UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS

National Oceanography Centre
School of Ocean and Earth Sciences

Taxonomy and biology of deep-sea polychaetes: Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean

By

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Dedicated to the memory of my loved and remembered father

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ABSTRACT

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TAXONOMY AND BIOLOGY OF DEEP-SEA POLYCHAETES: TEMPORAL VARIABILITY IN POLYCHAETE ASSEMBLAGES OF THE ABYSSAL NE ATLANTIC OCEAN

By Eulogio Hernán Soto Oyarzún

Taxonomy and temporal variability of deep-sea polychaete assemblages was assessed over a 9-year period. Macrofauna 300 *μ*m fraction samples, taken with USNEL box core (0.25 m^2), were studied from Porcupine Abyssal Plain, NE Atlantic Ocean from 8 cruises between August 1989 and September 1998.

A taxonomic study at species level was carried out for the two most abundant families: Cirratulidae and Spionidae. 15 different morphotypes of Cirratulidae and 13 of Spionidae were recognized and described. For Cirratulidae eight morphotypes belonged to *Chaetozone*, there were six species of *Aphelochaeta* and one of *Tharyx*. For Spionidae three morphotypes belonged to *Minuspio*, two to *Prionospio*, one to *Aquilaspio*, two to *Laonice*, two to *Spiophanes* and two to indeterminate spionids. *Aurospio dibranchiata* also was recorded.

The polychaete communities were characterized by high numbers of individuals (abundance) and high family richness. Highest abundance occurred in the upper 1 cm sediment layer (53.2% of total abundance). The most abundant families were the Cirratulidae, Spionidae, Opheliidae and Paraonidae. Surface deposit-feeders were the dominant trophic group (67.4% of total abundance). Significant temporal variability was evident with significant differences in polychaete abundance between sampling periods (cruises). There were stepwise increases in abundance in September 1996 and March

1997 coinciding with similar increases in abundance in large invertebrates (megafauna) in the same area (known as the '*Amperima* Event' after a species of holothurian that increased in abundance by over three orders of magnitude). A similar trend was observed for abundance within different layers of the sediment, main families and trophic groups showing significant differences between cruises. A comparison made of samples taken 1) before the '*Amperima* Event' (1989-1994) and 2) during the '*Amperima* Event' (1996-1998) showed significant differences in the polychaete abundance in the upper 3 cm of the sediment. There were significant differences in some trophic groups (predators, deposit-feeders and burrowers) and the dominant families (Cirratulidae, Spionidae and Opheliidae). Changes in surface deposit feeders were particularly evident. The temporal variability is likely to be related to seasonal and interannual variability in organic matter input. Greater food supply in some years may allow the growth and development of deposit feeding polychaetes. However, not all elements of the polychaete community showed a response (e.g. the Paraonidae).

At the species level, the most abundant cirratulid and spionid species not always appear to respond in the same way as the family. Only *Aphelochaeta* sp. 647D, *Minuspio* sp. 4 and *Prionospio* sp. 81 showed a clear response, with significant differences between cruises and between pre '*Amperima* Event' and '*Amperima* Event' periods. *Chaetozone* sp. 1, *Chaetozone* sp. 55A and *Prionospio* sp. 613 only showed significant differences between cruises, while *Aphelochaeta* sp. 13A and *Aurospio dibranchiata* did not show any significant change with time. In the Paraonidae, where no apparent response was detected, the species level response in the most abundant species was similar.

Temporal changes in some polychaete species could be attributed to '*Amperima* Event' conditions. However, for polychaete species that did not response in a clear way to the '*Amperima* Event', their temporal variability observed appear to be related to interannual variations in organic matter input to the seabed throughout the deposition of phytodetritus. In general, seasonal and interannual fluxes in food supply appear to determine changes in polychaete assemblages at the Porcupine Abyssal Plain, affecting to a greater degree polychaete abundance, and to a lesser extent faunal composition.

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CHAPTER 1

1. INTRODUCTION

1.1. Deep-sea environment

Oceans cover more than two-thirds of the Earth's surface with an average depth of almost 4 km (Rice, 2000). They may be divided in five main big zones: the continental shelf, the continental slope, the continental rise, the mid ocean ridges and abyssal plains.

Continental shelves extend, on average, to about 60 km from the shoreline and represent only about 20% of the total area of the oceans. Continental slope and rise have a range in gradient from 1:40 and 1:100 at a depth of about 3000 m, respectively, and they together represent around one quarter of the total surface of the oceans. Mid-ocean ridges occupy about 33% of the area of ocean floor and are usually about 2.5 km below sea level. Abyssal plains extend gently from 3 to 6 km depth, have imperceptible slope (1:1000) and underlie well over half of the ocean surface (Gage & Tyler, 1991; Rice, 2000).

The deep-sea environment is one of the largest biomes (Paterson *et al.*, 1994, Thistle, 2003) with abyssal plains representing approximately 40% of the surface of the Earth (Paterson *et al.*, 1994). Deep-sea habitats are considered among the most diverse on the planet in terms of species richness (Grassle & Maciolek, 1992; Blake, 1993; Gage, 1996).

Topographically, the deep sea starts at the edge of the continental shelf and hydrographically it is the zone lying below the permanent thermocline (Gage & Tyler, 1991). With the exception of hydrostatic pressure and current energy (bottom currents), the physical properties of the deep-sea environment shows a narrow range below the permanent thermocline, being currently characterized as a physically variable environment with a predictable seasonality in some of its ecological processes (Gage & Tyler, 1991).

Pressure increases proportionately with depth, varying from 20 N/m^2 at the shelf-slope break to > 1000 N/m^2 in the deepest parts of the trenches. This parameter can affect the

physiology and biogeochemistry of some organisms changing the performance of proteins (e.g. enzymes) and lipid structures (e.g. membranes).

Bottom-energy currents are important parameters which have a direct relation to sediment transport. At the interface between the water and the seafloor, frictional forces reduce the current speed to zero. The currents increase gradually with distance from the bottom until the free-flow velocity is reached. The intermediate region is known as the '*Benthic Boundary Layer'* BBL and its thickness depends on the bottom current speed (Herring, 2002). This layer has important consequences for the suspension of particles and their availability as a food source, affecting the recruitment of larvae to the benthos and the survival of filter feeders especially during 'benthic storms' (Thistle *et al.*, 1991).

In physical terms, diurnal variations in bottom currents caused by deep-sea tides and the major hydrodynamic disturbances caused by benthic storms resulting from vorticity transmitted to the bottom, suggest a hydrodynamic regime far more energetic and subject to much more episodic variation than was previously conceived (Gage & Tyler, 1991). This type of regime may be of wide spread occurrence. Temperatures beneath 2000 m almost never arise above about 4º C (the exceptions being the Mediterranean and Red Seas), lying often between -1º and 3º C. Salinity remains to 34.8 at depths greater than 2000 m. Oxygen concentration values are high in the North Atlantic and Antarctica waters (6-7 ml L^{-1}) but lower in the north Pacific <3.6 ml L^{-1} and northern Indian Ocean, where oxygen concentrations are < 0.5 ml L^{-1} (Menzies, 1965; Mantyla & Reid, 1983; Demopoulos *et al.*, 2003)**.** There are extensive midwater regions where oxygen is depleted; these occur between 100 and 1200 m depth. These zones, referred as oxygen minimum zones (OMZs), defined as areas where O_2 < 0.5 mL^{-1}, persist over geologic time (Levin *et al*., 2001). Where these low oxygen regions intercept the continental seabed, the benthos experiences either permanent hypoxia or an oxygen gradient. Sedimentation rates vary and are related to downward flux of material (Sibuet *et al*., 1989) often very slow sediment accumulation rates (0.1-10 cm per thousands years), and an absence of sunlight (Gage & Tyler, 1991; Smith & Demopoulos, 2003).

The abyssal seabed is predominantly a soft-sediment environment. Exposed hard rock is relatively uncommon (e.g., mid-ocean ridges, seamounts) and the few solid substrates are formed by inorganic precipitation from seawater such as phosphate deposits, metallic oxide formations and sulphide deposits (Gage & Tyler, 1991).

Depending on the productivity of the overlying water, abyssal plains are covered mainly with biogenic oozes being considered an important energy source for deep-sea organisms (Gooday & Turley, 1990; Pfannkuche, 1993). Abyssal red clay is also important and it consists of terrigenous particles. Red clay sediments are fine-grained (median grain size <2 *μ*m) and poor in organic material (<0.25% organic carbon). They are found below depths of 4000 m in the central gyres of the North and South Pacific (Berger, 1974), while in the Atlantic red clays are restricted to deep (>5000 m), relatively small basin where the calcium carbonate (calcite) compensation depth (CCD) which is much deeper. Accumulation rates are low, *c.* 0.5 mm per thousand years. This sediment is produced when only a small amount of terrigenous material reaches the areas farthest from land, but the productivity of the overlying waters in these areas (oceanic central gyres) is so small that the few shells that are produced and fall to the seafloor are dissolved away (Thistle, 2003). Where productivity is high, the production rate of both siliceous and calcium carbonate shells is high. If the water is deep, the calcium carbonate shells that reach the seafloor dissolve. The sediment will be composed of terrigenous and siliceous particles. Radiolarian ooze occurs under the band of high productivity along the equator in the Pacific. Some productive regions occur where the underlying water is relatively shallow with rates of calcium carbonate dissolution more reduced. Biological oozes accumulate at a relatively rapid rate of centimetres per thousand years. Near continents, deep-sea sediments also consist, in part, of particles derived from weathering of rock on land (terrigenous particles), which are transported to the sea by wind or rivers (Thistle, 2003). Biogenic pelagic sediments contain >30% biogenic skeletal material. They are composed mainly of calcium carbonate, silicon and aragonite, only in depth shallower than the calcium carbonate compensation depth, and are derived from foraminifera, diatoms, radiolarians and pteropod molluscs. Over much (67%) of the Atlantic Ocean, the surface sediments are carbonate oozes ($CaCO_3$ content 30-50%) with a mean particle size of <100 *μ*m (Lampitt *et al.,* 1986; Udintsev, 1990), a sand-sized fraction consisting predominantly of planktonic foraminiferal tests, and an organic-carbon content generally <0.5% (Emery & Uchupi, 1984). Most of the deep Pacific seafloor is covered with soft sediments. Along the continental margin, the sediment is mainly terrigenous mud consisting of mineral grains, combined with diatoms fragments, the calcareous tests of planktonic Foraminifera and minute pieces of vascular plants (Smith & Demopoulos, 2003). The organic matter content is about 1-2% organic carbon by weight (Jahnke & Jackson, 1992). Calcareous sediments may be

found at depths between 4000-4600 m. This kind of sediment is often coarse-grained with more sand-sized particles than most deep-sea sediments and poor in organic material (0.3% by weight) (Jahnke & Jackson, 1992).

The discovery of all these parameters, phenomena and perturbations has overturned the previous concepts of great constancy in deep ocean ecosystems. Dynamic processes have been demonstrated to play an important role in the structure and development of deep-sea communities, because the rates are faster than expected. For example: variations in current energy (Thistle *et al.*, 1985, Paterson & Lambshead, 1995), seasonal flux from the surface productivity and its resulting deposition on the ocean floor (Billett *et al.*, 1983; Tyler, 1988).

1.2. Food supply, seasonality and benthic response

The deep sea is a food-limited environment (Hessler, 1974; Gage & Tyler, 1991; Thistle, 2003). Benthic biomass and abundance are directly related to the amount of organic material reaching the sediment surface, that originating from the pelagic layer (Sibuet *et al.*, 1989; Paterson *et al.*, 1998; Glover *et al.*, 2001, Smith *et al.,* 2001, 2002). However, the relationship between benthic biomass and productivity is not clear caused by variability in organic carbon export to the deep-sea floor (Paterson *et al.*, 1998; Smith *et al.,* 2002). Increases in primary production may not always result in an increase in POC flux to the seabed (Lampitt & Antia, 1997). Nevertheless, the deep-sea is highly dependent on sinking food material, the quality and quantity of which varies spatially and temporally across the ocean surface in seasonal, interannual and decadal time scales (Glover & Smith, 2003). Food supplies at the seafloor can arrive directly from the simple sinking of phytoplankton material and marine snow, or in the form of larger organic parcels such as fish, whale carcasses and macrophytic debris (e.g. kelp and *Sargassum* weed). Further evidence for the variability in the supply of nutrients came from two lines of research. First, it was found that the flux of settling particles may have a distinct seasonal component (Billett *et al*., 1983) and, second, in areas of the North Atlantic which experience a strong spring bloom, this seasonal flux is dominated by sinking aggregates of phytoplankton detritus (phytodetritus) (Levin & Gooday, 2003). North Atlantic phytodetritus is composed of the remains of various organisms derived from the euphotic zone (including Cyanobacteria, small chlorophytes algae, diatoms, coccolitophorids, silicoflagellates,

dinoflagellates, tintinnids, radiolarians and Foraminifera), crustacean moults, small fecal pellets, bound together in a gelatinous matrix to form aggregates up to about 1 cm in diameter (Billett *et al.*, 1983; Thiel *et al.*, 1989). The aggregates form an often extremely patchy layer on the seafloor and are typically, concentrated in depressions or behind mounds and other obstacles (Rice *et al.*, 1994). Phytodetritus is consumed by motile surface deposit feeders, incorporated to the sediment through the action of bioturbators, easily resuspended and redistributed by currents (Lampitt, 1985; Hecker, 1990). Pulses of phytodetritus and other forms of organic matter typically evoke a rapid response by the benthic community and serve to couple processes on the deep sea floor and in the upper water column (Gooday & Turley, 1990). Current evidence indicates that smaller biota such as microbes and foraminifera, show a rapid population response to episodic food input at the deep-sea floor, whereas larger, longer-lived taxa generally integrate seasonal changes and may only respond to interannual and decadal changes (Gooday, 2002). Some megafaunal animals such as echinoderms may respond to the arrival of food by synchronizing their reproductive activity (Tyler, 1988). This link has also been shown for actinians, bivalves, brachiopods and decapods (Gage & Tyler, 1991). Holothurians may actively select and consume phytodetritus; ophiuroids and echinoids are attracted to patches of phytodetritus (Billett *et al.*, 1998). Within the polychaetes, Paterson *et al.*, (1994, 1998) and Glover *et al.*, (2001, 2002) have shown a complex relationship between levels of nutrient flux and abyssal polychaete biodiversity. In the Pacific, polychaete abundance appears directly related to particulate carbon flux (POC), while in the Atlantic there is no obvious link. Cosson-Sarradin *et al.*, (1998) have reported a close link between deep-sea polychaete diversity and the nature of organic inputs off the west African upwelling system. Body sizes response of abyssal polychaetes to different nutrient regimes have also been documented with smaller polychaetes occurring from seasonal or periodic input of phytodetritus zones (Paterson *et al.*, 2006) and the largest polychaetes found at the most food impoverished sites (Glover, 2000). At larger bodies' sizes, individuals become metabolically more efficient, and require less food per unit of mass (Rex & Etter, 1998; Glover, 2000). Organically enriched settlement trays indicated the importance of opportunistic spionid and capitellid polychaetes in the deep-sea (Grassle & Morse-Porteous, 1987). It is possible that phytodetrital input may affect different polychaete taxa, influencing the body size of

those taxa. As a result, polychaetes are larger in the deeper layers of the sediment, where food is more scarce.

1.3. Deep-sea benthic communities

1.3.1. Characteristics

The fauna of the benthic boundary is comprised of those animals living either on the ocean floor or those associated with the immediately overlying water (Gage & Tyler, 1991). This is 'the benthos' and represents about 90% of known marine species.

Deep-sea, intertidal and sublittoral soft-sediment benthic communities share similar characteristics in terms of faunal composition. Megafauna, macrofauna and meiofauna found in shallow-water environments are also present in deep-sea habitats, both in sessile and errant forms, although generally in different relative abundances between taxa.

Deep-sea megafauna comprises a great variety of forms and marine animals that includes both errant (mobile) and sessile components. Megafauna are usually considered to have a lower size limit of centimetres. They can be seen in photographs and are normally caught in trawls and dredges. The errant megafauna includes echinoderms such as holothurians, ophiuroids, asteroids, echinoids, megabenthic worms such as scale worms i.e. *Laetmonice* spp., sea spiders (pycnogonids), giant scavenging amphipods, higher crustaceans such as crabs, shrimps and lobsters, cephalopods and benthic fishes.

Sessile megafauna are often found on hard substratum and include forms associated with hydrothermal vent and cold seep. It is characterized by sponges, hydroids, anemones, corals, gorgonians, crinoids, barnacles, brachiopods, bryozoans and mussels (Lampitt *et al.*, 1986; Gage & Tyler, 1991; Herring, 2002).

Sessile elements of the sediment include burrowing polychaetes such as species of the family Ampharetidae, hemichordates, hexactinalid sponges and pennatulids. The deep-sea macrofauna comprises small invertebrates that are generally not obvious in deep-sea photographs. However, they are highly abundant, diverse and most occur within the sediment (Hessler & Sanders, 1967; Grassle & Sanders, 1973; Grassle *et al.*, 1990).

In terms of faunal composition, deep-sea macrofauna are similar to shallow–water soft bottoms (Gage, 1978). Factors such as bathymetry and food input seem to have had remarkably little effect on the overall phylogenetic balance (Gage & Tyler, 1991). Polychaetes worms, peracarid crustaceans, such as amphipods, isopods, cumaceans

and tanaids, and bivalve and gastropod molluscs are the dominant taxa (Grassle & Maciolek, 1992). Sipunculids, priapulids, echiurans, pogonophorans and oligochaetes are also important in certain areas. The larger species of some of these groups can also be considered as megafauna.

Deep-sea meiofaunal communities also show high diversity (Lambshead, 1993). Meiofauna are those animals that pass through the macrofauna screen and are retained on the finest meshes, down to about 0.45 mm (Herring, 2002). Meiofauna consist mainly of both multicelled (metazoan) invertebrates such as nematodes and harpacticoids copepods, and larger single-celled protozoans, such as Foraminifera. Deep-sea nematodes have still not been studied extensively and many experts think that there may be tens of thousands of species yet to be described (Lambshead *et al*., 2000). Foraminifera may dominate the meiofaunal community in terms of biomass and are thought to be an important early link in benthic metazoan food chains (Gooday, 1988). Other significant meiofauna groups are ostracods, kinorhynchs, tardigrades and loriciferans. Deep-sea soft-sediment communities often exhibit very high local species diversity, with 0.25 m^2 of the deep-sea mud containing 21-250 macrofaunal species (Snelgrove & Smith, 2002). The biomass of deep benthic communities is typically only 0.001-1% of that in shallow-water benthic communities because of the low flux of organic energy. Low food flux in concert with low temperatures (-1- 4ºC), yield relatively low rates of growth, respiration, reproduction, recruitment and bioturbation in the deep-sea (Gage & Tyler, 1991; Young, 2003).

1.3.2. Polychaete assemblages

The Class Polychaeta comprises the bulk of the diversity of Phylum Annelida and polychaetes are found nearly every marine habitat, from intertidal to the deepest sediments. Some polychaetes are dominant parts of hydrothermal vent communities (Blake, 1985; Desbruyères & Segonzac 1997), while minute forms make up a significant component of the deep-sea interstitial meiofauna (Rouse & Pleijel, 2001).

Polychaetes are considered a monophyletic group based on the presence of nuchal organ; these are ciliated sensory structures just behind the prostomium (Rouse & Fauchald, 1997). The Pogonophora (including the former phylum Vestimentifera) appeared within the traditionally formulated Annelida, and represent a derived clade of polychaetes, therefore must now be regarded as a family among the polychaetes (Mc Hugh, 1997; Kojima, 1998). In ecological terms, pogonophorans (beard worms) are

highly abundant at some hydrothermal vents and cold seeps. The largest worms (*Riftia*) live in thickets of tubes, each tube up to 25 mm in diameter and a metre or more in length. Most species exhibit some form of endosymbiosis.

Together with the peracarid crustacean and bivalve molluscs, polychaete annelids are regarded as the core organisms of the macrofauna and among the most abundant and diverse macrofaunal organisms in the deep sea (Hartman, 1965; Hartman & Fauchald, 1971; Grassle & Maciolek, 1992). The polychaetes typically make up around half of the total numbers of individuals, and around a third to nearly a half the number of species, of the macrofauna. They are the dominant component of the deep-sea macrofauna constituting between 30 to 70% of the macrofaunal abundance (Gage & Tyler, 1991; Glover *et al.*, 2001; Grassle & Maciolek, 1992; Paterson, 1993; Paterson *et al.*, 1994) and they are often dominant in terms of biomass (Brown, 1991).

Recent surveys on the diversity of deep-sea polychaetes have shown a similar pattern, namely dominance in terms of individuals and taxa (Grassle & Maciolek, 1992; Paterson *et al.*, 1998; Glover *et al.*, 2002). Bathymetric species diversity gradients showing a parabolic pattern have been established for deep-sea polychaetes assemblages in the north Atlantic (Rex, 1983; Paterson & Lambshead, 1995; Cosson *et al.*, 1997; Narayanaswamy *et al.*, 2005). Diversity, species richness and abundance are also influenced by the oxygen minimum zone (OMZ) at specific depths (Levin & Gage, 1998; Hilbig & Blake, 2006).

Deep-sea polychaetes tend to be small (<1 cm), and often with a reduced number of body segments at maturity compared to shallow-water species (Hartman & Fauchald, 1971). They are taxonomically diverse class, their morphology is varied, reflecting their different lifestyles and feeding strategies. Many deep-sea polychaetes live buried, or partially buried, in the soft sediments. Many of them live in tubes constructed out of sediment particles and secretions, while a small number live as commensals of big sea cucumbers (Kirkegaard & Billett, 1980) or bivalve molluscs (Blake, 1993). Dweller polychaetes often have elaborate tentacles to sweep the sediment surface while burrowers ingest the sediment, like the sublittoral lugworms. Those polychaetes that live in tubes are sessile, projecting their feeding appendages from the tube and either collecting food from the surrounding surfaces or filtering it directly from the water (Fauchald, 1977).

Most are surface deposit feeders (e.g. Cirratulidae, Spionidae and Sabellidae), depending directly on detrital material falling from above, although other more

specialized feeding strategies are recorded such as raptorial feeding (e.g. Phyllodocida) and filter feeders (Fauchald & Jumars, 1979). Blake (1994) has suggested that deep-sea polychaetes, which feed directly on superficial sediments, are more likely to respond to organic pulses impinging on the bottom than species that feed at depth in the sediment or on other resources. Their subsurface activities, and abundance, greatly modify the sediment structure and chemistry, adding to the heterogeneity of the deep-sea benthic environment (Herring, 2002).

Since the discovery of seasonality in the deep sea in the 1980's, several investigations have focussed on the reproductive biology and recruitment of different invertebrate groups (Tyler, 1988; Young & Eckelbarger, 1994). The reproductive and population dynamics of some bathyal polychaetes species have been studied (Hilbig & Blake, 1991; Blake, 1993) and seasonality in egg maturation has been observed (Blake & Watling, 1994). Also clear evidence of seasonal and synchronised recruitment in small juvenile opheliid individuals was recorded (Vanreusel *et al.*, 2001). However, reproduction in abysal polychaetes remains largely unknown.

The majority of deep-sea polychaetes appear to have separate sexes (Young, 2003), where oocytes always originate within distinct ovaries. In some cases, sperm are of the primitive type associated with free spawning and external fertilization, however the variety is striking and the morphology changes between such as elongate, normal or modified forms. Fecundity in non-vent deep-sea species is lower than those that have been reported for various hydrothermal vents species (Zal *et al.*, 1995). In shallow-water species the pattern of brooding within the Spionidae are diverse; some brooding larvae in the tubes, others employing specialized brood pouches, and still others having the larvae attached directly to the segments of the mother. Direct and indirect modes of development have been observed, however, the situation is further confused in polychaetes by the prevalence of mixed developments that involve several later larval stages (Wilson, 1991b; Young, 2003). Whether such patterns are also widespread in deep-sea species remains to be discovered. The Cirratulidae, one of the most dominant components of the northeast Atlantic deep-sea sediments a wide variety of reproduction and development way have been recorded (Petersen, 1999). However, there is inadequate information about longevity, spawning frequency, and the speed of the gametogenic cycle in deep-sea polychaetes.

Polychaetes are not well represented in the fossil record and the time of radiation into the deep sea environment is unknown. Palaeozoic polychaetes fossils are present

from the Cambrian and Ordovician. The main differentiation of these Palaeozoic polychaetes suggests that most of the major families' clades had already appeared before the break up of Pangaea at the end on the Permian. It is suggested that major extinctions in the deep sea were caused by anoxia during the Mesozoic and beginning of the Palaeocene, indicating that the modern deep-sea fauna originates from after this time, with species re-invading from the bathyal refugia (Rogers, 2000).

1.4. Deep-sea time series

Long-term datasets are required to establish baseline data to allow evaluation of the direction and magnitude of changes to deep-sea ecosystems. In the 1980s, long-term ecological studies were initiated to explore temporal variability in the abyssal north-east Atlantic and north-east Pacific. Recent process-based studies have elucidated long-term trends in the surface ocean (Karl, 2002).

In the Pacific, there have been two long-term time series centred on Station M, north-east Pacific (Smith & Druffel, 1998) and on the HOT station, off Hawaii (Smith *et al.*, 2002; Karl *et al.*, 1996). Studies have focused on the flux of sinking particulate matter through Benthic Boundary Layer (BBL) but only at Station M a detailed long-time series investigation of food supply and demand at the benthos was carried out between 1989 and 2004 (Smith & Kauffmann, 1999, Smith *et al.*, 2002, 2006). Researchers have measured the particulate organic carbon (POC) flux into deep sediment traps, sediment community oxygen consumption and have taken time-lapse photographic images over period of seven years, allowing investigation of both seasonal and interannual changes in a number of ecosystem parameters. Changes were observed both in the abundances of benthic communities (larger macrofauna and megafauna) and community oxygen consumption over seven-year study period. These variations have been tentatively linked to seasonality in food supply (Lauerman *et al.*, 1996; Smith & Druffel, 1998).

The Porcupine Abyssal Plain (PAP) in the north-east Atlantic has been intensively studied since the mid 1980s, with research programmes investigating the downward flux and fate of organic material at the deep-sea floor (Billett & Rice, 2001). Considerable seasonal fluctuations in the downward particle fluxes with peaks occurring during the mid-summer and little seasonal variation in the gross composition of the sedimentary flux have been determined (Lampitt *et al.*, 2001), though inter-annual variability was evident. Seasonal changes in composition of specific organic

compounds such as labile lipids (Kiriakoulakis *et al.,* 2001) and phytopigments (Fabiano *et al*., 2001) were recorded. Vanucci *et al*., (2001), established that micro-organisms contributed about 2% to the Particulate Organic Carbon (POC) flux, being significantly correlated with DNA fluxes. Measurements made of near-bed currents and particle concentrations show evidence of resuspension of smaller particles by bottom currents, but the resuspension of large particles could not be correlated to observed variations in current speed and direction during the summer months. This resuspension would be influenced because feeding and sediment re-working made by the megafauna. A dataset extending over ten years has recently revealed a long-term change in the abundance and faunal composition of the invertebrate megafauna (Billett *et al.*, 2001). Two major trends were apparent. First, a general increase in the abundance of megafaunal animals (such as actiniarians, annelids, pycnogonids, ophiuroids and holothurians) over the 1989-1999 sampling period has occurred, and secondly, there has been a shift in megafaunal community composition. Two holothurian species *Amperima rosea* and *Ellipinion molle*, increased in abundance by more than two orders of magnitude. Before 1996 these holothurians were always minor component of the megafauna. From 1996 to 1999 *A. rosea* was abundant over a wide area of the PAP indicating that the event was not localised. Inter-annual variability and long-term trends in organic matter supply to the seabed may be responsible for the observed changes in abundance, species dominance and size distributions (Billett *et al.*, 2001).

The data both from the north-east Atlantic and the north-east Pacific indicate the major ecological changes can and do occur in the abyssal deep-sea over timescales of roughly 10 years (Glover & Smith, 2003).

1.5. Long-term temporal variability

Research has shown that deep-sea ecosystems change with time (Tyler, 1995; Gage, 1991; Tyler, 2003). While seasonal and short-term responses in deep-sea populations have been well documented (Billett & Hansen, 1982; Tyler, 1988; Gage & Tyler; 1991; Pfannkuche, 1993; Young & Eckelbarger, 1994; Gooday, 2002), it is now apparent that several ecological parameters, such as family and species abundance, richness and diversity, may also change over longer periods (Gage *et al.*, 2000; Glover *et al.*, 2001; Gooday & Rathburn, 1999). Few studies have investigated long-term temporal variability in deep-sea macrobenthic communities (Lauerman *et al.*, 1996; Druffel &

Smith, 1998). Macrofaunal studies at the PAP over ten years indicated that there were much longer-term changes taking place. An apparent increasing in the abundance of opportunistic species was recorded, with various taxa, such as foraminiferans, opheliid polychaetes and other polychaetes, responding to the changes on the seabed at different rates (Galéron *et al.*, 2001; Vanreusel *et al.*, 2001). Long-term changes were most clearly seen in the abundances of the invertebrate megafauna. Changes occurred in the abundances of actiniarians, annelids, ophiuroids, pycnogonids and tunicates and particularly in holothurians (Billett *et al.*, 2001). In particular, long-term variability deep-sea polychaete assemblages are very poorly known. To date there are no studies on long-term temporal variability in deep-sea polychaete communities at the assemblage level. There are long-term studies about dynamics of the polychaete fauna from shallow sublittoral sites (Carrasco & Moreno, 2006; Hilbig & Blake, 2000) and several short-term and spatial observations on the biology and ecology of polychaetes (Glover *et al.*, 2002; Grassle & Maciolek, 1992; Paterson *et al.*, 1994; Vanreusel *et al.*, 2001). Long-term time series investigations of temporal variability have revealed periods of stability and persistence as well as others of instability due to physical disturbances affecting species abundance and richness (Buchanan & Moore, 1986; Dauvin & Ibáñez, 1986). However, long-term studies are needed to be able to assess population succession, recruitment and reproductive patterns in polychaete communities (Gage, 1991). Many years of consistent data collection are a necessity in order to identify natural patterns (Hilbig & Blake, 2000).

1.6. The '*Amperima* Event'

One of the most exciting discoveries to come out of European deep-sea investigations carried out between 1989 and 1999 was the significant change in the abundance and species dominance in some size classes of benthic fauna on the Porcupine Abyssal Plain. Nowhere was this more apparent than in the invertebrate megafauna, where a dramatic change was observed in the structure of the holothurians community. An increase in abundance of two orders of magnitude was recorded for the holothurians, accompanied by a dramatic shift in the pattern of species dominance. Prior to 1996 the holothurians community was dominated by the elasipodid holothurians *Oneirophanta mutabilis* and *Psychropotes longicauda*, and the aspidochirotid *Pseudostichopus villosus*. Post-1996 the trawl catches from Porcupine Abyssal Plain

were dominated by *Amperima rosea* and *Ellipinion molle*, two small gelatinous holothurian species from the family Elpidiidae (Elasipodida) (Billett *et al*., 2001).

Sampling at other locations on the abyssal plain, away from the centrally located PAP observatory, showed that the "*Amperima* Event" was not localised, but covered a vast area of the NE Atlantic. Apart from the holothurians significant increases occurred in a number of other faunal groups (Actiniarians, Polychaetes, Ophiuroids, Pycnogonids and Tunicates). Sampling in 2002 showed that *Amperima* was more abundant in this year than ever before. The "*Amperima* Event", has lasted for more than 6 years and was more in the nature of a regime shift than a short-term population explosion. In all sampling on the Porcupine Abyssal Plain since 1977 *Amperima rosea* has been a minor component of the fauna until 1996. Only in one sample, taken in 1911, has *Amperima* occurred in such large numbers. It led Hérouard (1923), to conclude that the distribution of *Amperima* must be very localised. The inference was that it was localised in space, but equally it may be localised in time.

The species that have increased in abundance all appear to be specialist feeders on phytodetritus (Iken *et al*., 2001). Phytodetritus is deposited on the seabed in the area during the spring and summer months (Billett *et al.*, 1983; Lampitt, 1985). It is derived from surface water production and falls to the seabed from the sunlit surface waters within a few weeks. Generally, it covers the seabed in a layer of detritus several centimetres thick (Thiel *et al.*, 1990). Different holothurian species appear to feed on different fractions of the detritus, as shown by pigment analyses of their stomach contents (Wigham *et al.*, 2003). The pigments carotenoids selected appear to play a critical role in the reproduction of the holothurians. It is thought that the holothurians are unable to synthesise sterols (Ginger *et al.*, 2001) and so they are dependent on their diet for these critical compounds. The hypothesis is that small variations on critical compounds may lead to large ecosystem changes in the food limited environment of the deep sea, where only about 1% of surface production reaches abyssal depths. The changes in megafauna abundance may be related to environmental forcing (food supply) rather than to localised stochastic population variations. Inter-annual variability and long-term trends in organic matter supply to the seabed may be responsible for the observed changes in abundance, species dominance and size distributions.

1.7. Deep-sea polychaete taxonomy

Recent quantitative studies from deep-sea areas have shown that taxonomists should not be out of work for a long time yet (Glover, 2000). Studies carried out by Grassle and Maciolek (1992) have suggested that there may be over ten million deep-sea macrofaunal species waiting to be discovered and described; where about 60% could be polychaetes and only a few hundred have been described so far. The taxonomic work in this thesis will attempt describing and identifying the greatest possible number of species for the main polychaete families studied.

Identification of deep-sea fauna to species level is often difficult; hence identification to family level may facilitate deep-sea studies should family level identification prove adequate (Narayanaswamy *et al.*, 2003). Though some studies in taxonomic sufficiency have been undertaken in relatively shallow water areas and all have found that it is possible to use results from a higher taxonomic resolution, e.g. family, to determine the response of the benthic community to environmental gradients, Narayanaswamy *et al.*, (2003) conclude that in the deep-sea, species level identifications of polychaetes is preferable to that family-level identification.

The number of formal taxonomic treatments of polychaetes ranges from the pioneering studies made by McIntosh (1875), Hartmann (1965) and Hartmann & Fauchald (1971) to the investigations carried out by Blake (1996, 2006), Blake *et al.* (2000) and Chambers & Woodham (2003). Yet there is a lag in making taxonomic information available from the many ecological programmes that have been undertaken in recent years. The Abyssal Polychaete Inter-calibration Project (APIP), which is supported by Census of the Diversity of Abyssal Marine Life (CeDAMar) aims to address this lag by creating a unified database of abyssal polychaetes (Glover, 2007).

The taxonomy of deep-sea polychaetes is complex. The reduced size, smaller number of body segments and the generalized tendency for character loss or reduction are the main problems for the identification taxonomic work. For example, the absence of the abdominal section for many cirratulids specimens (Glover, 2000) and paranoids as well as the loss of branchial pairs in Spionidae (Maciolek, 1981) are condition routinely seen in deep-sea specimens. In opheliids, often there are differences in the development of adult features, which some species undergo metamorphosis earlier than in others. From PAP samples specimens show similar development of anal

papillae/cirri, and individuals of similar size show similar levels of development. A remaining difficult is in assigning these juveniles to a specific species. The range of individuals often does not provide a complete developmental series, and none of the individuals show full adult characteristics (Vanreusel *et al.*, 2001). Many of the morphological modifications and adaptations of shallow-water genera are reduced or absent in deep-sea forms. Therefore, new characters have to be found for morphological groupings to be made (Glover, 2000), as well as measurements of the total number of chaetigers to determine the best fit in some soft-bodied polychaetes (Blake & Baptiste, 1985).

1.8. Aims and Hypothesis

1.8.1. AIMS

The main goal of this study was to investigate how long-term variability and changes in the seasonally fluctuating food supply affected to polychaetes assemblages. Also test whether there are changes in the distribution of polychaetes within the sediment, main families and trophic groups with time. The high numbers of megafaunal sediment deposit feeders was thought to affect the quantity and quality of nutrient available in the surface layers. Finally, to answer the question is the fauna before the '*Amperima* Event' significantly different from after? determining which are the main differences in polychaetes assemblages among 'pre-*Amperima*' and '*Amperima* Event' periods.

A comprehensive taxonomic research will allow an assessment of the species that play a leading role on this long-term variability.

1.8.2. OBJECTIVE

The study examined temporal changes, correlating them with nutrients inputs and other biogeochemical parameters. Comparisons were made with the responses of the other abyssal benthic macrofauna to changes in the biogeochemical environment.

1.8.2.1. Specific objectives

- To increase the understanding of deep-sea polychaetes, providing a unified dataset bringing together previously identified MAST I, II material with BENGAL unidentified specimens, revising the taxonomy where necessary.

- To understand long-term change at the community level and to place biodiversity studies within a temporal context.
- To assess inter- and intra-annual variability in abyssal sediment polychaetes.
- To contribute biodiversity information on abyssal polychaetes to existing databases on temporal change in NE Atlantic fauna.

1.8.3. HYPOTHESIS

H1: Considering the seasonal variations of organic matter input such as the deposition of phytodetritus, and the large increase in some holothurian populations on the Porcupine Abyssal Plain during the periods 1996 to 1998, hypothesize polychaete community structure, in terms of ecological parameters such as abundance and family richness, increased at the time of '*Amperima* Event'.

Hypothesize that abundance of polychaetes, particularly surface deposit feeders may be depressed as a result.

CHAPTER 2

2. MATERIALS AND METHODS

2.1. Study area

2.1.1. Northeast Atlantic Ocean and Porcupine Abyssal Plain

The NE Atlantic Ocean extends northwards from the equator and encompasses all the water masses to the east of the mid-Atlantic ridge up to the continental boundaries of Western Europe and Africa. It has a complex topography that divides the ocean into several basins separated by ridges and banks. It is delimited to the northwest by the Reykjanes Ridge, by Iceland to the north and the Iceland-Faroe-Shetland-Ridge to the northeast. To the east it is bordered by the continent of Europe and on the continental slope southwest of Ireland, can be found the Porcupine Bank, Porcupine Seabight and Goban Spur. Heading further south the Porcupine Abyssal Plain is part of the West European Basin that extends down to the equator and includes also the Madeira and Cape Verde Abyssal Plains. The northeast Atlantic is a well-studied area and there are numerous oceanographic and biological data. Particularly, well-studied area localities include the Rockall Trough (Gage *et al.,* 1985; New & Smythe-Wright, 2001), the Faroe-Shetland Channel (Bett, 2001), the Porcupine Seabight (Rice *et al*., 1991) and the Porcupine Abyssal Plain (Billett *et al.*, 2001).

The current research was carried out at the Porcupine Abyssal Plain (PAP), which is located at 48º 50' N 16º 30' W (central location), about 270 km southwest of Ireland in 4850 m of depth (Fig. 1) The site lies between two other important localities in the NE Atlantic; the foothills of the Mid-Atlantic Ridge, and the European continental margin southwest of Ireland (Billett & Rice, 2001).

The study site has been particularly well studied (Thurston *et al*., 1998; Billett & Rice, 2001), including its oceanographic and biological settings. Details of the hydrography, primary productivity and upper ocean mixed layer dynamics can be found in Lampitt *et al.*, (2001). The main water mass in contact with the benthic fauna is the Lower Deep Water (LDW). Deep currents on the PAP have a cyclonic circulation, flowing northwards at 1-2 cm s^{-1}, up the central and eastern part of the abyssal plain, turning westward and southward as the basin shoals to the north, then southward or

westward along the eastern flank of the Mid-Atlantic Ridge (van Aken, 2000; New & Smythe-Wright, 2001). The circulation pattern is characterized as vigorous, systematic and superimposed on this residual current are semi-diurnal oscillations with current speeds of around 5 cm s^{-1} reaching until 13 cm s^{-1}. The main sources of current variability are the semi-diurnal tidal oscillations (Vangriesheim *et al*., 2001). No evidence of benthic storms has been recorded (Lampitt *et al*., 2001). The depth of winter mixing of the upper water column is about 500 m, leading to significant seasonal fluctuations in primary productivity and fluxes of organic matter to the seabed (Rice *et al*., 1994). The seasonal thermocline in this area is around 50 m depth during the summer months, where as the permanent thermocline can be found between 600-1400 m depth with an associated temperature decrease of 10º C to ~4º C (Rice *et al*., 1991). The sediment at the site is calcareous ooze with a median grain size of 8 to 8.6 *μ*m (Rice *et al*., 1991). The sedimentation rate is ~3.5 cm ky^{-1} (Rice *et al*., 1991). The surficial sediment has a total organic carbon (TOC) content of about 0.35%. The POC flux varies between 0.8–3 $g/m^{-2}/y^{-1}$ (Smith & Rabouille, 2002). The C:N ratio varies between 4.8 and 7.8 (Santos *et al*., 1994). Much of the knowledge concerning the benthic community structure of the PAP such as megafauna (Thurston *et al*., 1994; Billett *et al*., 2001) and macrofauna and meiofauna (Galéron *et al.,* 2001; Gooday & Alve, 2001, Vanreusel *et al.,* 2001) comes from numerous studies conducted at a central location. This abyssal region is known to be subject to strong seasonal fluctuations in fluxes of organic material that reflect the seasonal cycle of the primary production in the euphotic layer (Rice *et al.*, 1994).

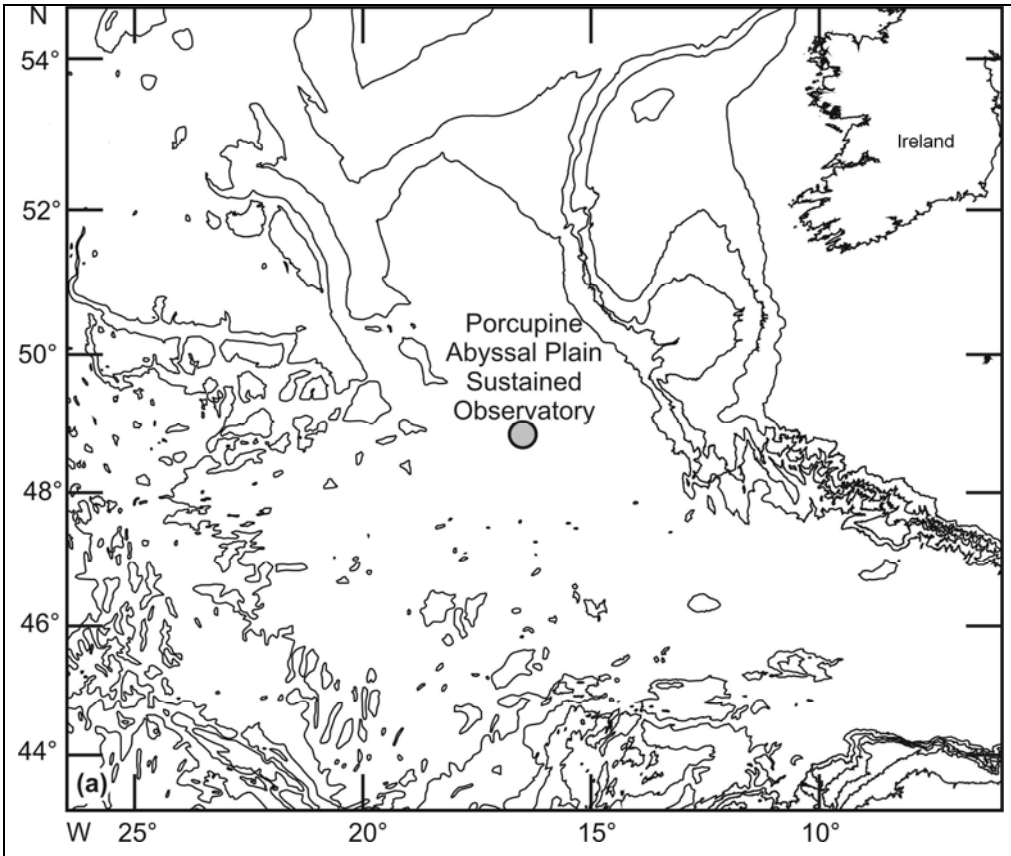


Figure 2.1. Study site at Porcupine Abyssal Plain (PAP). NE Atlantic Ocean

2.1.2. Long-term sampling programmes

The study site was sampled between 1989 and 1994, during EU-funded MAST I and MAST II projects (Rice, 1995). These investigations studied the environmental and biological variability at different temporal and spatial time scales and investigating effects of disturbance of benthos (MAST I) and compared benthic communities receiving seasonal phytodetritus inputs with undisturbed communities (MAST II).

Most of the information, data and samples used on the present study have come from BENGAL project (High-resolution temporal and spatial study of the **Ben**thic Biology and **G**eochemistry of a north-eastern Atlantic **A**byssal **L**ocality).

The BENGAL project was a multidisciplinary study of how the abyssal benthic boundary layer (BBL) responds to, and modifies, the incoming material flux to the seafloor. In particular, to determine how the geochemistry of abyssal sediments and the characteristics of the BBL community change seasonally in response to a highly seasonal input of organic matter from the overlying water column. The BENGAL project was a three-year study (1996 -1998) which undertook a sampling programme

within one season. This approach avoided the problems of temporal pseudoreplication that arises when comparing interannual samples and then trying to recreate patterns (Billett & Rice, 2001).

BENGAL locality was selected because, 1) it is a relatively flat area with simple topography, which facilitates a variety of types of benthic sampling and reduces spatial heterogeneity; 2) it is remote from both continental slope to the east and mid-ocean ridge reducing the effects of downslope sediment transport and the influence of the continental shelf; 3) it is unlikely to be influenced by strong downslope or advective processes and 4) it is as close to European ports as is possible for a remote abyssal location.

Cruise	Date	Station	Number of box core samples
RRS *Discovery* 185	**18 August – 17 September 1989**	**11908**	**1**
RRS *Challenger* 79	**12 May – 3 June 1991**	**52701**	**6**
RRS *Challenger* 111	**29 March – 25 April 1994**	**53201** **53205**	**4**
RRS *Discovery* 222	**29 August – 24 September 1996**	**12930**	**7**
RRS *Discovery* 226	**12 March – 10 April 1997**	**13077**	**6**
RRS *Discovery* 229	**2-31 July 1997**	**13200**	**5**
RRS *Discovery* 231	**1-31 March 1998**	**13368**	**2**
RRS *Discovery* 237	**25 September – 8 October 1998**	**13627**	**3**

Table 2.1. Cruise, sampling period, station number and samples number

2.2. Sampling and processing

All samples and data were taken during eight oceanographic cruises between 1989 and 1998 (Table 2.1). Three first cruises carried out among 1989-1994 belonged to EU-funded MAST I and MAST II projects. The five following cruises, September 1996 to September-October 1998 were conducted as part of the BENGAL project (Rice *et al.,* 1991; Thurston *et al.,* 1998; Billet & Rice, 2001) (Table 2.1).

All macrofauna samples were collected using an USNEL spade boxcorer (total surface area 0.25 m^2) (Hessler & Jumars, 1974) from different stations situated in the middle of the Porcupine Abyssal Plain. Samples were processed immediately after recovery. The core was routinely subsampled using a subcore with a square cross section (92 x

92 mm) and another with a circular cross section (55 mm diameter). Large megafauna' animals, xenophyophores and perforated tubes were removed before vertical subdivision of the core. The front panel of the box was removed and the core was then divided into six horizontal layers (0-1, 1-3, 3-5, 5-10, 10-15, 15-20 cm), which were removed manually with a trowel. The 0-1 and 1-3 cm layers were immediately placed into 4% borax-buffered formaldehyde until sieving, in order to avoid the deterioration of organisms, which were the most abundant in these two layers. Remaining layers were placed in cold sea-water. Sieving was carried out on a stack of 1 mm, 500 *μ*m, 300 *μ*m and 250 *μ*m sieves for the four upper layers, while the two deepest (10-15 cm and 15-20 cm) layers were washed through two sieves (1 mm and 500 *μ*m). In the laboratory, all preserved samples were sorted into higher taxa (Polychaeta, Peracarida, Mollusca, etc.) and counted using a stereomicroscope. Macrofauna sensu stricto was considered, excluding any meiofaunal taxa such as ostracods, nematodes and harpacticoid copepods (Hessler & Jumars, 1974).

2.3. Taxonomy

2.3.1. Identification

Polychaetes samples were first identified at family level. This process was carried out using stereo microscope (Leica, model WILD MZ8) and light microscope (Olympus BH-2) with video camera support (Panasonic F10 CCD). Unknown specimens were drawn using a light microscope with camera lucida attachment (Olympus). Identifications were supported with reference to key species in the *Discovery Collections* and at the Natural History Museum (NHM), as well as drawings provided by Dr. Gordon Paterson and taxonomic keys published by Fauchald, (1977); Hartmann, (1965); Rouse & Pleijel, (2001) and Rozbaczylo, (1980). General genus and species level identifications were supported with species identified by Dr. Gordon Paterson and Dr. Adrian Glover from previous studies (MAST I and MAST II). The Cirratulidae, Spionidae and Paraonidae families were the most abundant in the study and were revisited to identify new morphotypes and species and detecting those species principally associated with the observed temporal variability in species composition.

2.3.1.1. Cirratulidae, Spionidae and Paraonidae identifications

Observation and identification of species were carried out using stereo microscope (NIKON, model SMZ800) and light microscope (Olympus CX31). A photographic record of unknown specimens, main families and all described species was kept using a digital photograph camera in both stereo microscope and light microscope. The photographic equipments used were a digital camera NIKON, COOLPIX S10, 6.0 megapixeles for stereo microscope and a digital camera CANON, Power Shot A640, 10 megapixeles for light microscope.

The Cirratulidae was the most common and abundant family. Genus and species level identifications of Cirratulidae were supported and made considering descriptions and taxonomic characters used from several publications and works, such as Woodham & Chambers (1994), Chambers (2000), Chambers & Woodham (2003), Blake (1991, 1996a and 2006), Glover (2000), Doner & Blake (2006), Dean & Blake (2007) and Doner *et al*., (2008). Specimens were also checked with NHM samples from previous investigations. They were also compared with Pacific specimens as part of the 'Abyssal Polychaete Intercalibration Project' (APIP). As part of the APIP project the character sets for this polychaete family was revised and all specimens were examined or in the case of previously identified material re-examined. Thus it was possible to unify the identifications of all samples across the different sample sets.

The identifications and descriptions for Spionidae species were supported and compared with taxonomic keys and publications developed by Blake & Kudenov (1978), Blake (1996b), Maciolek (1981, 1985 and 2000) and Meißner (2005). The Paraonidae identifications and descriptions were supported using the Blake's taxonomic key (1996c) and the work written by Strelzov (1979). The descriptions of Paraonidae are in progress, so they were not included in the current work. Spionidae and Paraonidae specimens were also compared with NHM samples from previous investigations. A list of taxonomic characters and species versus characters matrix was made for each family before descriptions. Drawings, figures and pictures for each morphotype were recorded.

2.4. Ecology

2.4.1. Parameters and variables studied

2.4.1.1. Family level

The structure of the polychaete community was analysed using the number of individuals as the main ecological parameter. Total and mean numbers of individuals were obtained together to the standard deviation (SD), standard error (SE) and confidence intervals (CI). Mean abundance per unit area (0.25 m^2) was evaluated temporally and in relation to sediment depth (0-1, 1-3 and 3-5 centimetres layers), trophic groups (surface deposit-feeders, predators and burrowers) and main polychaetes families (Cirratulidae, Spionidae, Opheliidae and Paraonidae). Family richness also was calculated.

The trophic groups classification applied for each family was based and simplified from the scheme proposed by Fauchald and Jumars (1979), with individuals being assigned to broad feeding categories –predators (carnivores plus omnivores), surface deposit feeders and burrowing subsurface deposit feeders (here after termed burrowers) (Table 2.2.).

Table 2.2. Trophic groups assigned for each polychaetes family recorded in this study (after Fauchald & Jumars, 1979).

Family	Trophic group
Acrocirridae	**Surface deposit feeder**
Ampharetidae	**Surface deposit feeder**
Amphinomidae	**Predator**
Apistobranchidae	**Surface deposit feeder**
Arenicolidae	**Burrower**
Capitellidae	**Burrower**
Chaetopteridae	**Surface deposit feeder**
Chrysopetalidae	**Predator**
Cirratulidae	**Surface deposit feeder**
Cossuridae	**Burrower**
Ctenodrilidae	**Burrower**
Dorvilleidae	**Predator/Surface deposit feeder**
Fauveliopsidae	**Burrower**
Flabelligeridae	**Surface deposit feeder**
Glyceridae	**Predator**
Goniadidae	**Predator**
Hesionidae	**Predator**
Heterospionidae	**Surface deposit feeder**
Lacydonidae	**Predator**
Lopadorhynchidae	**Predator**
Lumbrineridae	**Predator/Burrower**
Magelonidae	**Surface deposit feeder**

Maldanidae	**Burrower**
Nepthyidae	**Predator**
Nereididae	**Predator**
Oenonidae	**Predator**
Opheliidae	**Burrower**
Orbiniidae	**Burrower**
Oweniidae	**Surface deposit feeder**
Paraonidae	**Surface deposit feeder**
Pectinaridae	**Burrower**
Phyllodocidae	**Predator**
Pilargidae	**Predator**
Pisionidae	**Predator**
Poecilochetidae	**Surface deposit feeder**
Polynoidae	**Predator**
Sabellidae	**Surface deposit feeder**
Scalibgrematidae	**Burrower**
Sigalionidae	**Predator**
Sphaerodoridae	**Burrower**
Spionidae	**Surface deposit feeder**
Sternapsidae	**Burrower**
Syllidae	**Predator**
Terebellidae	**Surface deposit feeder**
Trochochaetidae	**Surface deposit feeder**

In order to obtain a consistent data set the presented results and statistical analyses were made only on a specific subset of samples. This was necessitated by

1. The high variability in the number of samples available for each sampling period,
2. The different types of data available for each cruise
3. The loss of some samples.

The specific samples subset was individuals retained in the 300–500 μm fractions. This sieve fraction still constitutes a representative component of the polychaetes fauna. The greatest abundance of polychaetes 62.9 % occurred in this size fraction (Fig. 2.2).

2.4.1.2. Species level

The temporal variability study for polychaete species considered those belonging to Cirratulidae, Spionidae, Paraonidae, Pilargidae and Glyceridae families. The Opheliidae was not identified at species level due to high presence of small size juveniles in samples. These specimens should match up with meiofauna category. For each species total and mean abundance was studied. Species richness was also calculated. To determine if there were changes in the polychaete composition associated with the '*Amperima* Event' a comparison between periods was made.

2.4.2. Statistical analyses

Only cruises with more than two replicate samples were used in statistical comparisons. To assess temporal variations of polychaete assemblages and detecting significant differences occurred in each parameter with time (cruises) a range of tests were undertaken. To attempt to meet the assumptions of parametric statistical analyses the data were log transformed (i.e. y=Log(x+1)) before analysis to ensure normality. Box-plot graphs were made to visualise on details differences among cruises. One way Analyses of Variance (ANOVA, Sokal & Rohlf, 1995) and non parametric Kruskal-Wallis test were undertaken to assess variations in abundance and testing for significant differences between sample times. Post Hoc tests were performed using Tukey Kramer's Test. ANOVAs and Kruskal-Wallis were carried out on abundance values for all polychaete assemblages; 0-1, 1-3 and 3-5 centimetres sediment layers; main polychaetes families such as the Cirratulidae, Spionidae, Opheliidae and Paraonidae, trophic groups such as surface deposit-feeders, predators and burrowers and in the most dominant species. 'STATISTICA' statistical software was used. Differences in the fauna between samples, cruises and particularly before and after the '*Amperima* Event' were analysed for families and species using various multivariate analyses techniques such as Non-metric Multidimensional Scaling (NMDS) and Analyses of similarity (ANOSIM) using the PRIMER 5 ecological software package (Clarke & Warwick, 2001; Clarke & Gorley, 2001). Bray Curtis Similarity Index was used, data was not standardised and either fourth or square root transformed for species analyses. Stress was defined by the number of times that model occur. A dendrogram made by Hierarchical Cluster analyses for families was also produced to indicate sample grouping.

2.4.3. '*Amperima* Event' comparison

A comparison between 'pre-*Amperima* Event' samples and '*Amperima* Event' samples for each parameter was also made. Statistical analyses were carried out with the aim to validate the results obtained, to identify temporal trends and test for there are significant changes between variables such as abundance with time, per sediment layers, main families, trophic groups and at species level. T-tests, which considered two samples with unequal variances, were made to detect differences between 'pre-*Amperima* Event' samples (1989-1994) and '*Amperima* Event' samples (1996-1998).

Data were log transformed (i.e. y=Log(X+1)) prior to analyses. Mann-Whitney U test were undertaken on raw data to compare and supporting before analyses. Both tests were carried out using a nonparametric statistical tool from 'STATISTICA' software. For the comparison between 'pre-*Amperima* Event' samples and '*Amperima* Event' samples from August 1989, May 1991 and April 1994 cruises were used as 'pre-*Amperima* Event'; and samples from September 1996, March 1997, July 1997, March 1998 and September 1998 cruises were used as '*Amperima* Event'.

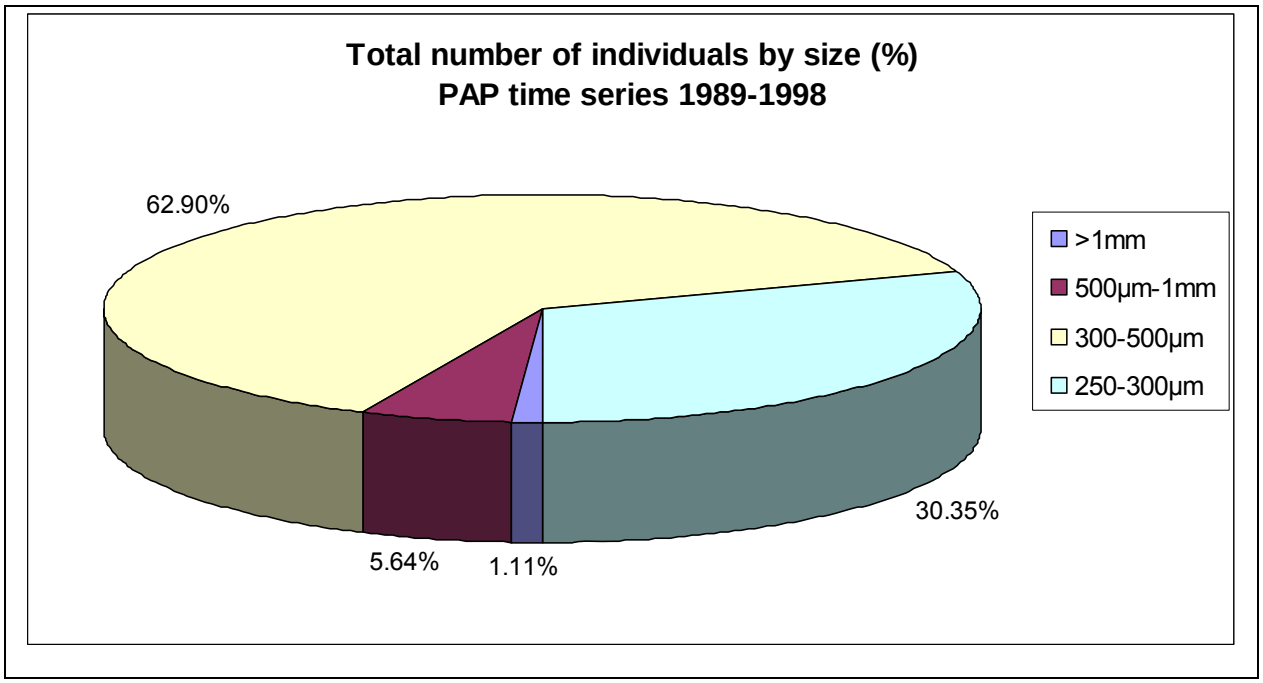


Figure 2.2. Total number of individuals by size (mesh diameter). All sieve fractions considered

CHAPTER 3

3. TAXONOMY

3.1. Cirratulidae

3.1.1. Introduction

Deep-sea cirratulids are common and abundant in the north-east Atlantic they may represent up to 25% of the total number of individuals (Glover *et al*., 2001; Soto *et al*., *in press*) and appear to be one of the four numerically dominant polychaetes families in the Atlantic margin (Chambers & Woodham, 2003). Cirratulids are also highly diverse in deep-sea sediments. Studies from recent programmes in the Atlantic, Pacific and Southern Oceans have revealed a wealth of new species. This species richness has posed two problems: 1) the need to review and expand the characters to describe species and 2) the definitions of the genera and species are inadequate and need to be revised (Doner *et al*., *submitted*).

Polychaetes belonging to the family Cirratulidae Rickholdt, 1851 are poorly known and many common species are often called by different names. There are few taxonomic characters and these are often descriptions misconstrued such that different generic designations are applied to a single species. Most of the older descriptions are not sufficient to adequately characterize species and many species are currently being misidentified. Some characters, such as the first appearance of acicular spines, are often related to growth. Because this character has been considered important in the differentiation of one species from another (Banse & Hobson, 1968), it is likely that single species are known under different names according to their stage of development (adapted from Blake, 1996).

The concept of the Cirratulidae has changed in the last years as many groups have been removed to separate families (e.g. Acrocirridae, Cossuridae, and Ctenodrilidae). The remaining genera are roughly divided into three groups: 1) the multitentaculate genera (e.g., *Cirratulus, Cirriformia, Protocirrineris* and *Timarete*); 2) the bitentaculate soft-substrate genera (e.g., *Aphelochaeta*, *Caulleriella, Chaetozone, Monticellina* and *Tharyx*); and 3) the bitentaculate hard-substrate genera (e.g., *Dodecaceria*). As the bitentaculate soft-substrate genera was the main group recorded in the current research, I will focus on these species.

The infaunal bitentaculate genera include several species, many undescribed, which are poorly known and difficult to distinguish from one another. The definitions of *Chaetozone, Caulleriella* and *Tharyx* were those established by Hartman (1961). All three genera were considered similar in the placement of the single pair of dorsal tentacles, reduction of the parapodia, and general appearance of the anterior and posterior ends of the body. The only reliable differences were in the form and arrangement of the chaetae. According to Hartman's system, species of *Tharyx* had only capillary-tipped chaetae; species of *Caulleriella* had acicular chaetae with bifid tips; whereas species of *Chaetozone* had acicular spines with distally entire tips. Hartman's concept of *Caulleriella* and *Chaetozone* differed from definitions of Fauvel (1927), Berkeley & Berkeley (1952), and Day (1967), who defined *Chaetozone* on the basis of whether or not the spines formed cinctures encircling the posterior body segments.

Blake (1991) established that the type species of the genus *Tharyx*, *T. acutus* Webster & Benedict, had knob-tipped hooks or spines in addition to capillaries. Blake (1991) therefore, restricted *Tharyx* to species having knob-tipped spines and established a new genus, *Aphelochaeta*, for those former species of *Tharyx* having simple, non-serrated capillary chaetae. *Tharyx monilaris* Hartman was designated as the type species of this new genus. Species having serrated capillaries were referred to the genus *Monticellina* Laubier. Further refinement of the definitions of *Caulleriella* and *Chaetozone* is now necessary because some species of *Chaetozone* have been discovered with one or more bidentate spines among the posterior cinctures of unidentate spines, especially in juveniles (Christie, 1985:242, fig. 2C). (Adapted from Blake, 1991).

In common with other deep-sea polychaetes, the Cirratulidae show a tendency for character loss. Some morphological adaptations are absent or reduced in deep-sea species. Therefore the taxonomy is more difficult and so new characters have to be considered to develop better descriptions. Doner & Blake (2006) have demonstrated for *Chaetozone* that characters associated with segmentation patterns and branchial distribution, details of posterior spines, and placement and form of the nuchal organ may be important in developing a phylogenetic analysis of the family. In the same way, Blake (2006) suggests that modifications to the digestive tract and the formation of spherical faecal pellets as seen in *C. brunea* may also serve as useful characters. Modifications to the peristomium, parapodia, and pygidium may be coded as part of a

monographic and phylogenetic analysis of *Chaetozone* and closely related cirratulids. Glover (2000) considered new characters based on the shape and relative sizes of various features associated with the thoracic region, although these characters were subjective for the observer. The same author considers that the absence of the abdominal section on specimens generates a big problem. The presence, position and nature of abdominal acicular spines are very important generic and specific taxonomic character for *Chaetozone*, *Tharyx* and *Aphelochaeta*.

Currently preliminary results from the CeDAMar database have revealed 3,389 polychaete records representing 803 species. Yet many more species have been identified but not formally classified and remain as morphotypes in a number of collections. To make this information available and calibrate the results from these studies a collaborative taxonomic project has been started – Abyssal Polychaete Inter-calibration Project (APIP). This project supported by CeDAMar aims to create a unified database of abyssal polychaetes. To this end several working groups have been set up to revise different families (http//:polychaetes.info).

For Cirratulidae the first activity was to agree on a common character set. The group is using key generating software, initially DELTA (Dallwitz *et al*., 1993), to collate the characters and to test morphotype species concepts from different localities. The main characters sets investigated were: 1) general body shape, 2) prostomial shape, 3) peristomial shape and organisation, 4) distribution and types of chaetae. This review has revealed a range of features previously ignored which are proving to be taxonomically robust. So far, a total of 80 characters for Cirratulidae have been established.

In the current investigation 15 different morphotypes of Cirratulidae have been recognized and described from 34 box-core studied samples*. 6 morphotypes belonged to genus *Aphelochaeta*, 8 to *Chaetozone* and 1 to *Tharyx*. The diversity of Cirratulidae is very high, considering that the 1 mm, 500 *μ*m, and 250 *μ*m sieve size fractions, and the deeper sediment layers such as 5-10 cm and 10-15 cm were not considered in this study. Identifications were carried out on the basis of taxonomic morphological characters where a list of them was considered and adapted from Glover (2000) and APIP (Glover, 2007). A key for genus (Blake, 1996a) was also considered. Around 80% of examined specimens had incomplete bodies with missing palps, branchiae and abdominal region, important taxonomic region areas. As a result the main species characters considered were the prostomium shape, the thoracic

body shape, the position of the palps, buccal region length, the presence or absence of ‘bottle-brush’ chaetae and their starting position, and the presence of acicular spines. Also the use of Methyl green staining was very useful as the staining pattern can be used to distinguish one species from another.

Species descriptions have been carried out using morphological characters detailed in the ‘List of characters’ (Appendix 3). Due to body conditions of the examined specimens most of these characters were not found therefore they were not considered in descriptions. Pictures from each species are showed in separate plates with the purpose to show the general shape of the body and some important taxonomic characters.

* 300-500 *μ*m, 0-1 cm, 1-3 cm and 3-5 cm sediment layers. Pre and Bengal samples

3.1.2. Results

3.1.2.1. Description of morphotypes

Genus: *Aphelochaeta*. Blake, 1991

***Aphelochaeta* sp. 13A**

268 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 185, August 1989 5 individuals; RRS *Challenger* 79 May 1991 46 individuals; RRS *Challenger* 111, April 1994 28 individuals; RRS *Discovery* 222, September 1996 49 individuals; RRS *Discovery* 226, March 1997 47 individuals; RRS *Discovery* 229, July 1997 47 individuals; RRS *Discovery* 231, March 1998 18 individuals and RRS *Discovery* 237, September 1998 28 individuals).

Description: The longest specimen with incomplete body, 4 mm long and 0.3 mm wide for 41 chaetigers. Thoracic body shape slightly swollen in mid to posterior region. Prostomium short widely conical duck-bill shaped. Elongate buccal region 3 times as long as broad. Peristomial region smooth and hunchbacked from lateral view in dorsal region. Three annulations on peristomium were observed. Palps less than 2 branchial widths to chaetiger 1. Short branchiae in dorsal position to notochaetae. Thoracic region about 20-25 chaetigers in length

Thoracic notochaetae and neurochaetae are simple capillaries 1-2 chaetigers in length, from chaetiger 11 long 'bottle-brush' chaetae present until chaetiger 13-14. Acicular spines not observed in thoracic and abdominal region. Incomplete abdominal region present with simple capillaries 1 chaetiger in length and 'bottle-brush' chaetae. Pygidium not observed.

Methyl green staining (MGS): Strong MGS pattern observed. Horizontal sidelines across prostomium and peristomial region.

Remarks: Though complete specimens were not found this species may be easily recognized by its duck-bill prostomium shape and the presence of long 'bottle-brush' chaetae from chaetiger 11. These taxonomic characters plus the thoracic body shape and buccal region length allow differ it from the rest of *Aphelochaeta* species. This species looks like some species of *Tharyx* (e.g. *Tharyx kirkegaardi*) described by Blake from Eastern North Pacific, mainly on prostomium shape and peristomium

length. However, knob-tipped spines, which are a characteristic taxonomic character of *Tharyx*, were not found in this species.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

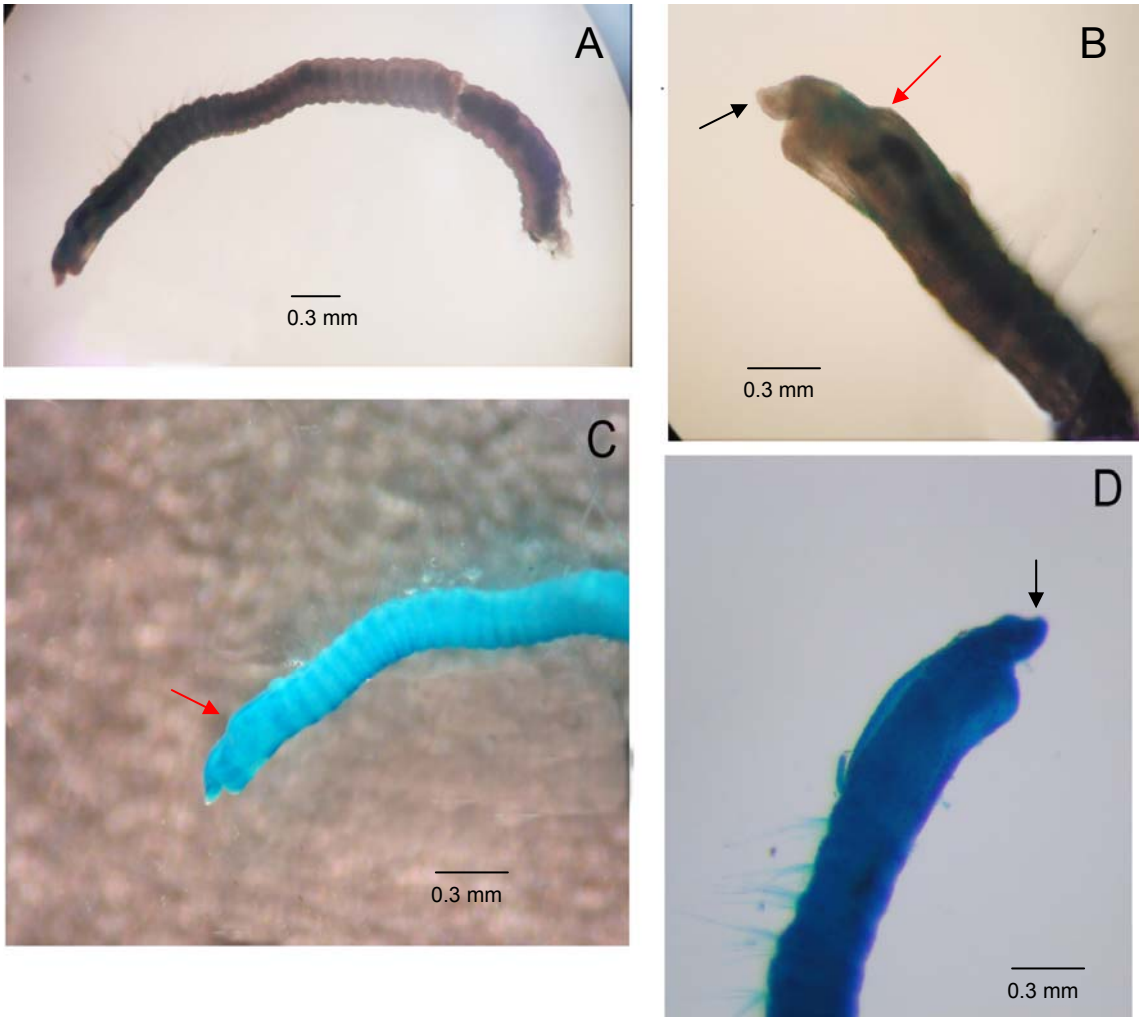


Figure 3.1. *Aphelochaeta* sp.13A a) incomplete body, lateral view 10x, b) anterior end lateral view 4x, c) anterior end, lateral view, methyl green staining 32x and d) anterior end, lateral view 10x.
The black arrows show the 'duck-bill' shaped prostomium and the red arrows show the hunchbacked peristomial region.

***Aphelochaeta* sp. 643C**

32 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79, May 1991 8 individuals; RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 6 individuals; RRS *Discovery* 226, March 1997 7 individuals; RRS *Discovery* 229, July 1997 2 individuals; RRS *Discovery* 231, March 1998 6 individuals and RRS *Discovery* 237, September 1998 2 individuals).

Description: The longest specimen with incomplete body, 3.5 mm long and 0.6 mm wide for 26 chaetigers. Thoracic body shape swollen in mid region tapering towards abdominal region. Prostomium pointed conical, with blunt tip. Elongate buccal region (greater than 4 chaetigers in length) with 3 achaetous annulations. Five black stains (spots) like dots on peristomium (lateral-ventral position) and between chaetiger 1 and end of peristomium (dorsal position). Longitudinal dorsal channel in thoracic zone. Palps more than 2 branchial widths to chaetiger 1. Short branchiae in dorsal-posterior position to notochaetae. Thoracic region 10-12 chaetigers in length.
Thoracic notochaetae and neurochaetae from chaetiger 1 are simple capillaries, 6 per fascicle, 1-3 chaetiger in length. Very long 'bottle-brush' chaetae from chaetiger 12. Thoracic acicular spines absent. Incomplete abdominal region with capillaries and 'bottle-brush' chaetae. Pygidium not observed.

Methyl green staining: Smooth and uniformly diffused green. Prostomium did not stained

Remarks: This species mainly differs from *Aphelochaeta* sp. 13A in the prostomium and peristomium shape, length of thoracic capillaries, thoracic body shape and the starting position of the 'bottle-brush' chaetae.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

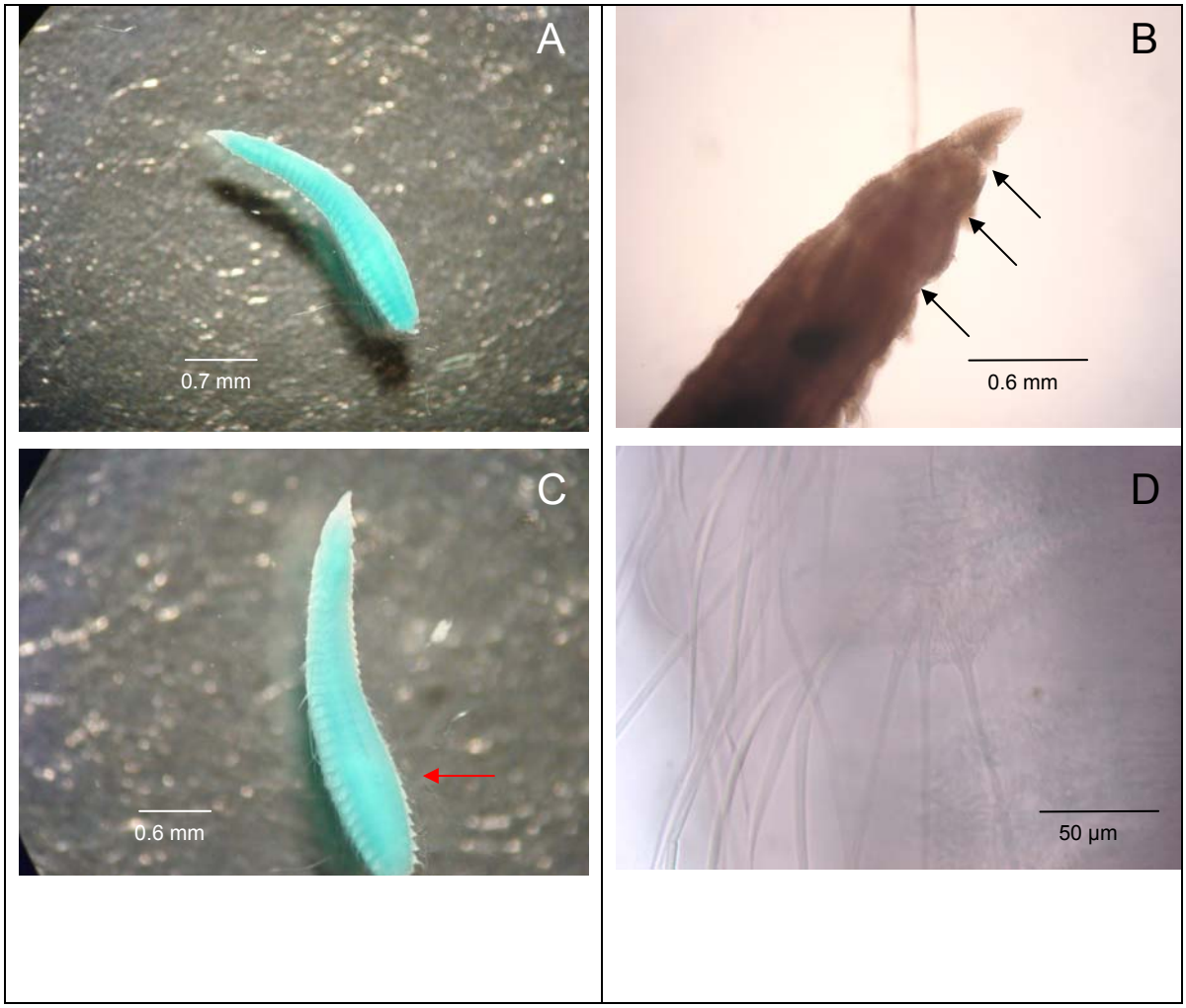


Figure 3.2. *Aphelochaeta* sp. 643C a) incomplete body, lateral view 10x, b) anterior end, lateral view 4x, c) incomplete body, ventral view 12x and d) neurochaetae capillaries, chaetiger 25, 40x.
The black arrows show 3 achaetous annulations and the red arrow shows the swollen body in mid region.

***Aphelochaeta* sp. 7**

10 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 3 individuals; RRS *Discovery* 226, March 1997 3 individuals; RRS *Discovery* 229, July 1997 2 individuals and RRS *Discovery* 237, September 1998 1 individual).

Description: The examined specimens with incomplete body. The longest specimen 2.6 mm long and 0.2 mm wide for 15 chaetigers in length. Thoracic body shape varied between slightly 'hour-glass' and swollen in mid region. Prostomium widely conical, small snout-like tapering from peristomium. Elongate buccal region 2-3 times as long as broad approximately. Palps more than 2 branchial widths to chaetiger 1. Branchiae in dorso-posterior position to chaetae. Thoracic region 7-8 chaetigers in length.
Thoracic notochaetae and neurochaetae from chaetiger 1 are simple capillaries of 1-2 chaetiger in length. On chaetiger 5-6 long chaetae 4 chaetigers in length. On chaetiger 1, 7 capillaries per fascicle in neuropodia and 6 capillaries per fascicle in notopodia. From chaetiger 7-8 very long 'bottle-brush' chaetae presents. Thoracic acicular spines absent. Intermediary body region presents simple capillaries and 'bottle-brush' chaetaes sited in segment chaetigers longer than thoracic region. Abdominal region missing.

Methyl green staining: Uniform

Remarks: *Aphelochaeta* sp.7 differs mainly from other *Aphelochaeta* species described in prostomium shape, length and shape of the buccal region, starting position of 'bottle-brush' chaetae and length of anterior capillaries

Habitat: This species was found within the sediment at a depth of 0-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

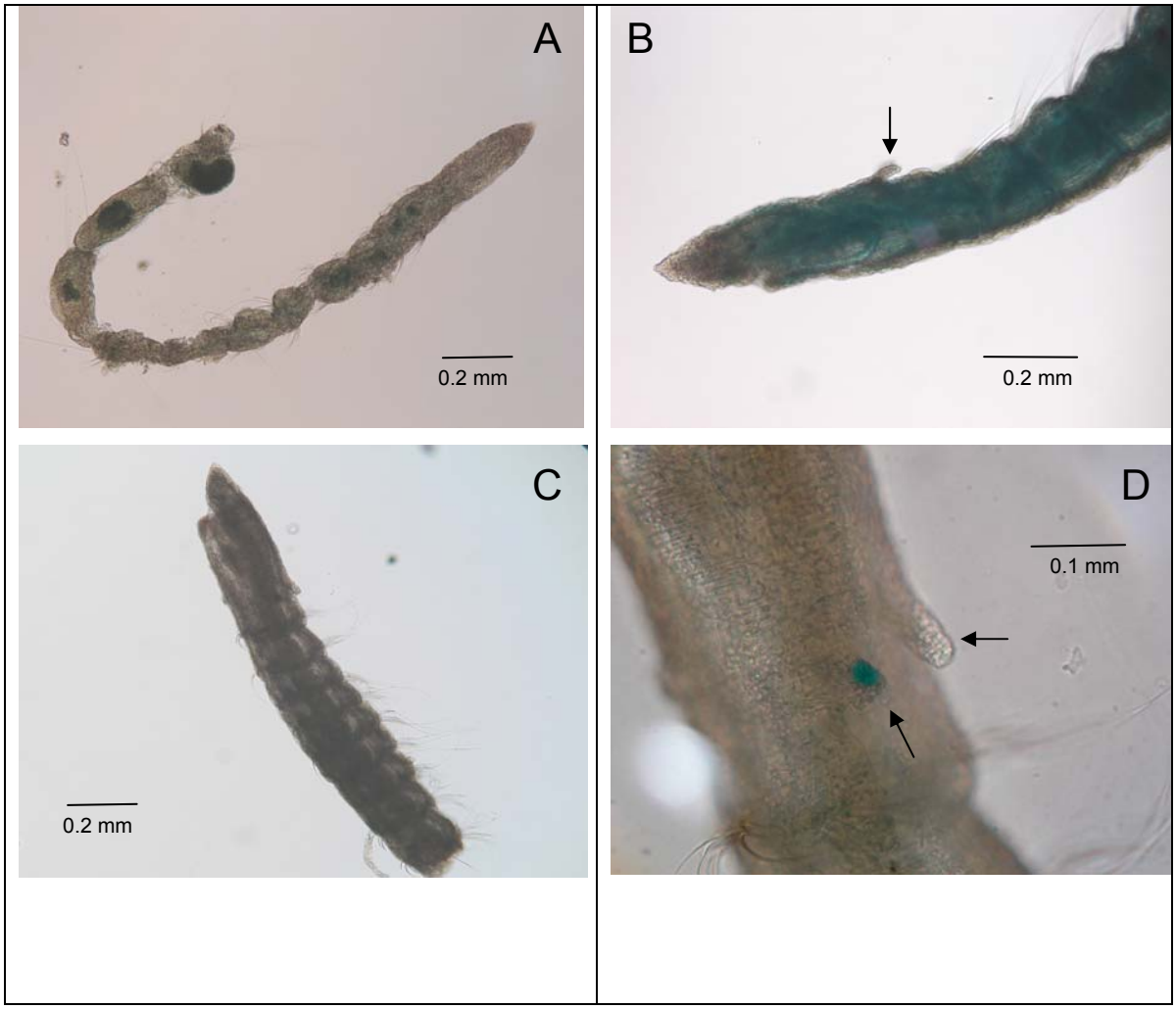


Figure 3.3. *Aphelochaeta* sp. 7 a) incomplete body 10x, b) anterior end, dorso-lateral view 10x, c) anterior end, dorso-lateral view 10x and d) scars palps, dorsal view 40x.
The black arrows show the scars palps.

***Aphelochaeta* sp. 9**

21 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 222, September 1996 13 individuals; RRS *Discovery* 226, March 1997 4 individuals; RRS *Discovery* 229, July 1997 3 individuals and RRS *Discovery* 237, September 1998 1 individual).

Description: Examined specimens with incomplete and deteriorated bodies. The largest specimen presented 3 mm long and 0.3 mm wide for 23 chaetigers approximately. Thoracic body shape widely swollen in anterior region. Prostomium short widely conical tapering from peristomium with rounded tip. Buccal region compact 1.5 times as long as broad. Palps more than 2 branchial widths to chaetiger 1. Long branchiae sited in dorsal position to chaetae. Thoracic region 16 chaetigers in length, with first anterior chaetigers crowded.

Thoracic notochaetae and neurochaetae are simple capillaries comprising short chaetae of 2-3 chaetigers in length (6-7 per fascicle) and long 'bottle-brush' chaetae 4-5 chaetigers in length present from chaetiger 1-9. Very long thoracic 'bottle-brush' chaetae 7-8 chaetiger in length present from chaetiger 8-15 forming hair-like tangle. Thoracic acicular spines absent. Acicular spines in mid region were observed in only one specimen. Abdominal region incomplete with simple capillaries.

Methyl green staining: Uniform and diffused

Remarks: *Aphelochaeta* sp. 9 differs from other *Aphelochaeta* species in prostomium and thoracic body shape; length of buccal region and starting position of 'bottle-brush' chaetae. The absence of abdominal region in specimens examined did not allow a better description. Some specimens with pharynx everted were observed. Taxonomic characters observed on examined specimens such as simple non-serrated capillary chaetae, 'bottle-brush' chaetae and absence of thoracic acicular spines suggest these specimens belong to *Aphelochaeta*.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

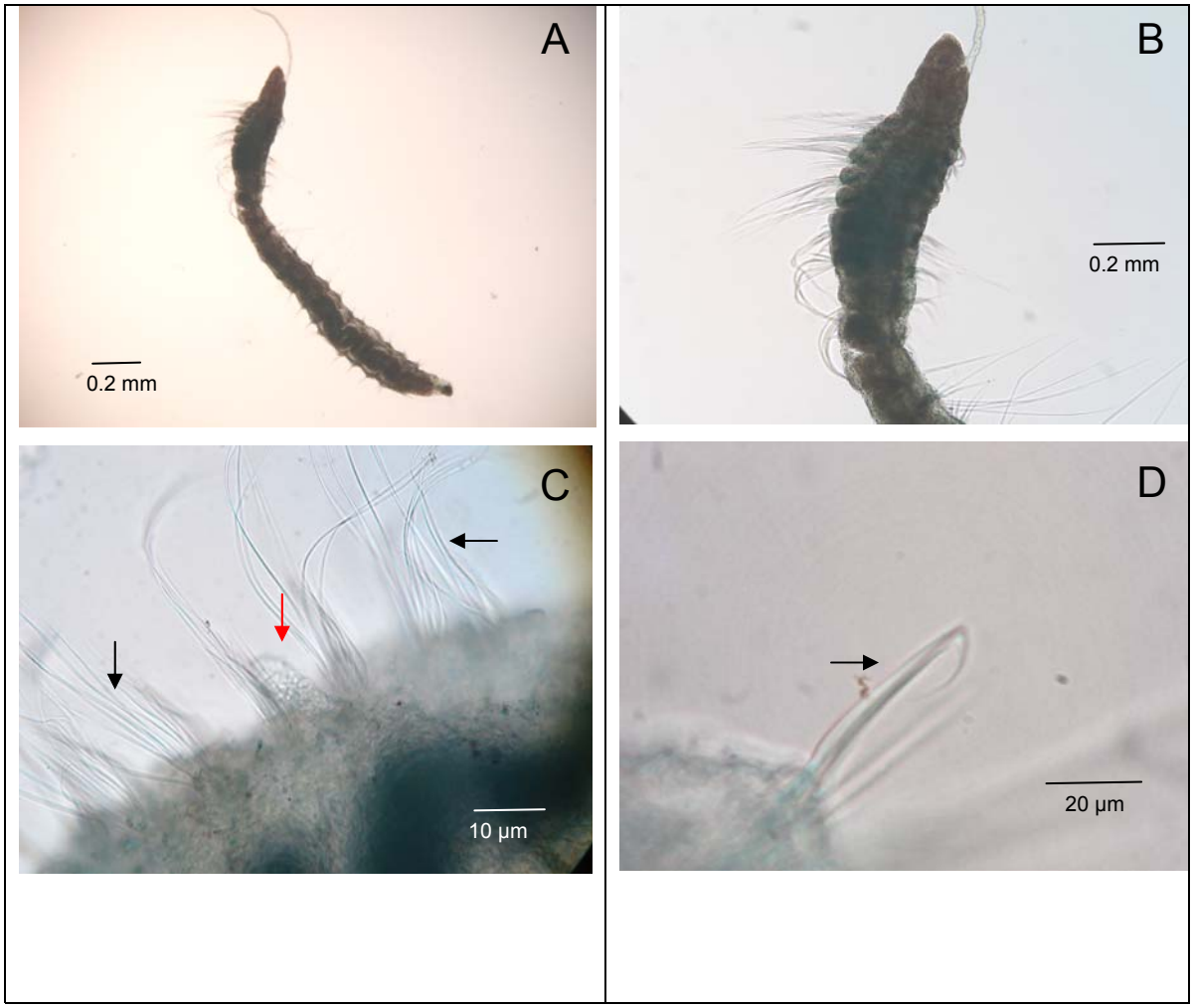


Figure 3.4. *Aphelochaeta* sp. 9 a) complete body, ventral view 4x, b) anterior end, ventral view 10x, c) capillaries and branchiae (red arrow), anterior region 40x and d) acicular spine chaetiger 23, 100x.
The black arrows show the thoracic capillaries (Fig. 3.4.C) and acicular spine (Fig. 3.4.D).

***Aphelochaeta* sp. 11**

15 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 3 individuals; RRS *Discovery* 222, September 1996 2 individuals; RRS *Discovery* 226, March 1997 5 individuals; RRS *Discovery* 229, July 1997 3 individuals; RRS *Discovery* 231, March 1998 1 individual and RRS *Discovery* 237, September 1998 1 individual).

Description: All observed specimens with incomplete bodies. The longest specimen recorded 20 mm long and 0.2 mm wide for 42 chaetigers in length. Thoracic body shape of uniform width throughout, slightly moniliform in mid region, with first chaetigers shorter than posterior chaetigers. Prostomium long widely conical with rounded-blunt tip. Buccal region elongate 2.5 to 3 times as long as broad. Palps less than 2 branchial widths to chaetiger 1. Branchiae scars in dorsal-anterior position to chaetae. Thoracic region 8-10 chaetigers in length.

Thoracic notochaetae and neurochaetae from chaetiger 1 are simple capillaries of 1-2 chaetigers in length; on chaetiger 1, 5-6 capillaries per fascicle in notopodia and 5-7 capillaries per fascicle in neuropodia. Long chaetae 4 chaetigers in length on chaetiger 8 and chaetiger 9. Bottle-brush chaetae from chaetiger 7 and presents in following chaetigers until abdominal region. Thoracic acicular spines absent. Chaetiger segments longer and moniliform in mid and abdominal region. Intermediary body region between thorax and abdomen with short capillaries and bottle-brush chaetae. Abdominal region long 20-22 chaetigers in length. Pygidium not observed.

Methyl green staining: Soft and uniformly diffused.

Remarks: Differs mainly from other PAP *Aphelochaeta* species described in body and prostomium shape, bottle-brush chaetae length and the presence of crowded chaetiger segments on anterior thoracic region and moniliform chaetigers from mid region .

Habitat: This species was found within the sediment at a depth of 0-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

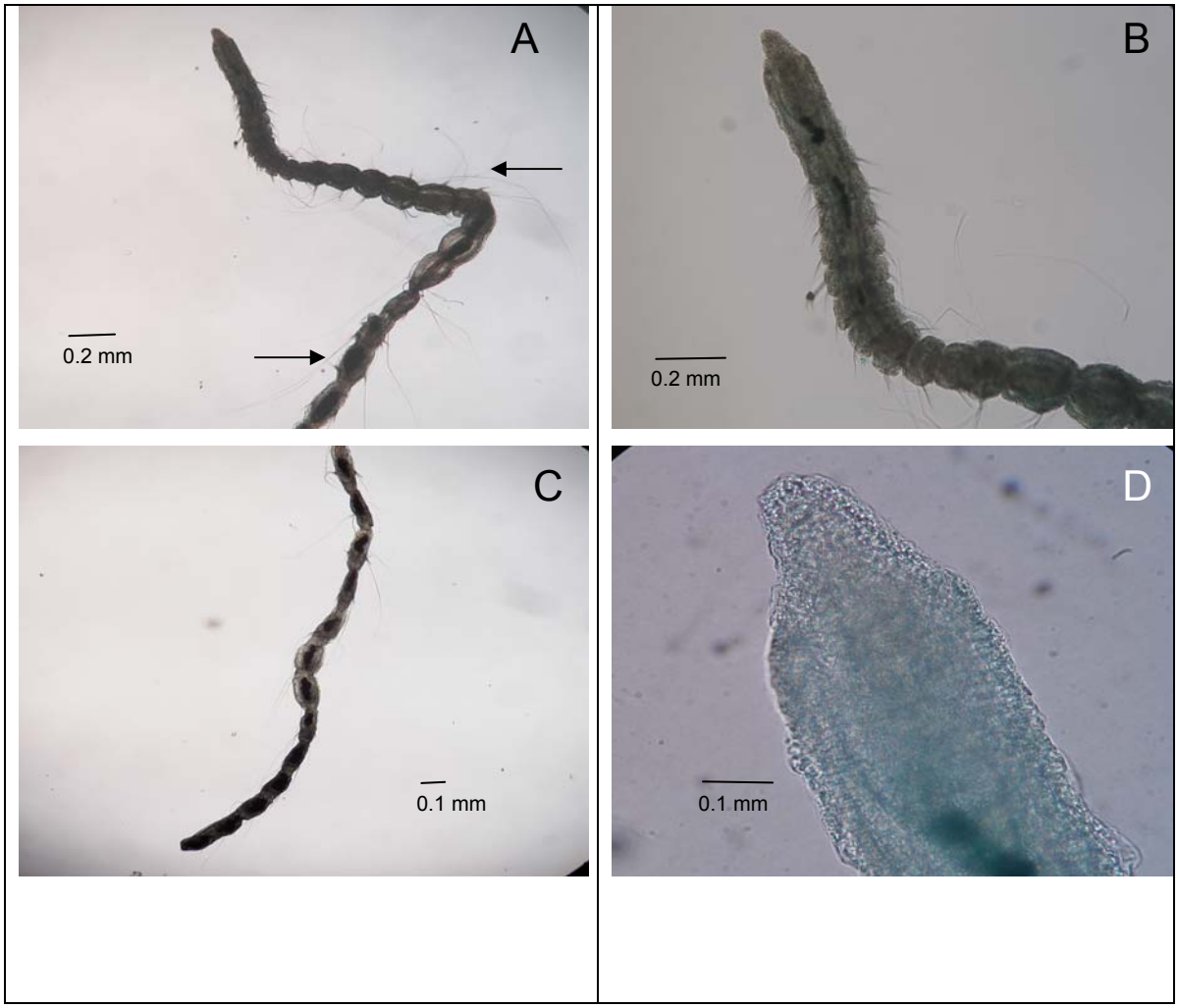


Figure 3.5. *Aphelochaeta* sp. 11 a) anterior end and mid region, 4x, b) anterior end, ventral view 10x, c) posterior region 4x and d) prostomium detail 40x.
The black arrows show the 'bottle-brush' chaetae.

***Aphelochaeta* sp. 647D**

104 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79, May 1991 1 individual; RRS *Challenger* 111, April 1994 9 individuals; RRS *Discovery* 222, September 1996 18 individuals; RRS *Discovery* 226, March 1997 17 individuals; RRS *Discovery* 229, July 1997 21 individuals; RRS *Discovery* 231, March 1998 11 individuals and RRS *Discovery* 237, September 1998 27 individuals).

Description: The specimen with complete body 4.5 mm long and 0.3 mm wide for 29 chaetigers in length. Thoracic body shape slightly hour-glass shaped changing to uniform width throughout in some specimens. Prostomium long and conical tapering between blunt and pointed tip (snout-like). Buccal region elongate 2-3 times as long as broad. Palp scars visible more than 2 branchial widths from junction with chaetiger 1. Branchiae sited posterior to chaetae. Thoracic region 10-11 chaetigers in length.
Thoracic notochaetae and neurochaetae from chaetiger 1 simple capillaries of 1-2 chaetiger in length. Long chaetae 4 chaetigers in length from chaetiger 2 to chaetiger 9. On chaetiger 1, 7-9 capillaries per fascicle in notopodia and neuropodia decreasing in number to posterior chaetigers. Long 'bottle-brush' chaetae from ch10 also present in abdominal chaetigers. Thoracic acicular spines absent. Pygidium as a simple and short lobe ending rounded tip in dorsal position.

Methyl green staining: Prostomium and peristomium darker than thoracic region. Chaetiger 10 and chaetiger 11 darker than the rest stained in ventral region.

Remarks: This species differs from other PAP *Aphelochaeta* species in general body shape, prostomium shape, starting position of bottle-brush chaetae and pygidium shape.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

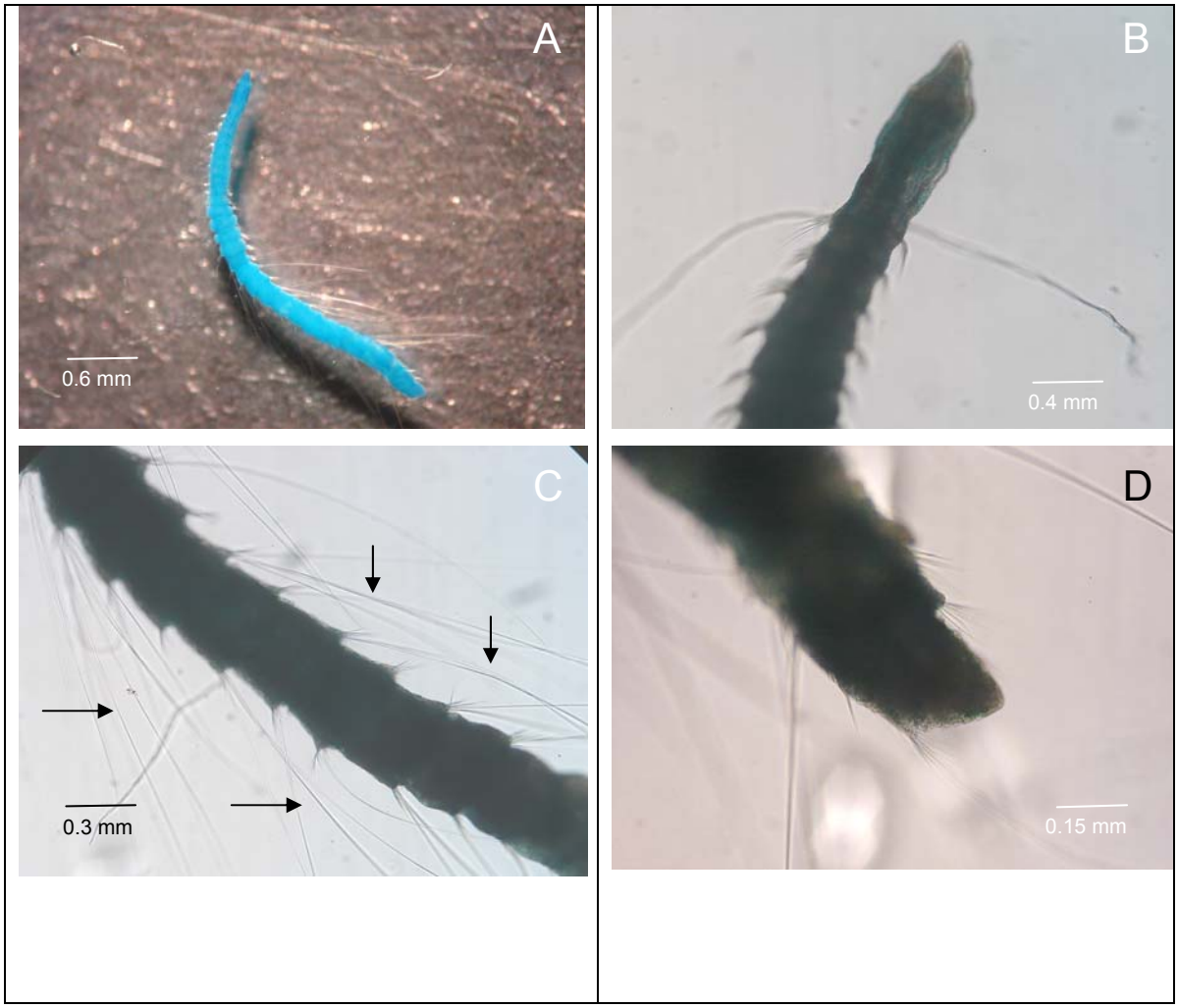


Figure 3.6. *Aphelochaeta* sp. 647D a) complete body, dorsal view 23x, b) anterior end, dorsal view 10x, c) 'bottle-brush' chaetae abdominal region (black arrows), 10x and d) pygidium 10x.

Species	Prostomium	Thorax	Buccal region	Branchial scars position	'Bottle-brush' chaetae
***Aphelochaeta* sp. 13A**	Duck-bill	Slightly swollen in mid to posterior	3 times as long as broad	Dorsal to chaetae	From ch11
***Aphelochaeta* sp. 643C**	Pointed conical, blunt tip	Swollen in mid tapering abdominal	Elongate, greater than 4 chaetigers	Dorsal-posterior to chaetae	From ch12
***Aphelochaeta* sp. 7**	Small, snout-like	'Slightly Hour-glass' to swollen	2-3 times as long as broad	Dorsal-posterior to chaetae	From ch7-8
***Aphelochaeta* sp. 9**	Short, widely conical, rounded tip	Widely swollen in anterior	Compact, 1.5 times as long as broad	Dorsal to chaetae	From ch1
***Aphelochaeta* sp. 11**	Long, conical, rounded blunt tip	Uniform	2.5-3 times as long as broad	Dorsal-anterior to chaetae	From ch7
***Aphelochaeta* sp. 647D**	Long, conical with pointed tip	Slightly 'hour-glass' to uniform	2-3 times as long as broad	Posterior to chaetae	From ch10

Table 3.1. Taxonomic characters of *Aphelochaeta* species. ch: chaetiger

Genus: *Chaetozone*. Malmgren, 1867

***Chaetozone* sp. 685**

20 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79, May 1991 4 individuals; RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 6 individuals; RRS *Discovery* 226, March 1997 5 individuals and RRS *Discovery* 229, July 1997 4 individuals).

Description: The largest specimen with complete body, 1.2 cm long and 1.1 mm wide for 58 chaetigers. Thoracic body shape swollen in mid to posterior region. Prostomium long, conical with a blunt and rounded tip. Elongated buccal region almost 3 times as long as broad. Peristomial region smooth in dorsal region. Palps less than 2 branchial widths to chaetiger 1. Long branchiae observed. Thoracic region 34-36 chaetigers in length

Thoracic notochaetae with short simple capillaries 1-2 chaetigers in length from chaetiger 1, becoming long like 'bottle-brush' (>5 chaetigers) from chaetiger 11 until chaetiger 13-14. Acicular spines present appearing from chaetiger 8.

Thoracic neurochaetae, from chaetiger 1 are short simple capillaries of 1-2 chaetigers in length. Acicular spines present appearing from chaetiger 5. Abdominal region not constricted between segments with 22-24 chaetigers in length. Incomplete abdominal cinctures present with simple capillaries of 1 chaetiger in length and acicular spines. Seven acicular spines per fascicle in neuropodia. Six acicular spines per fascicle in notopodia. 'Banana' shaped acicular spines in thoracic and mid region. Pygidium long, with simple lobe.

Methyl green staining: Horizontal sidelines were observed in peristomium and anterior region

Remarks: The allocation of the genus *Chaetozone* Malmgren 1867 is debatable owing to the presence of acicular spines in the thoracic region. However, acicular spines are most common in mid and abdominal region of *Chaetozone* species. This species can be identified by prostomium shape, starting position of thoracic acicular spines and 'bottle brush' chaetae.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

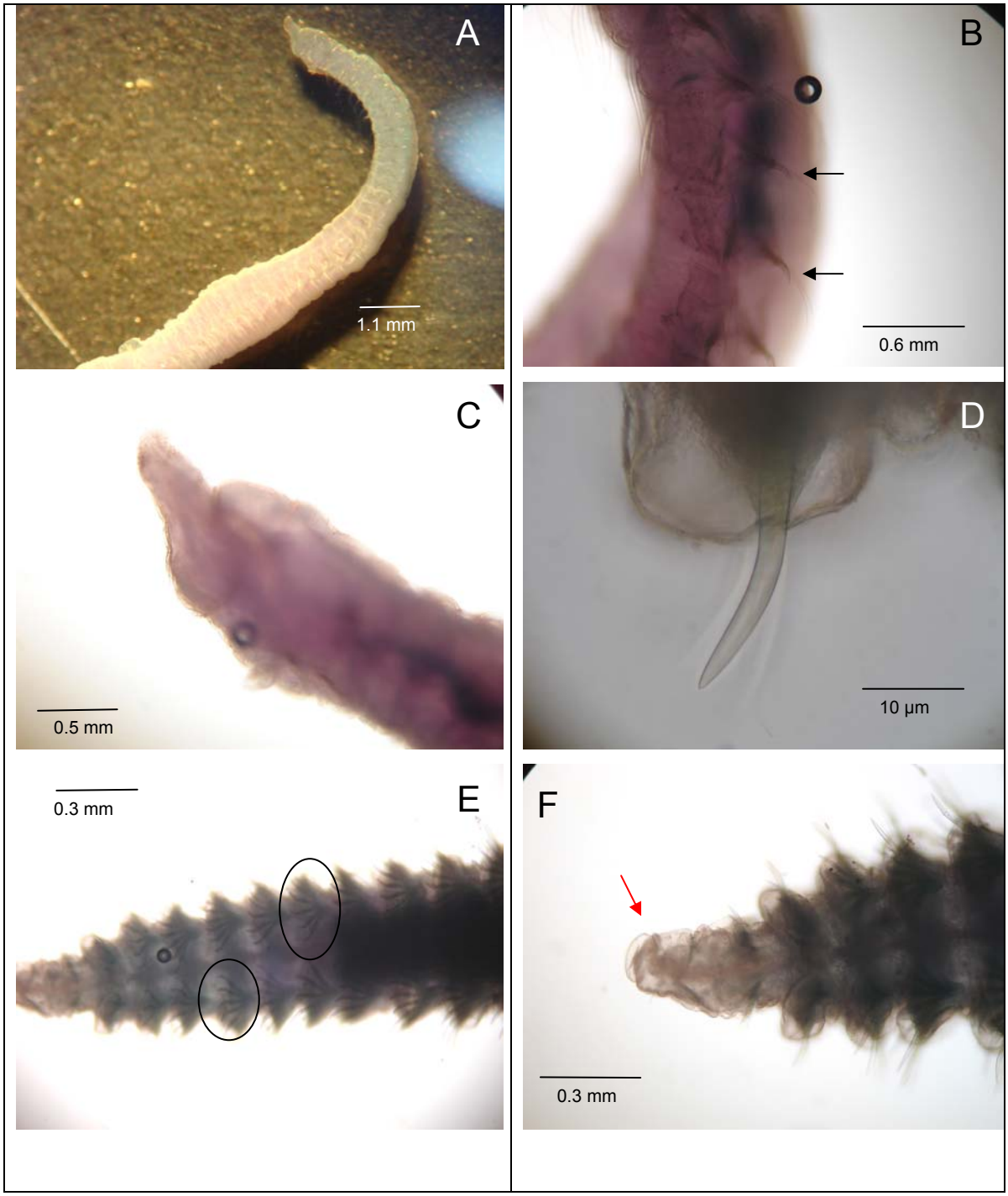


Figure 3.7. *Chaetozone* sp. 685 a) anterior end 16x, b) thoracic acicular spines 10x, c) peristomium detail 10x, d) 'banana' shaped spine, mid region 40x, e) posterior end, ventral view, acicular spines 4x and f) pygidium detail, ventral view 10x.
The black arrows show the thoracic acicular spines, the black circles show the incomplete cinctures and the red arrow shows the pygidium.

***Chaetozone* sp. 55A**

128 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 185, August 1989 3 individuals; RRS *Challenger* 79, May 1991 34 individuals; RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 24 individuals; RRS *Discovery* 226, March 1997 29 individuals; RRS *Discovery* 229, July 1997 21 individuals; RRS *Discovery* 231, March 1998 7 individuals and RRS *Discovery* 237, September 1998 9 individuals).

Description: The largest specimen with complete body recorded 9 mm long and 1 mm wide for 34-35 chaetigers. Thoracic body shape swollen in mid region. Prostomium short, pointed conical with blunt tip, while some specimens with rounded prostomium were also observed. Buccal region compact and wider than prostomium; 1-2 times as long as broad. Palps less than 2 branchial widths to chaetiger 1. Branchial scars present, visible in some thoracic chaetigers. Thoracic region 19-20 chaetigers in length.

Long 'bottle-brush' chaetae from chaetiger 1, in one specimen presents from chaetiger 5. ‘Bottle brush’ capillary chaetaes 6-7 chaetigers in length approximately.

Thoracic notochaetae and neurochaetae from chaetiger 1 are simple capillaries of 1-2 chaetigers in length. Thoracic acicular spines were not observed. Ventral channel observed in thoracic zone. Chaetigers on part intermediate (between thoracic and abdominal region) were not observed. Abdominal region constricted between segments tapering to pygidium, 16 chaetigers in length. Abdominal cinctures present in partial distribution with simple capillaries 1 chaetiger in length sited on parapodia and acicular spines. ‘Bottle-brush’ chaetae absent. Pygidium short and rounded

Methyl green staining: Entire body staining a uniformly diffused green.

Remarks: This species mainly differs from *Chaetozone* sp. 685 in prostomium length and shape, buccal region length, starting position and length of long chaetae (‘bottle-brush’), the absence of acicular spines in thoracic region and pygidium shape. The presence of eggs in intermediary body region (between thorax and abdomen) was observed in some specimens.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

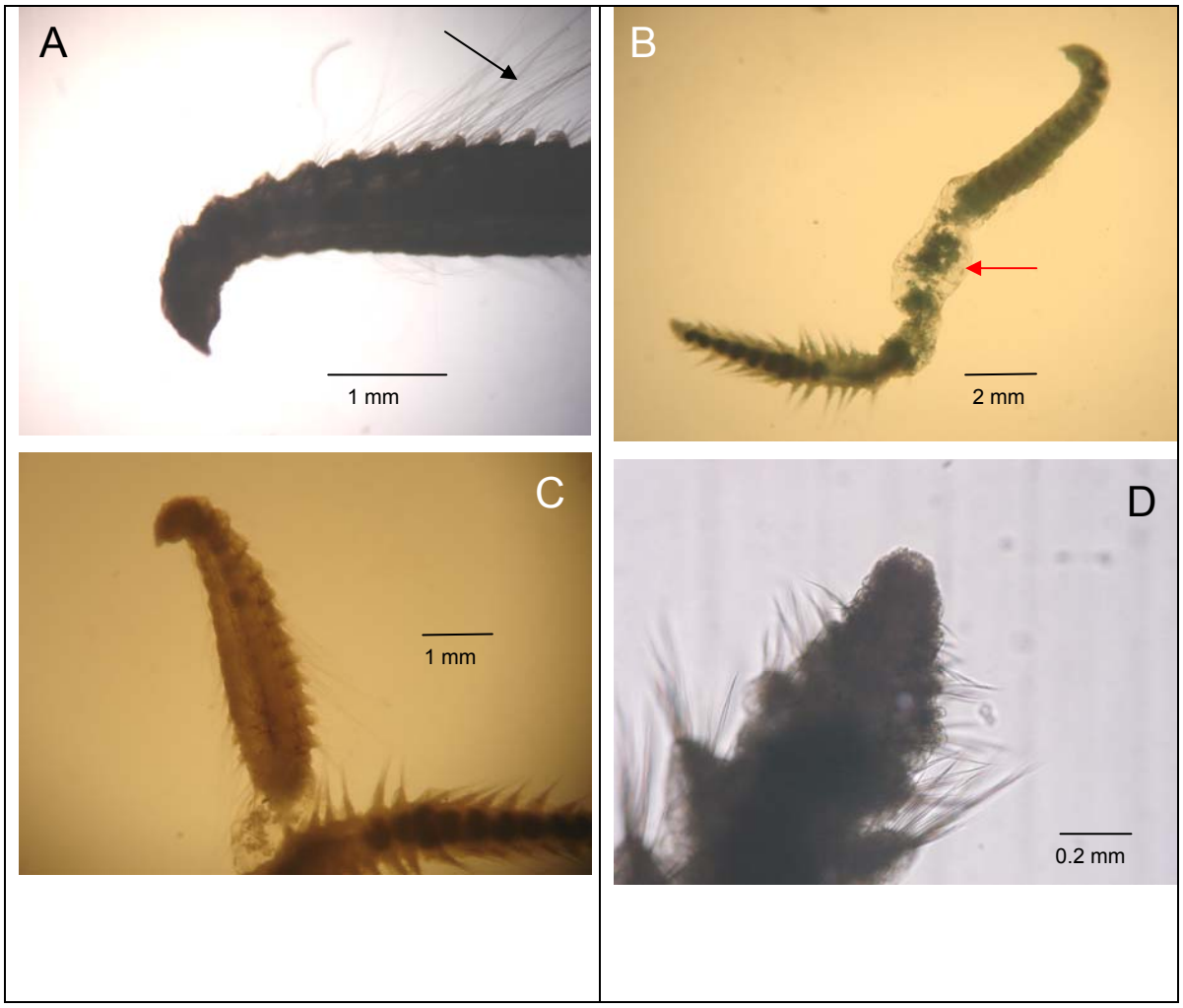


Figure 3.8. *Chaetozone* sp. 55A a) anterior end, lateral view 13x, b) complete body 6x, c) complete body, ventral view 10x and d) posterior end 15x.
The black arrow shows the thoracic 'bottle-brush' chaetae and the red arrow shows the achaetous part intermediate.

***Chaetozone* sp. 657E**

16 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79, May 1991 1 individual; RRS *Challenger* 111, April 1994 2 individuals; RRS *Discovery* 222, September 1996 1 individual; RRS *Discovery* 226, March 1997 5 individuals; RRS *Discovery* 229, July 1997 4 individuals; RRS *Discovery* 231, March 1998 2 individuals and RRS *Discovery* 237, September 1998 1 individual).

Description: The largest specimen with complete body, 2.4 mm long and 0.2 mm wide for 27 chaetigers. Thoracic body shape uniform width throughout. Prostomium pointed, widely conical with rounded tip. Elongate buccal region 2 times as long as broad. Peristomial region smooth. Palps scars present more than 2 branchial widths to chaetiger 1. Branchiae scars present. Thoracic region 7-9 chaetigers in length.
Thoracic notochaetae and neurochaetae with short simple capillaries 1-2 chaetigers in length from chaetiger 1. Long 'bottle-brush' chaetae present from ch1, longer than 5 chaetigers in length. Thoracic acicular spines not observed. Intermediary body region between thorax and abdomen was not observed. Abdominal region necklace-shaped (moniliform) tapering to pygidium 18 chaetigers in length. Long abdominal acicular spines present forming complete cinctures together to simple capillaries 1 chaetiger in length (10 per fascicle). Pygidium present, long and ending as a rounded lobe.

Methyl green staining: Uniform. Prostomium not stained.

Remarks: This species mainly differs from other PAP *Chaetozone* species already described in thoracic body shape, shape of the prostomium, buccal region length, number of chaetigers with long ’bottle-brush’ chaetae, palp scars location, acicular spines forming complete cinctures and abdominal region shape.

Habitat: This species was found within the sediment at a depth of 0-10 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

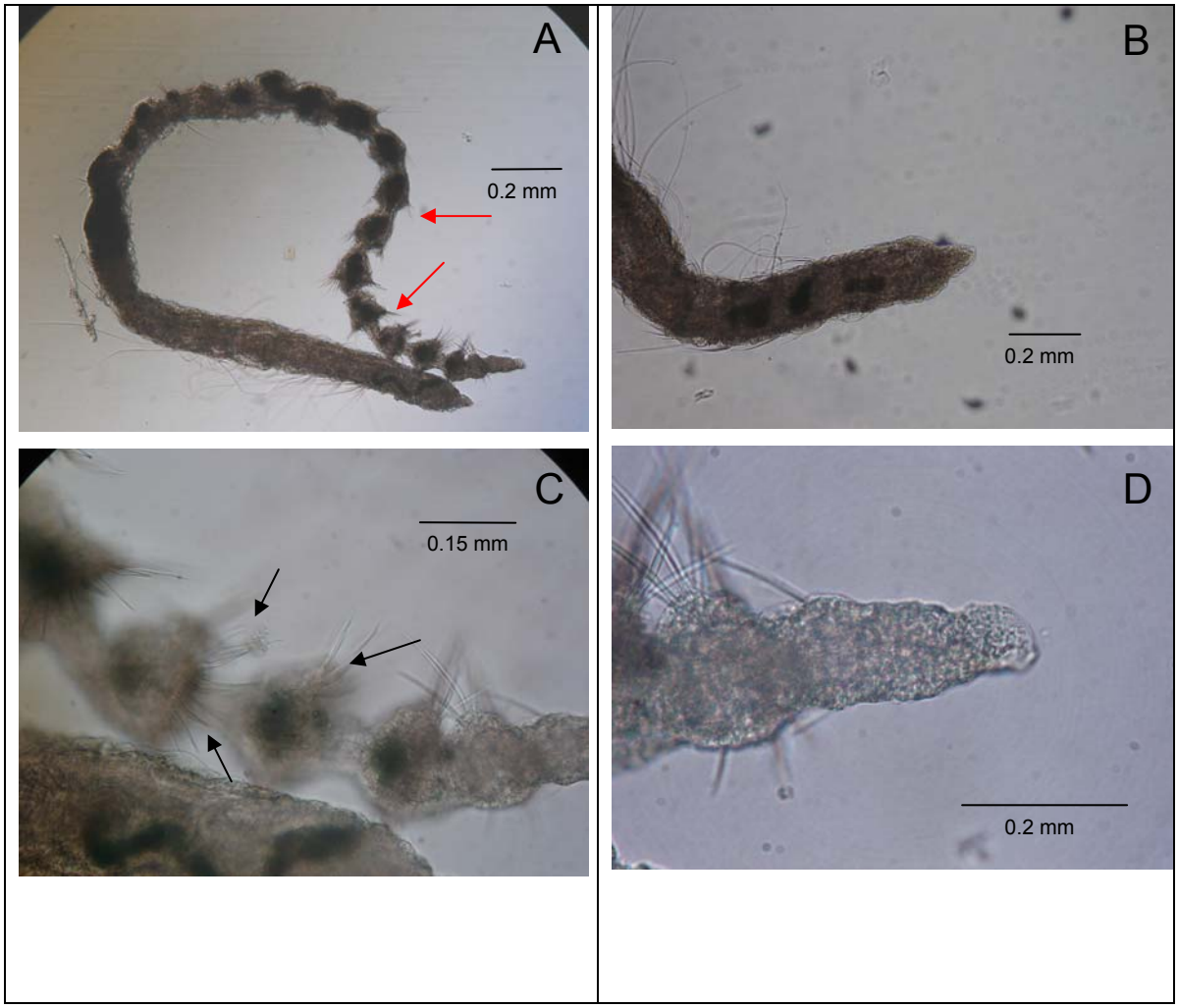


Figure 3.9. *Chaetozone* sp. 657E a) complete body 10x, b) anterior end 10x, c) acicular spines in abdominal region 40x and d) pygidium detail 40x.
The red arrows show the moniliform abdominal region and the black arrows show the acicular spines.

***Chaetozone* sp. 605B**

27 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79, May 1991 4 individuals; RRS *Challenger* 111, April 1994 3 individuals; RRS *Discovery* 222, September 1996 7 individuals; RRS *Discovery* 226, March 1997 9 individuals and RRS *Discovery* 229, July 1997 4 individuals).

Description: The specimens with incomplete body, the largest specimen recorded 2.3 mm long and 0.2 mm wide for 18 chaetigers approximately. Thoracic body shape changes between uniform and swollen in anterior region. Prostomium pointed, widely conical with blunt tip. Semi elongate buccal region 1.5 times as long as broad. Two specimens with peristomial region wider than thoracic region. Palps less than 2 branchial widths to chaetiger 1. Branchiae scars were not observed. Thoracic region 9-10 chaetigers in length

Thoracic notochaetae and neurochaetae all simple and short capillaries of 1-2 chaetiger in length or shorter. Chaetae 3 chaetigers in length from chaetiger 4 were observed in one specimen. Long 'bottle-brush' chaetae and thoracic acicular spines absent. Incomplete abdominal region with acicular spines present in some specimens. Pygidium not observed.

Methyl green staining: Uniform. Prostomium not stained.

Remarks: This species differs from other *Chaetozone* species described in the prostomium tip shape, width of peristomial region about thorax, buccal region length, length of capillaries and absence of 'bottle-brush' chaetae. Unfortunately, the absence of abdominal region in the majority of specimens revisited did not allow a better description. Hence further observations are required.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

Figure 3.10. *Chaetozone* sp. 605B a) incomplete body lateral view 10x and b) anterior end, ventral view 10x.
The black arrows show the short thoracic capillaries.

***Chaetozone* sp. 10**

19 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 2 individuals; RRS *Discovery* 222, September 1996 3 individuals; RRS *Discovery* 226, March 1997 9 individuals; RRS *Discovery* 229, July 1997 1 individual and RRS *Discovery* 237, September 1998 4 individuals).

Description: The largest specimen with complete body, 5 mm long and 0.5 mm wide for 34 chaetigers. Thoracic body shape slightly swollen in mid region. Prostomium long, widely conical with blunt tip. Elongate buccal region long, wider than prostomium 2-3 times as long as broad. Palps more than 2 branchial widths to chaetiger 1. Palps scars present. Branchiae visible in some thoracic chaetigers in dorsal-posterior position to notochaetae. Thoracic region 20-22 chaetigers in length.

Thoracic notochaetae and neurochaetae from chaetiger 1 are simple capillaries, 7-8 per fascicle 1-2 chaetigers in length. Thoracic acicular spines not observed. The appearance and long of 'bottle-brush' chaetae were variable. It was present from chaetiger 1 and 5. Abdominal region shape varies between uniform width and necklace-shaped. Complete abdominal cinctures composed by acicular spines, 18 per fascicle, and simple capillaries were observed. Abdominal region 14 chaetigers in length. Pygidium short with terminal anus.

Methyl green staining: Smooth and uniformly diffused green.

Remarks: The presence of simple acicular spines in posterior chaetigers arranged in cinctures would be indicating the genus *Chaetozone*. This species differs from other PAP *Chaetozone* species described in shape and length of the peristomium, starting position of long chaetaes (bottle-brush), shape of abdominal region and the presence of terminal anus in the pygidium.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

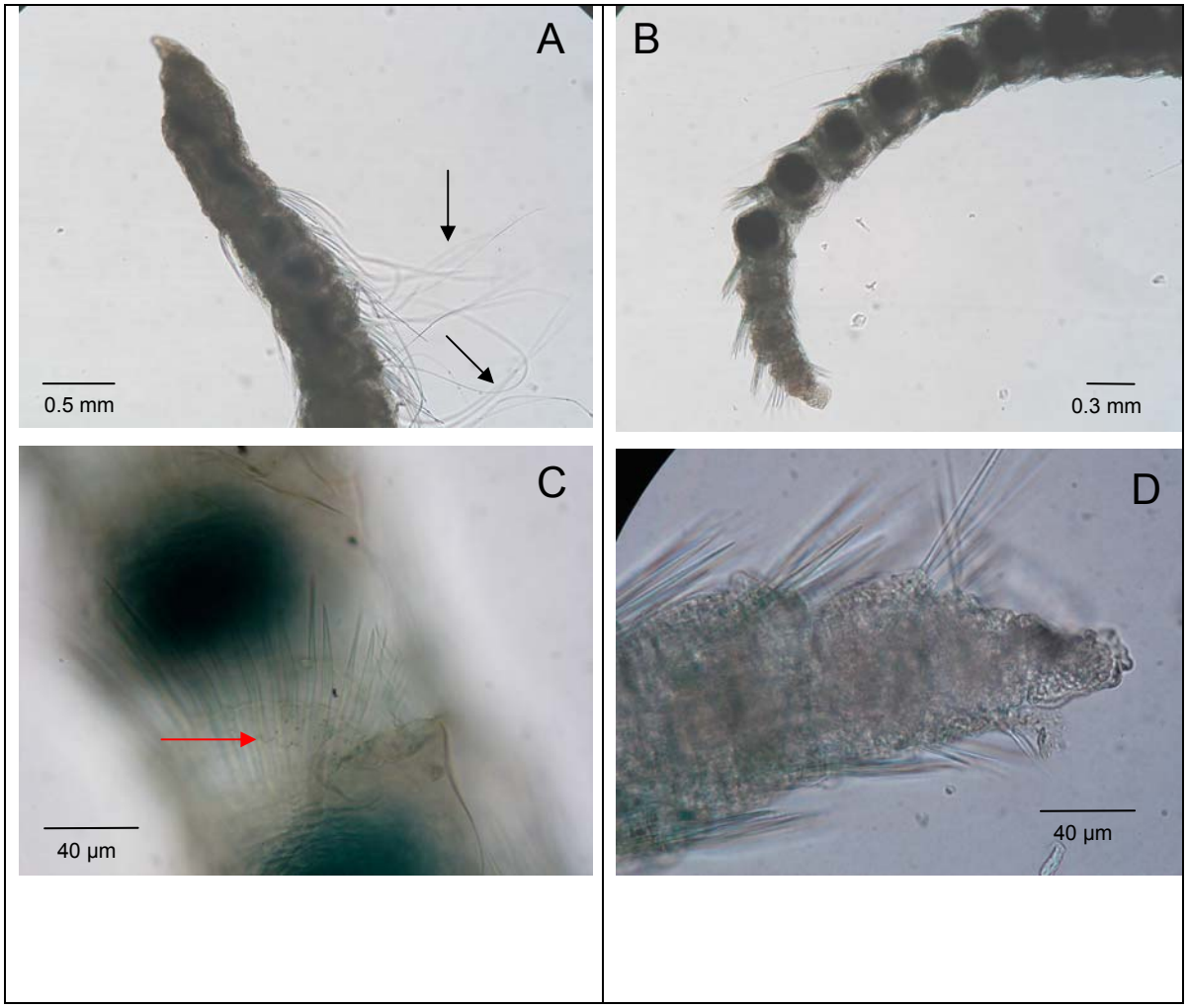


Figure 3.11. *Chaetozone* sp. 10 a) anterior end, lateral view 10x, b) posterior end lateral view 10x, c) cinctures, posterior end 40x and d) pygidium 40x.
The black arrows show the 'bottle-bush' chaetae and the red arrow shows the complete abdominal cinctures.

***Chaetozone* sp. 12**

8 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 3 individuals; RRS *Discovery* 222, September 1996 3 individuals; RRS *Discovery* 229, July 1997 1 individual and RRS *Discovery* 237, September 1998 1 individual)

Description: The longest specimen with incomplete body, 3 mm long and 0.6 mm wide for 19 chaetigers. Thoracic body shape swollen in mid region increasing gradually from peristomial to mid region. Prostomium long, conical, with blunt tip. Semi-elongate buccal region 2 times as long as broad with 3 achaetous annulations. Big palps more than 2 branchial widths to chaetiger 1. Long branchiae visible in thoracic chaetigers dorsal to notochaetae. Thoracic region 16 chaetigers in length.
Thoracic notochaetae and neurochaetae from chaetiger 1 simple capillaries, 4 per fascicle; 1-2 chaetigers in length, from chaetiger 3 very long 'bottle-brush' chaetae greater than 12 chaetigers appear hair-like around the body of the animal. Thoracic acicular spines absent. Unidentate acicular spines were observed in posterior region from some specimens, however cinctures arrangement was not observed. Abdominal region missing.

Methyl green staining: Darker in peristomium region. Smooth and uniformly diffused green.

Remarks: *Chaetozone* sp. 12 differs from other PAP *Chaetozone* species described in the shape of the buccal region, prostomium and peristomium and the starting position and length of 'bottle-brush' chaetae. Unfortunately, the lack of complete individuals did not allow further descriptions about abdominal region

Habitat: This species was found within the sediment at a depth of 0-1 and 3-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

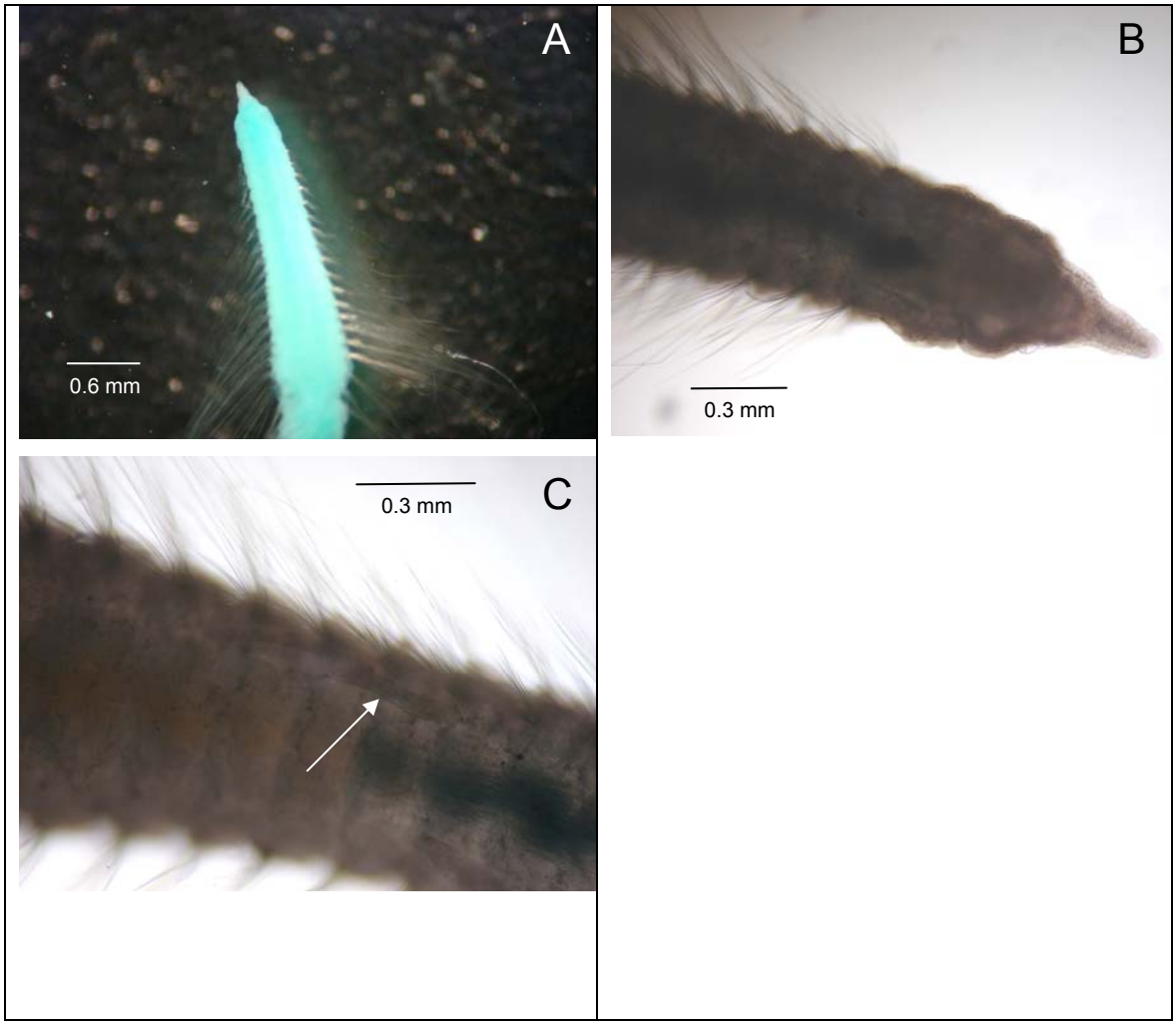


Figure 3.12. *Chaetozone* sp. 12 a) anterior end dorsal view 20x, b) anterior end dorsal view 10x and c) thoracic region showing a branchiae (white arrow) 6x.

***Chaetozone* sp. 1**

231 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 185, August 1989 7 individuals; RRS *Challenger* 79, May 1991 14 individuals; RRS *Challenger* 111, April 1994 30 individuals; RRS *Discovery* 222, September 1996 22 individuals; RRS *Discovery* 226, March 1997 44 individuals; RRS *Discovery* 229, July 1997 68 individuals; RRS *Discovery* 231, March 1998 21 individuals and RRS *Discovery* 237, September 1998 25 individuals).

Description: The largest examined specimen with incomplete body, 9 mm long and 1 mm wide for 32 chaetigers. Shorter and smaller complete specimens were examined. Thoracic body shape swollen in mid region. Prostomium long and pointed, acutely conical, dummy-like with blunt tip. Semi-elongate buccal region 2 times as long as broad. Peristomial region with three achaetous annulations. Big palp scars less than 2 branchial widths to first chaetiger. Branchiae scars in dorsal position to notochaetae. First branchia starts on peristomium (before the first chaetiger). Thoracic region 7 chaetigers in length.

Thoracic notochaetae and neurochaetae are short simple capillaries 1-3 chaetigers in length from ch1. Capillaries vary from 3-5 per fascicle in notopodia to 2-5 per fascicle in neuropodia. Intermediary body region between thorax and abdomen chaetae was not observed. Long 'bottle-brush' chaetae absent. Thoracic acicular spines present, from chaetiger 5 in neuropodia and chaetiger 8-9 in notopodia. More than one acicular spine observed in some chaetigers. Abdominal region necklace-shaped (moniliform), 12 chaetigers in length. Small abdominal acicular spines present, forming incomplete cinctures together with simple capillaries 1 chaetiger in length (5 per fascicle). Pygidium long and simple lobe in dorsal position.

Methyl green staining: Uniform, mainly on prostomium and acicular spines.

Remarks: This species mainly differs from other PAP cirratulids already described in length and shape of the prostomium, absence of ‘bottle-brush chaetae and presence of thoracic acicular spines. Because the presence of acicular spines in the thoracic region this species could be allocated as genus *Chaetozone*.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

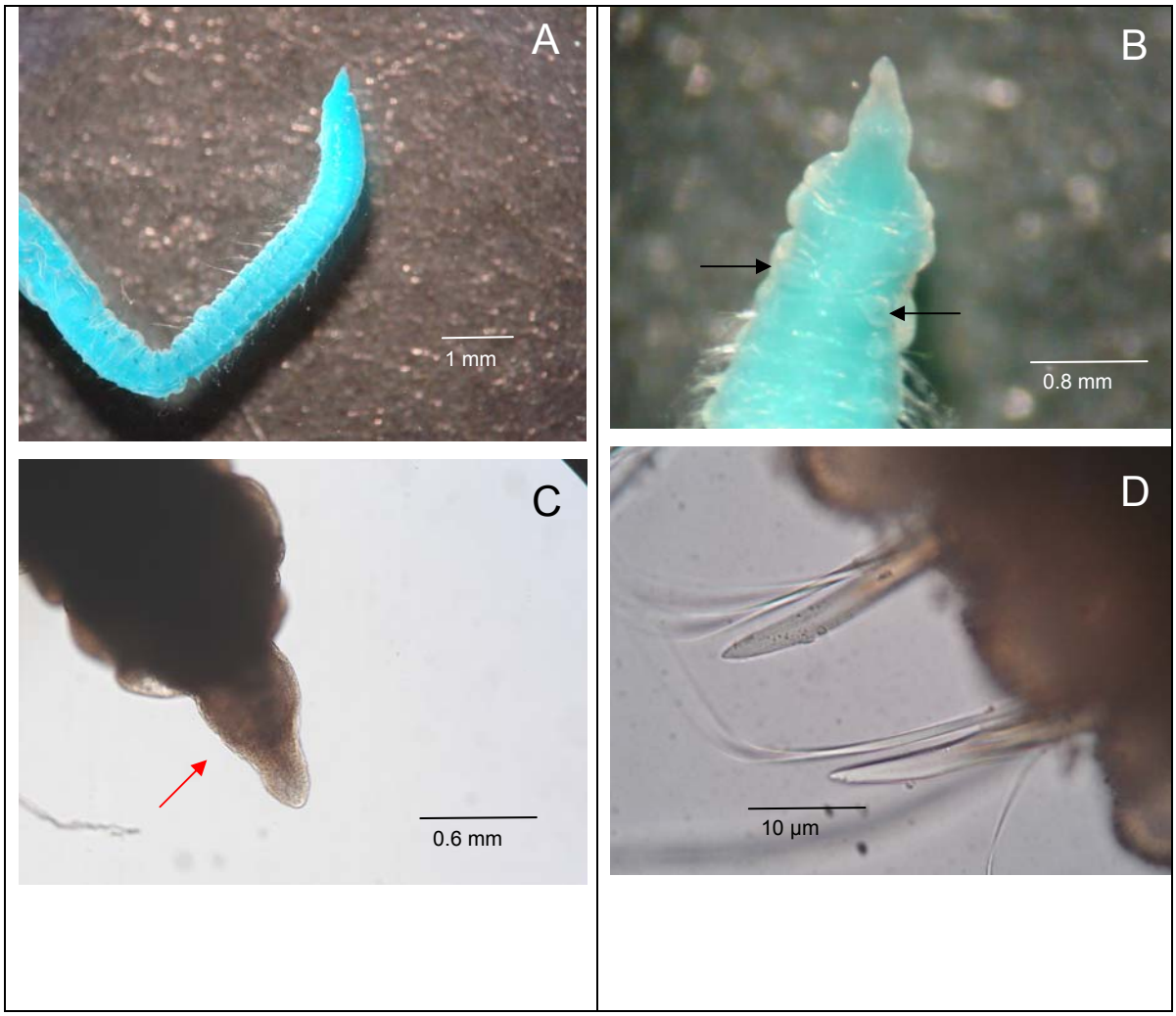


Figure 3.13. *Chaetozone* sp. 1 a) incomplete body, ventral view 21x, b) anterior end, dorsal view and palps scars 32x c) prostomium detail ventral view 10x and d) acicular spines in notopodia 40x.
The black arrows show the palps scars and the red arrow shows the 'dummy-like' prostomium.

***Chaetozone* sp. 2**

14 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79, May 1991 2 individuals; RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 2 individuals; RRS *Discovery* 226, March 1997 1 individual; RRS *Discovery* 229, July 1997 7 individuals and RRS *Discovery* 237, September 1998 1 individual)

Description: All specimens with incomplete body, the most complete 3.0 mm long and 0.8 mm wide for 22 chaetigers in length. Thoracic body shape swollen in mid region. Prostomium widely conical with blunt tip changing to snout-like. Buccal region compact 1 time as long as broad approximately. Palp scars less than 2 branchial widths to chaetiger 1, in anterior position to peristomium. Peristomium with three annulations. Branchiae in dorsal position to notochaetae. Thoracic region with crowded chaetiger segments 16 chaetigers in length and ventral channel.

Thoracic notochaetae and neurochaetae from chaetiger 1 simple capillaries of 1-4 chaetigers in length. On chaetiger 1, 7-9 capillaries per fascicle in notopodia and 7 in neuropodia. From chaetiger 6 'bottle-brush' chaetae 5 chaetiger in length also observed in posterior region. Thoracic acicular spines from chaetiger 6-7 in neuropodia increasing in number to posterior chaetigers (mid region). Acicular spines in notopodia were not observed. Banana and hooked shape spines in mid region were observed in some specimens. Abdominal region missing.

Methyl green staining: Uniform.

Remarks: This species differs from *Chaetozone* sp. 1 in the shape of prostomium and peristomium, buccal region length, number and shape of thoracic acicular spines and presence of 'bottle-brush' chaetae. The presence of thoracic acicular spines (hooked-shape) would indicate the presence of the genus *Chaetozone*.

Habitat: This species was found within the sediment at a depth of 1-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

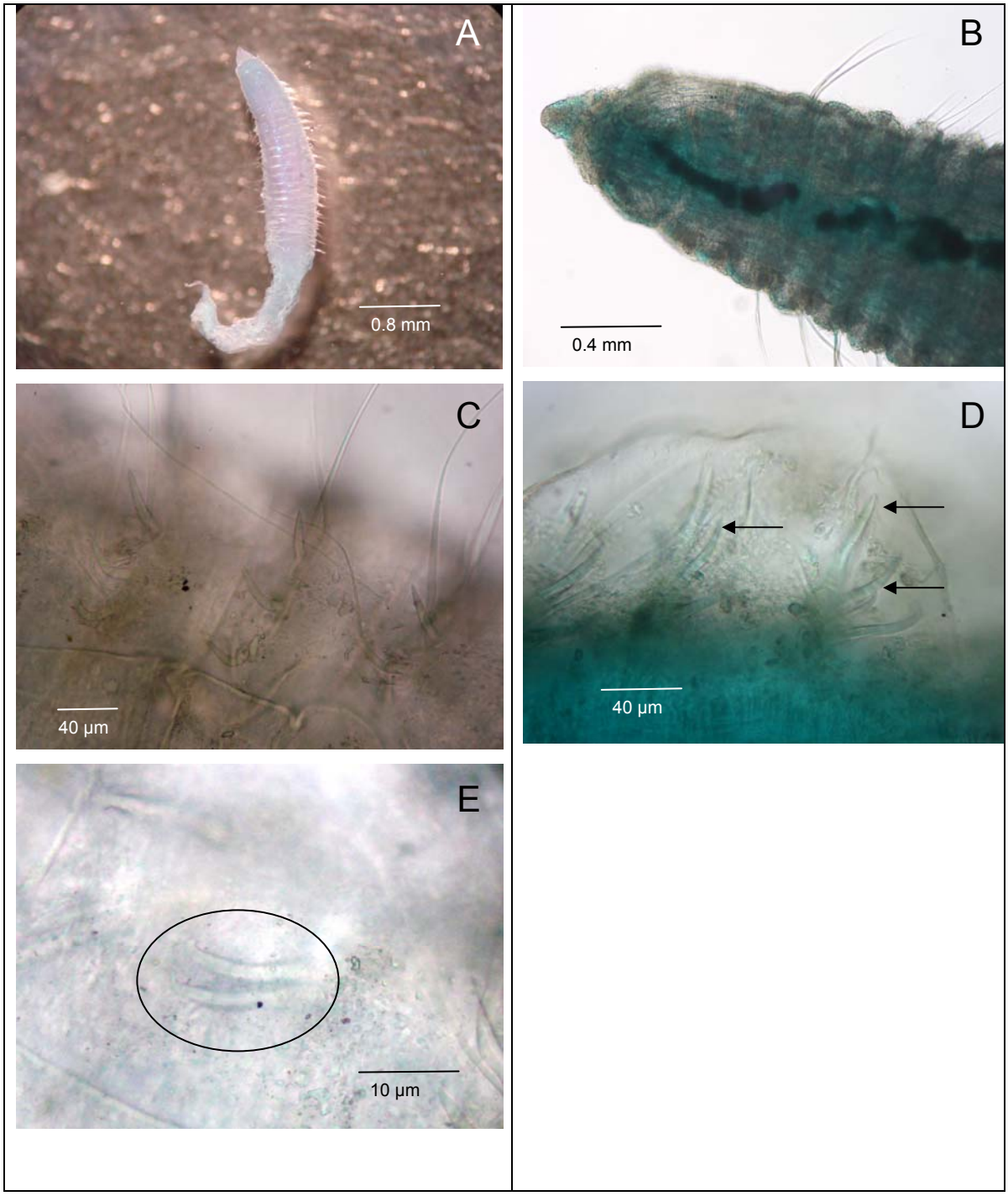


Figure 3.14. *Chaetozone* sp. 2 a) incomplete body, ventral view 25x, b) anterior end, dorso-lateral view 10x c) acicular spines anterior end ventral view 40x d) acicular spines (black arrows) ch14-16 ventral view 40x and e) hooked shape spines (black circle), ventral view 40x

Species	Prostomium shape	Thoracic acicular spines	Buccal region	'Bottle-brush' chaetae	Cinctures	Abdominal region shape
***Chaetozone* sp. 685**	Long, conical with blunt and rounded tip	From ch8 noto, ch5 neuro	3 times as long as broad	From ch11	Partial	Not constricted. Rectangular
***Chaetozone* sp. 55A**	Short, pointed with blunt tip	Not observed	1-2 times as long as broad	From ch1 and ch5	Partial	Constricted, tapering to pygidium
***Chaetozone* sp. 657E**	Pointed, widely conical rounded tip	Not observed	2 times as long as broad	From ch1	Full	Moniliform tapering to pygidium
***Chaetozone* sp. 605B**	Pointed, widely conical rounded tip	Not observed	1.5 times as long as broad	Not observed	Not observed	Elongated and incomplete
***Chaetozone* sp. 10**	Long, widely conical blunt tip	Not observed	2-3 times as long as broad	From ch1 and ch5	Full	Not constricted to moniliform
***Chaetozone* sp. 12**	Long conical blunt tip	Not observed	2 times as long as broad	From ch3	Not observed	Missing
***Chaetozone* sp. 1**	Long, acutely conical, 'dummy-like'	From ch8-9 noto, ch5 neuro	2 times as long as broad	Not observed	Partial (incomplete)	Moniliform (necklace-shaped)
***Chaetozone* sp. 2**	Widely conical to 'snout-like'	From ch? noto,ch6-7 neuro	1 times as long as broad	From ch6	Not observed	Missing

Table 3.2. Taxonomic characters of *Chaetozone* species. ch. chaetiger

Genus: *Tharyx*. Webster and Benedict, 1887

***Tharyx* sp. 1**

13 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 4 individuals; RRS *Discovery* 226, March 1997 6 individuals and RRS *Discovery* 237, September 1998 2 individuals).

Description: The longest specimen 5.0 mm long and 0.2 mm wide for 42 chaetigers in length. Thoracic body shape hour-glass shaped. Prostomium wide and rounded. Buccal region glove shape, compact 1-1.5 times as long as broad. Anterior thoracic region starting like a 'neck' composed by five short crowded chaetigers plus long chaetiger of the same length. Short palps less than 2 branchial widths to chaetiger 1. Long branchiae dorsal-posterior to chaetae. Thoracic region 14-15 chaetigers in length.

Thoracic notochaetae and neurochaetae from chaetiger 1 simple capillaries of 1-2 chaetiger in length. On chaetiger 1, 4 capillaries per fascicle in notopodia and 3 capillaries per fascicle in neuropodia. Very long 'bottle-brush' chaetae from chaetiger 7. Thoracic acicular spines absent. Chaetiger segments longer in mid and abdominal region. Intermediary body region between thorax and abdomen not defined. From chaetiger 24 bidentate knob-tipped spines and short capillaries 1/2-1 chaetiger in length. Abdominal region with long chaetigers segment 24-26 chaetigers in length. Pygidium not observed

Methyl green staining: Soft and diffused.

Remarks: The presence of abdominal bidentate knob-tipped spines would place to this species into the genus *Tharyx.* The rest of taxonomic characters such as prostomium and thoracic body shape, arrangement of the anterior thoracic chaetigers like 'neck' and length of the capillaries in abdominal region allow differencing the species from other PAP Cirratulids but they are not common to the genus *Tharyx*.

Habitat: This species was found within the sediment at a depth of 0-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

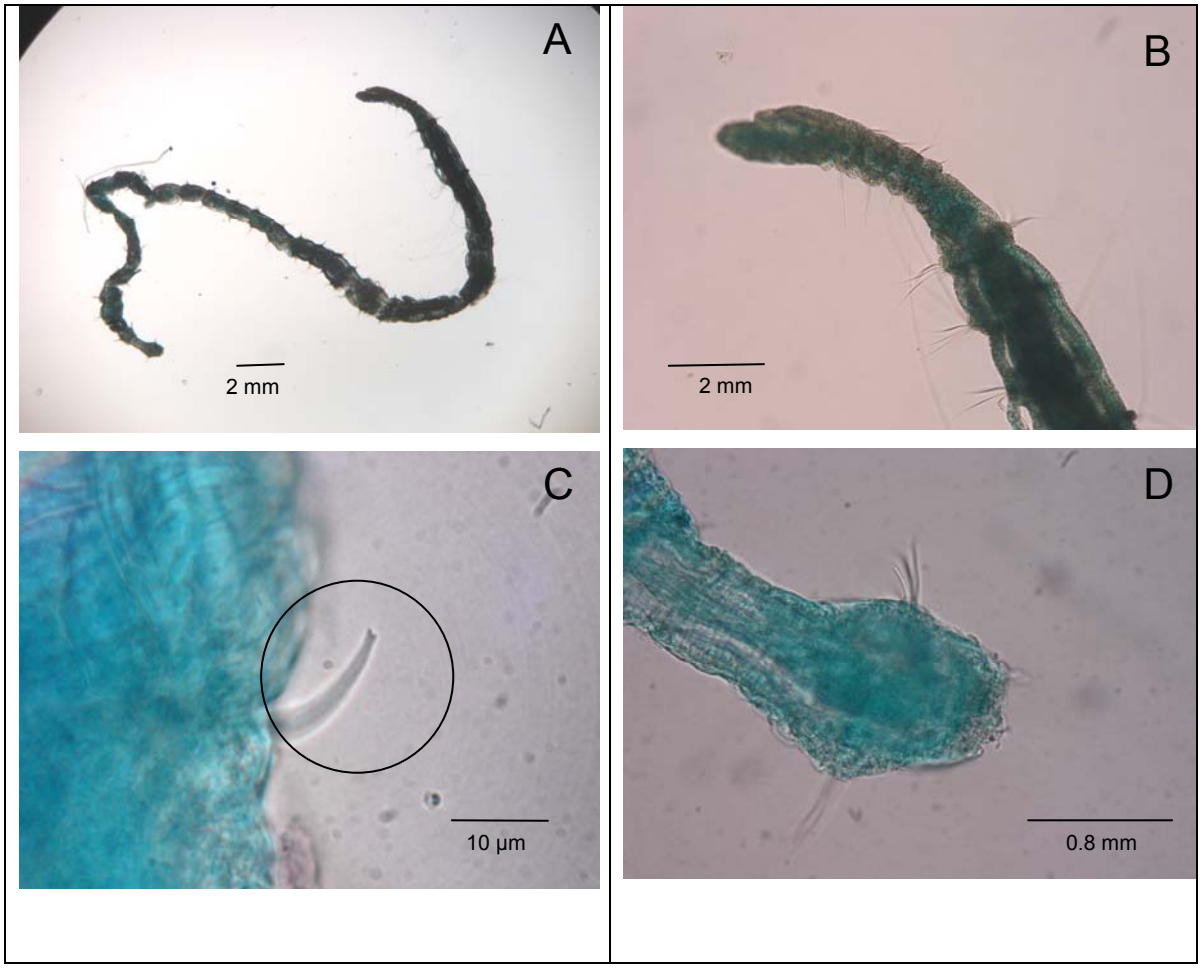


Figure 3.15. *Tharyx* sp. 1 a) complete body 4x, b) anterior end dorso-lateral view 10x c) abdominal knob-tipped spines 100x and d) pygidium detail 40x.
The black circle shows the 'knob-tipped' spines

3.1.3. Discussion

3.1.3.1. Introduction

The taxonomy of Cirratulidae has been very confused throughout history. Although several deep-sea Atlantic species have been treated by Blake (1991) Chambers (2000) and Chambers and Woodham (2003), the true diversity of west and east north Atlantic cirratulids is underestimated since species remain largely undescribed or are erroneously assigned European names. The problem lies in the relative lack of discrete morphological characters and the misleading descriptions of species (Blake, 1991) as well as the current confusion over the systematic of the group due to largely historical reasons (Woodham & Chambers, 1994).

Historically there have been few characters used to separate the various genera and species of bitentaculate cirratulids. Chamberlin (1919) separated the genera based on the number of branchiae (few in number to rather numerous), presence/absence of acicular chaetae encircling posterior segments, and chaetae either all fine, capillaries, or either entire or bidentate acicular chaetae occurring in both notopodia and neuropodia. The absence/presence of cinctures was the character used to separate *Chaetozone* and *Caulleriella*. Hartman (1961) established definitions for the genera *Chaetozone, Caulleriella and Tharyx* which were widely accepted. The three genera were distinguished solely on the type of chaetae present in posterior body segments i.e. *Tharyx* having capillary limbate chaetae with hair like tips and *Caulleriella* and *Chaetozone* having acicular chaetae. Hartman noted the unreliability of using arrangement of acicular spines in cinctures as a generic level character since these were often not observed in incomplete specimens. *Caulleriella* with acicular spines distally bifid and *Chaetozone* with acicular spines distally entire was proposed by Hartman (1961) as a means to separate the genera. Day (1967) identified three main diagnostic characters; head and feeding appendages, arrangement of branchial filaments, and chaetae. Once again emphasis was placed on the arrangement of acicular chaetae in either a continuous dorso-ventral arc of spines in the posterior end or chaetae remaining in two distinct bundles as the division between *Caulleriella* and *Chaetozone*. Difference in chaetal type was mentioned but only emphasized for *Tharyx*.

Blake (1991, 1996a) introduced new characters for separating the bitentaculate genera as well as individual species. Blake (1991) expanded the number of

bitentaculate genera from three to five following examination of *Tharyx acutus* Webster & Benedict, 1887, the type species of *Tharyx*. He restricted species of *Tharyx* to those having knob-tipped chaetae. Species having simple capillaries that were previously referred to *Tharyx* by Hartman and others were instead referred to a new genus, *Aphelochaeta.* Blake also re-established *Monticellina* Laubier (1961) for species having capillaries with denticulate or saw-toothed edges. The five genera as currently defined are separated primarily by chaetal type. Species level designations are made based upon origin of the first modified chaetae, peristomial annulations, number of spines per noto- and neuropodia, prostomial shape, presence of dorsal and/or ventral grooves along the body, inflation of posterior segments, and methyl green staining patterns to name a few. Recent species descriptions include a much wider range of characters but there is still no common set of characters used on a regular basis by taxonomists (Chambers & Woodham, 2003; Blake, 2006; Doner & Blake 2006; Dean & Blake, 2007).

The PAP species descriptions considered as differentiating taxonomic characters those commonly available and recognizable in the bodies of the specimens examined. As the lack of the several characters, even often the whole abdominal region, was a permanent characteristic, a combination of new characters based on the shape and relative sizes of various features associated with the thoracic region and kind of chaetae (Glover, 2000) together those developed by Blake (1996a) in its key to genera plus some concepts from a new list of characters for abyssal bitentaculate cirratulids (Doner *et al*, *submitted*) were used.

3.1.3.2. *Aphelochaeta*

The genus *Aphelochaeta* is one of the most diverse of PAP cirratulids, two of the four most abundant species of cirratulids belong to this genus: *Aphelochaeta* sp13A and *Aphelochaeta* sp647D. Doner & Blake (*unpublished*) also record this genus as one of the most diverse between all taxa found from deep water off Northern California. Among *Aphelochaeta* species found in the current study the most common taxonomic characters used to distinguish quickly one species from another were the prostomium shape, overall thoracic body shape, buccal region shape and length and its relation with the broad, branchial scars position in relation to chaetae, starting position of the long ‘bottle-brush’ chaetae and length of the capillaries. Blake (1996a), also consider these characters on his descriptions and key to species of *Aphelochaeta* from Santa

Maria Basin, north Pacific, but he add the Methyl green staining pattern, nature of segments across the body, presence of peristomial annulations and glandular segments in thorax as main characters. The presence of these new characters could be related to depth in the ocean in which the species are found. Doner & Blake (*unpublished*) describe 12 deep-water species (2400 to 3775 m depth) of *Aphelochaeta* from off Northern California. These authors consider the degree of inflation of the dorsal crest, the nature of posterior chaetigers and the number of peristomial annulations are characters that warrant further attention.

Descriptions of this genus usually note minor differences between species. Blake in 1991 assigned bitentaculate cirratulids species having only simple, non-serrated capillary chaetae to the genus *Aphelochaeta*, there are no formal taxonomic publications with new species descriptions of this genus from abyssal sites. The current study constitutes an important input for the knowledge of this group in deep-sea environments.

Aphelochaeta sp. 13A from PAP also has a very distinctive methyl green staining pattern, so this species is readily separated from other species by the staining method. A new species of *Aphelochaeta* from deep-water off Northern California (Doner & Blake, unpublished) also presents this property. From PAP species the nature of posterior chaetigers together pygidium shape were tricky characters due to the lack of abdominal regions in many specimens observed.

3.1.3.3. *Chaetozone*

Among bitentaculate cirratulids species, *Chaetozone* is perhaps the most common and diverse genus in the deep sea. Blake (2006) considers the genus among the dominant species in depths of 2400-3200 m from off Northern California, while Chambers & Woodham (2003) also show its high diversity in deep waters of the Greenland-Iceland-Faroe-Ridge. PAP *Chaetozone* species mainly differs in the prostomium shape, buccal region length, arrangement of abdominal acicular spines in cinctures, starting position of 'bottle-brush' chaetae and overall abdominal shape. Other important taxonomic characters were thoracic body shape, the length and shape of peristomium, pygidium shape, length of capillaries and palp scars location. Thoracic unidentate acicular spines from chaetiger 8 were observed in *Chaetozone* sp. 685, from chaetiger 5 in *Chaetozone* sp. 1 and from chaetiger 6-7 in *Chaetozone* sp. 2. This character is not common in *Chaetozone* species, with thoracic bidentate

spines being more frequent in *Caulleriella* species. Acicular spines often appear from posterior segments, although Chambers (2000), in her redescription of the genus does not point out where acicular spines appear. Chambers & Woodham (2003) shows that *Caulleriella zetlandica* is often confused with *Chaetozone* species and may well belong in this genus. The presence of eyes in *Caulleriella zetlandica,* which are readily visible also in *Chaetozone gibber*, would distinguish them from other *Chaetozone* species. These authors in their key to deep-water northeast Atlantic species consider the number of spines per ramus, the definition of constrictions between posterior chaetigers and the starting position of very long capillary chaetae as important characters to differentiate species.

Blake (2006) describes several new species of *Chaetozone* from deep-water off northern California, 2400-3200 m depth. He considers the placement of the tentacles and first pair of branchiae as the most obvious feature distinguishing his specimens from *Chaetozone setosa* (Malmgren, 1867). Other characters of importance considered by this author for *Chaetozone* include the presence, structure, and arrangement of the posterior spines for which there is a full range of development, in addition the position and nature of the nuchal organ. New descriptions for shallow water *Chaetozone* species suggest that the segmentation pattern also may be important in developing phylogenetic analyses of the family (Doner & Blake, 2006).

Not many species of *Chaetozone* have been described from northeast Atlantic waters. Currently four species are recorded many of them from shallow and continental shelf water, with the deep-sea abyssal plains remaining without records. The current investigation is a first study of the diversity and taxonomy of the genus at depths greater than 3000 m from northeast Atlantic Ocean.

3.1.3.4. *Tharyx*

One species of *Tharyx* was described from samples. This species *Tharyx sp.1* showed low abundance throughout temporal study in comparison with before dominant cirratulid species. However, the main taxonomic character to separate this species from the rest of PAP bitentaculate cirratulids was the presence of knob-tipped spines from middle and posterior region. This character is exclusive for the genus and it may be confused with broken chaetae, which has similar appearance. The overall body shape, prostomium and peristomium shape, arrangement of the anterior thoracic chaetigers narrowing to form a ‘neck’ and length of the capillaries in abdominal region

also were important characters. Blake (1991) established that the type species of the genus *Tharyx, T. acutus* Webster & Benedict, had knob-tipped hooks or spines in addition to capillaries. This changed the traditional concept of *Tharyx*, which was based upon specimens having all capillaries. Therefore this author restricted species of *Tharyx* to those having knob-tipped spines and moved species having simple and those with serrated capillaries to the genera *Aphelochaeta* and *Monticellina*, respectively. The genus *Tharyx* appears most closely related to *Caulleriella* in that both species have modified spines that are more or less bidentate. These spines also are not arranged in cinctures. However, like *Chaetozone*, the genus *Tharyx* also has closely spaced chaetal bundles with a relatively small gap between noto- and neuropodia. This character separates to *Tharyx* from *Caulleriella* who has widely spaced chaetal bundles (Dean & Blake, 2007).

Descriptions of new species of *Tharyx* from Atlantic waters are scarce and they have been recorded for shallow waters (Christie, 1984), who described a new species *Tharyx vivipara* from estuaries in north-east England. In the deep-sea, Blake (1991) described *Tharyx kirkegaardi* from western north Atlantic continental slope and rise between 255-3015 m depth, while in his study from Santa Maria Basin, northeast Pacific in 1996 he did not find any new species of this genus. Glover (2000), who in his doctoral work includes specimens from deep-sea Central equatorial Pacific Ocean 4400-4900 m depth, creates a group of 'abdominal knob-tipped spine polychaete species'. This author briefly described three species with this taxonomic character, arguing that they place in the genus *Tharyx*. The current description of *Tharyx* sp. 1 from PAP would be a first record for the genus in the deep-sea northeast Atlantic waters.

The bitentaculate cirratulids fauna of the Porcupine Abyssal Plain is rich in species. If we consider that only the 300 *μ*m sieve fractions were used in analyses (62.9% of the total abundance), a larger number of species might be expected from the whole sample set. 15 different species of Cirratulidae have been recognized and described in the current research, with eight species of *Chaetozone*, six species of *Aphelochaeta* and 1 species of *Tharyx* recorded.

The current investigation constitutes the first taxonomic study at species level on north Atlantic deep-sea bitentaculate cirratulids. Glover (2000) has previously studied the same group establishing new characters which were used in the creation of morphological groupings. He recognized different morphotypes but he did not

assigned generic names to their descriptions. This author recorded 22 species from northeast Atlantic and 18 species from Equatorial Pacific.

Cirratulids are abundant and highly diverse in deep-sea sediments. Studies from recent programs in the Atlantic, Pacific, and Southern Oceans have revealed a wealth of new species. Table 3.3. shows the relative abundance and number of undescribed species in the various collections from different geographical areas. What they show is that in many instances, the proportion of new species often exceeds 60%. In just six sampling programs 86 potential new species have been identified. This species richness has posed several problems. However, as a result of the APIP workshop, it was realized that many of the character concepts and species being studied from widely separated or even adjacent locations were very similar and that significant progress could be made by the different taxonomic teams exchanging information and working together. By developing a common language and set of characters it is now possible to make headway in solving these problems (Doner *et al*. 2008).

	ACSAR-South (Slope)	**SF-DODS (Rise)**	**ANDEEP II-III (Shelf, Abyssal)**	**KAPLAN NODINAUT (Abyssal)**	**DEEPSETS Porcupine Abyssal Plain (NE Atlantic)**	**NE ATLANTIC TAP & CVAP**
Polychaeta Total No. of Species	542	376	155	55	>106	115
Cirratulidae Total No. of Species	32	25	14	6	19	14
Cirratulidae No. of New Species	23 (72%)	16 (64%)	13 (93%)	5 (83%)	19 (100%)	10 (71%)
Total No. of Individuals (All polychaetes)	57,031	37,826	1983	485	3245	395
Total No. of Individuals (Cirratulidae)	2991	4420	174	19	935	95
Proportion of Total Polychaetes	5.2%	11.7%	8.8%	3.9%	28.8%	24%

Table 3.3. Relative Species Abundance of Cirratulidae from several deep-sea programs. ACSAR–Atlantic Continental Slope and Rise; SF–DODS–San Francisco; ANDEEP–Antarctic deep sea; KAPLAN & NAUDINAUT–Central Pacific Clipperton Clarion Fracture Zone; DEEPSETS–Porcupine Abyssal Plain; TAP–Tagus Abyssal Plain; CVAP–Cap Verde Abyssal Plain.

3.2. Spionidae

3.2.1. Introduction

The Spionidae is one of the largest taxonomic groupings of polychaetes. They are a dominant component in sand and mud habitats from intertidal to abyssal depths and have been recorded from all around the world.

Deep-sea spionids are highly abundant and diverse within the abyssal polychaete community in the north Pacific (Hilbig & Blake, 2006; Glover *et al.,* 2002) and in several areas of the Atlantic (Cosson-Sarradin *et al*., 1998; Paterson *et al*., 1998; Glover *et al*., 2001) with exception of Antarctica (Hilbig, 2001 and 2004; Blake & Narayanaswamy, 2004). The Spionidae are also found in dysoxic environments, such as hydrothermal vents (Sigvaldadóttir & Desbruyères, 2003; Blake & Maciolek, 1992), whale-falls (Goffredi *et al*., 2004) and oxygen minimum zones in the northern Arabian Sea (Lamont & Gage, 2000; Levin *et al*., 2000) and southern Pacific (Carrasco, 1997).

In some areas the Spionidae are particularly species rich such as the Pacific Ocean, where 90 nominal species have been described from waters off California (Blake, 1996b) and also from Atlantic continental slope and rise (Ebbe, *Pers. comm.).* While other regions such as Australia, Japan, North Carolina, the Gulf of Mexico, and the Caribbean Sea are widely known. However, little is known of abyssal plain polychaete species. Several deep-sea programmes are developing in the Pacific, Atlantic, Indian and Antarctic oceans and have a large number of new taxa waiting to be described.

Spionidae are generally recognized by hooded hooks and the anterior end which carries a pair of elongate grooved palps extending from the head, although some other polychaete groups have essentially the same kind of palps (e.g. Apistobranchus, Flabelligeridae and some Cirratulidae). The Spionidae has been grouped consistently with taxa such as *Heterospio, Poecilochaetus* and *Trochochaeta* into Spionida, including also *Magelona* and the Chaetopteridae (Rouse & Fauchald, 1997).

The systematics of the Spionidae has undergone a number of major revisions since the family was established by Grube in 1850. In 1896 Mesnil divided the family into two groups using characters such as the shape and presence of horns on the prostomium, the distribution of branchiae, the form of anal cirri, the occurrence of dorsal hooded hooks, and the presence of capillaries in segments with hooded hooks. Söderström (1920) created a classification based on the sexual reproductive patterns observed. He incorporated information on segmental organ structure, eggs

membranes, sperm shape and larval development in erecting Nerinae, Laonicinae and Spioninae. More recent studies on spionid phylogenetic relationships have been made by Mackie (1996), Sigvaldadóttir *et al.,* (1997) and Blake and Arnofsky (1999).

Recent revisions of some of the larger groups include Radashevsky (1993) on *Polydora*, Blake (1996b) of the genera and species from California, Sigvaldadóttir's (1998) cladistic study of *Prionospio*, Rice and Levin's (1998) analysis of *Streblospio* and Meißner's (2005) of the genus *Spiophanes*.

Spionidae currently have more than 450 nominal species grouped into around 38 genera. Large taxa such as *Prionospio* contain more than 100 nominal species. Features that have traditionally been used for identifying and naming *Prionospio* include the presence of frontal horns on the prostomium, the position, kind and number of branchiae, and the distribution and form of the hooks.

13 morphotypes or different species belonging to Spionidae were recognized and described in this research. Species that belong to the *Prionospio* complex were important. 3 morphotypes of *Minuspio*, 2 of *Prionospio* and 1 of *Aquilaspio* were recorded. Also 2 *Laonice* morphotypes were found and 2 morphotypes of *Spiophanes* were recorded. Finally, 2 different morphotypes with spionid affinities were observed and *Aurospio dibranchiata* was recorded.

The monograph of Spionidae published by Blake (1996b) was considered as the main guide to define the taxonomic characters involved on morphotypes descriptions. Other observations of taxonomic characters detailed and published by Maciolek (1981) for *Aurospio dibranchiata*, Maciolek (1985) for *Prionospio*, Meißner (2005) for *Spiophanes*, Maciolek (2000) for *Laonice* and *Spiophanes* and Blake and Kudenov (1978) for Spionidae were also considered.

The major taxonomic difficulties experienced in the identifying the species and descriptions making were the absence and poor condition of the branchiae and the absence or loss of posterior end and pygidium. Also owing to specimen preservation important characters such as occipital antenna, nuchal organ, dorsal crests, genital pouches, sabre chaetae and hooks, were not always present or well defined. Although the presence of palps is an important familial taxonomic character, they were found missing in the majority of specimens examined. Methyl green staining pattern (MGSP) was very important in the differentiation of the specimens observed. Descriptions were developed using the morphological characters detailed in the 'List of Characters' (Appendix 3). However, most of these characters were not found from analyzed

specimens. This list of characters shows the taxonomic characters used on morphotype descriptions by each genus recorded. Pictures from each specimen are attached with the purpose to show the general shape of the body or some important taxonomic character.

3.2.2. Results

3.2.2.1. Description of morphotypes

Genus: *Laonice*. Malmgren, 1867

***Laonice* sp. 1**

15 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 4 individuals; RRS *Discovery* 226, March 1997 2 individuals; RRS *Discovery* 229, July 1997 4 individuals and RRS *Discovery* 231, March 1998 4 individuals).

Description: All specimens with incomplete body, the longest fragment 1.9 mm long and 0.9 mm wide for 20 chaetigers. Prostomium bell-shaped, short broadest on anterior margin slightly sunk on mid part; posteriorly terminating at anterior border of chaetiger 1. Peristomium fused dorsally with chaetiger 1. Eyes not observed; occipital antenna small and present at posterior end of prostomium. Nuchal organ with two longitudinal grooves extending posteriorly. Peristomium with lateral wings.
On chaetigers 1 and 2 body shaped like neck narrower than following chaetigers. Interparapodial genital pouches not observed. Branchiae from chaetiger 2, apinnate, cirriform and long. Notopodial postchaetal lamellae well developed, triangular and subtriangular; thinner to posterior chaetigers. Neuropodial lamellae rounded and short. Capillary notochaetae and neurochaetae of anterior segments numerous and long appearing from well developed parapodia; neuropodial hooded hooks from ch16, 7 per ramus accompanied by non-granulated capillaries and long and thin sabre chaetae which starts from ch7. Pygidium not observed.

Methyl green staining: Uniform

Remarks: According with main characters observed this species could be considered as *Laonice*, however interparapodial genital pouches were not observed possibly due

to body was incomplete. Individuals with complete body are needed to make a full description of the species.

Habitat: This species was found within the sediment at a depth of 0-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

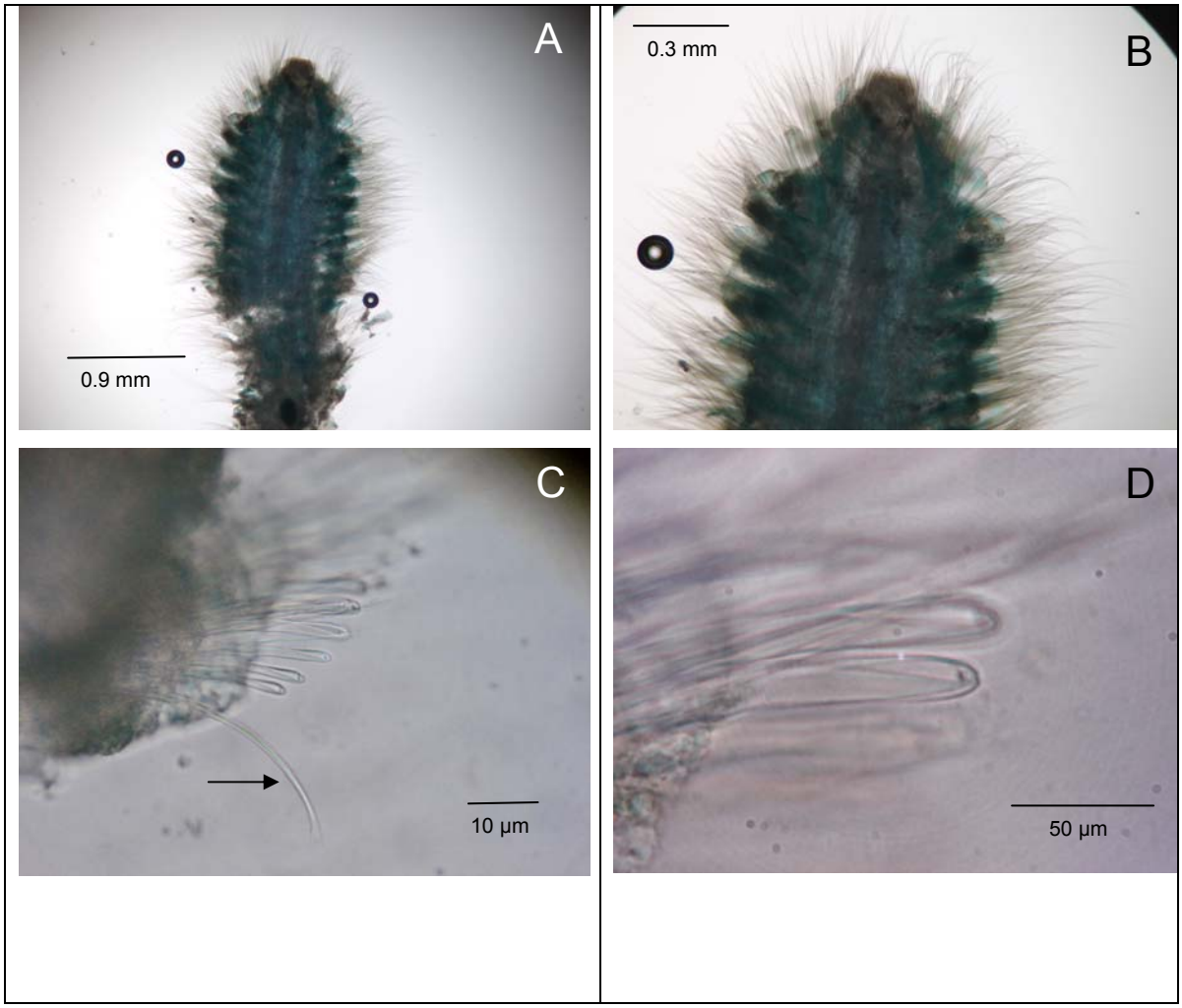


Figure 3.16. *Laonice* sp. 1 a) incomplete body, dorsal view 4x, b) anterior end dorsal view, 10x c) hooded hooks and sabre chaetae (black arrow) 40x and d) hooded hooks, chaetiger 20, 100x

***Laonice* sp. 640**

22 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 185, August 1989 1 individual; RRS *Challenger* 79 May 1991 1 individual; RRS *Challenger* 111, April 1994 2 individuals; RRS *Discovery* 222, September 1996 5 individuals; RRS *Discovery* 226, March 1997 8 individuals; RRS *Discovery* 229, July 1997 4 individuals and RRS *Discovery* 237, September 1998 1 individual).

Description: Specimen with incomplete body, the longest recorded 4 mm long and 1 mm wide for 15 chaetigers. Prostomium bell-shaped to triangular, long, broad anteriorly weakly incised in the middle, tapering posteriorly. Pair of eyes not observed; occipital antenna present at posterior region of prostomium. Peristomium well developed with small lateral wings; palps not observed. Nuchal organ paired and short extending posteriorly as two longitudinal ciliated grooves.

Branchiae cirriform from chaetiger 2, long and thin wider to posterior chaetigers. Notopodial lamellae on chaetiger 1 reduced and rounded, following leaf-like and rounded shape. Neuropodial lamellae rounded. On chaetiger 1 reduced. Genital pouches present from between chaetigers 3-4 until chaetigers 12-13.

Notochaetal and neurochaetal capillaries dense and normal length; neuropodial hooded hooks not observed due to short length of specimen. Ventral sabre chaetae from chaetiger 10, double and triple in some chaetigers. Pygidium not observed.

Methyl green staining: Branchiae and postchaetal lamellae strongly stained mainly on border.

Remarks: This species mainly differs from *Laonice* sp. 1 in the shape of the prostomium, notopodial lamellae and presence of genital pouches. The absence of complete bodies did not allow observing hooks in posterior regions.

Habitat: This species was found within the sediment at a depth of 0-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

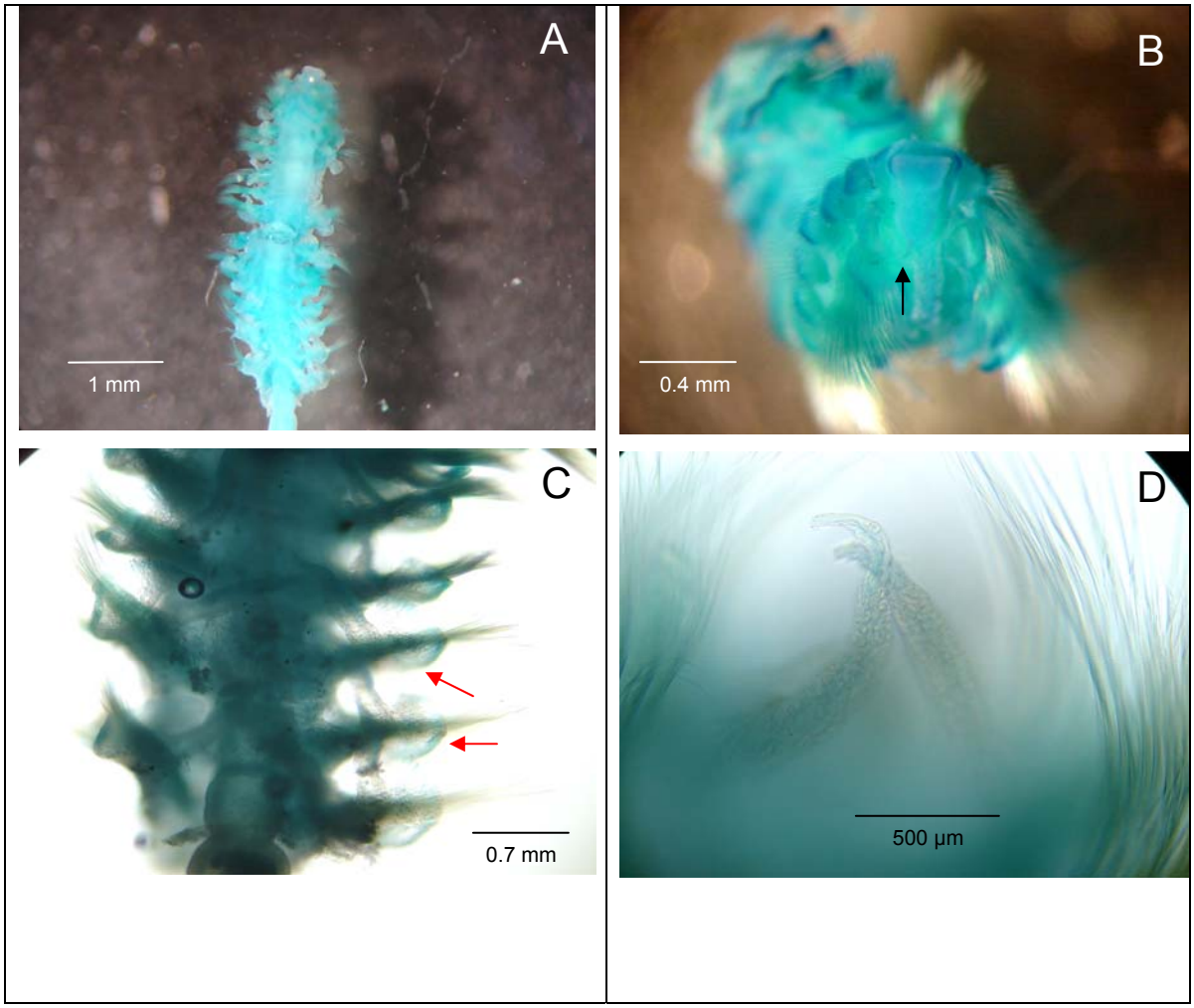


Figure 3.17. *Laonice* sp. 640 a) incomplete body dorsal view 30x b) anterior end dorsal view 33x c) anterior and mid region dorsal view 10x and d) anterior end, branchiae 40x.
The black arrow shows the occipital antenna and the red arrows show the lamellaes.

Species	Anterior prostomial shape	Nuchal organ	Branchiae	Lamellae	Genital pouches
***Laonice* sp. 1**	Bell-shaped, short	Longitudinal grooves	Cirriform. Long	Notopodia: triangular to subtriangular Neuropodia: rounded and short	Not observed
***Laonice* sp. 640**	Bell-shaped to triangular, long	Longitudinal grooves	Cirriform. Long and thin wider to posterior chaetigers	Notopodia: rounded to leaf-like Neuropodia: rounded	Present

Table 3.4. Taxonomic characters of *Laonice* species.

Genus: *Spiophanes*. Grube, 1860

***Spiophanes* sp. 1**

14 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 6 individuals; RRS *Discovery* 226, March 1997 4 individuals; RRS *Discovery* 229, July 1997 1 individual and RRS *Discovery* 237, September 1998 2 individuals).

Description: Longest specimen with incomplete body 6 mm long and 0.7 mm wide for 27 chaetigers. Prostomium bell-shaped to subtriangular, bluntly rounded posteriorly without frontal horns; pair of eyes present; occipital antenna present, short and rounded lying on posterior edge of prostomium. Peristomium well developed, not enclosing prostomium. Nuchal organs extending posteriorly as ciliated grooves.

Anterior notopodial postchaetal lamellae elongate and digitiform, changing to short, rounded well developed lamellae. Anterior neuropodial postchaetal lamellae well developed, rounded and digitiform. Parapodia well developed. Interparapodial lateral pouches and dorsal crests not well defined.

No dense capillaries granulated on anterior noto- and neurochaetae. Posterior chaetae non-granulated. On chaetiger 1 long capillary chaetae and 1 large curved crook-like chaetae. Neuropodial hooded hooks bi or tridentate from chaetigers 15-16, 6-4 per ramus accompanied by capillaries and granulated sabre chaetae which appear from chaetiger 4. Bacillary chaetae not observed. Pygidium not observed.

Methyl green staining: Parapodia from chaetiger 10 to 13 strongly stained. General pattern uniform and diffused.

Remarks: Taxonomic characters such as the absence of branchiae and chaetiger 1 with 1-2 large curved neuropodial hooks in addition to normal capillaries place this species into *Spiophanes*.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

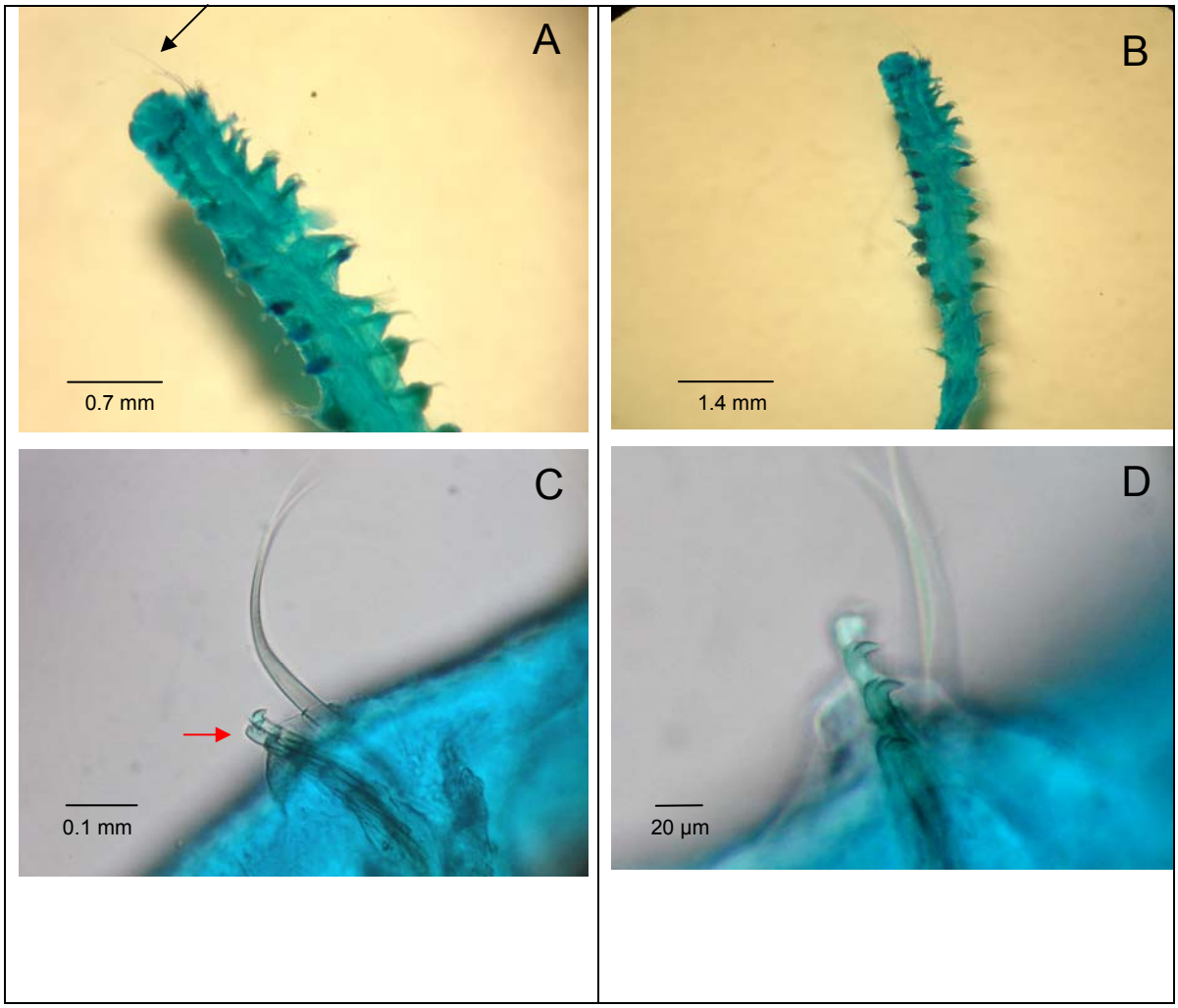


Figure 3.18. *Spiophanes* sp. 1 a) anterior end, dorsal view 25x b) incomplete body dorsal view 25x c) hooks (red arrow) and sabre chaetae, ventral view 40x and d) hooded hooks chaetiger 17, ventral view 40x.
The black arrow shows the long capillary chaetae on chaetiger 1.

***Spiophanes* sp. 619**

30 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 185, August 1989 3 individuals; RRS *Challenger* 79 May 1991 5 individuals; RRS *Discovery* 222, September 1996 4 individuals; RRS *Discovery* 226, March 1997 4 individuals; RRS *Discovery* 229, July 1997 6 individuals; RRS *Discovery* 231, March 1998 4 individuals and RRS *Discovery* 237, September 1998 4 individuals).

Description: The longest specimen with incomplete body, 9 mm long and 0.6 mm wide for 34 chaetigers. Prostomium broad anteriorly bell-shaped presenting frontal horns; sometimes incised, swollen or flat in the middle of the anterior region. Eyes absent. Small occipital antenna present. Peristomium reduced not fused to chaetiger 1. Nuchal organs paired extending posteriorly until chaetigers 7-8. Lateral bulges observed on peristomial region. Body swollen in anterior region. Pharynx observed in some specimens. Interparapodial pouches and dorsal crests not observed.

Notopodial postchaetal lamellae well developed, thin and digitiform between chaetigers 1-4; leaf-like and rounded on chaetigers 5-9 then changing to short and subtriangular shape on following chaetigers.

Neuropodial postchaetal lamellae subtriangular and short between chaetigers 1 to 4 varying to rounded on posterior chaetigers. Parapodia well developed from chaetiger 5 until chaetiger 14.

Anterior capillaries granulated. Long capillaries and large curved crook-like chaetae on chaetiger 1; long chaetae in mid region. Neuropodial hooded hooks from chaetiger 15, 4-6 per ramus, tridentate with main fang above a pair of smaller teeth. Slightly granulated sabre chaetae from chaetiger 4, double to posterior chaetigers. Bacillary chaetae on chaetiger 6. Pygidium not observed.

Methyl green staining: Horizontal bands on anterior ventral region. Parapodia strongly stained mainly on chaetiger 8 to 10

Remarks: This species differs from *Spiophanes* sp. 1 in prostomium shape, methyl green staining pattern, presence of bacillary chaetae, nuchal organ shape and lamellae shape.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

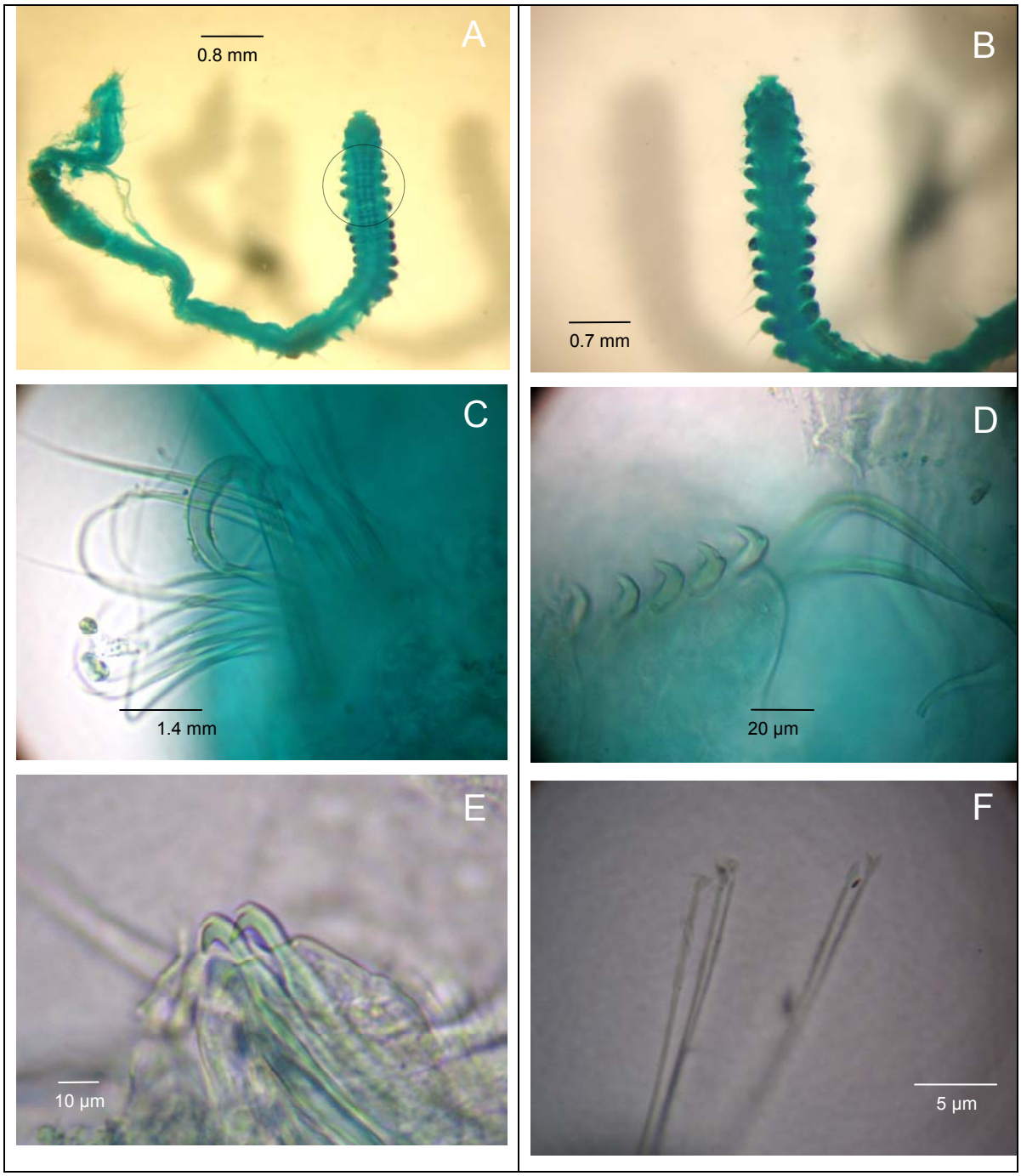


Figure 3.19. *Spiophanes* sp. 619 a) incomplete body ventral view 2x b) anterior end dorsal view 3.2x c) curved spine 40x d) hooded hooks chaetiger 15 and sabre chaetae 40x, e) hooded hooks posterior end 40x and f) bacillary chaetae, anterior end 40x.
The black circle shows the Methyl green staining pattern of the thoracic ventral region.

Species	Anterior prostomial shape	Occipital antenna	Hooded hooks from	No. teeth	Bacillary chaetae	Nuchal organ
***Spiophanes* sp.1**	Bell-shaped to subtriangular without frontal horns	Short and rounded	Chaetigers 15-16	2-3	Not apparent	Ciliated grooves
***Spiophanes* sp.619**	Bell-shaped with frontal horns	Small	Chaetiger 15	3	Present, brush-tipped	Paired extending to ch7-8

Table 3.5. Taxonomic characters of *Spiophanes* species. ch: chaetiger

Genus: *Aurospio*. Maciolek, 1981

***Aurospio dibranchiata* Maciolek, 1981**

152 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 185, August 1989 6 individuals; RRS *Challenger* 79 May 1991 29 individuals; RRS *Challenger* 111, April 1994 16 individuals; RRS *Discovery* 222, September 1996 30 individuals; RRS *Discovery* 226, March 1997 5 individuals; RRS *Discovery* 229, July 1997 34 individuals; RRS *Discovery* 231, March 1998 21 individuals and RRS *Discovery* 237, September 1998 11 individuals).

Description: Longest specimen with incomplete body, 2.4 mm long and 0.3 mm wide for 14 chaetigers, however several small complete specimens ranging between 1.6-2 mm long and 0.2-0.4 mm wide were observed. Body shape swollen in anterior region. Prostomium broad rounded anteriorly, sometimes with medial peak varying to subtriangular shape and prolonged posteriorly as a keel. Pair of eyes present; no occipital antenna. Peristomium partially fused to chaetiger 1, fused posteriorly to prostomium. Palps long and thick. Pharynx when everted big crater-shaped in ventral position, heavily muscularized on ventral region. Dorsal crests observed in some specimens.

Two pairs of branchiae on chaetigers 3-4, each partially fused to dorsal lamellae. Branchiae short and cirriform. Notopodia and neuropodia of chaetiger 1 reduced to rounded lamella. Notopodial lamellae foliaceous, leaf-like varying to round posteriorly. Neuropodial lamellae round shape, thin and long; decreasing in size to posterior segments. Nuchal organ present

Notochaetal and neurochaetal capillaries numerous and long arranged in two rows; neuropodial quadridentate hooded hooks always present from chaetiger 10, 6 per

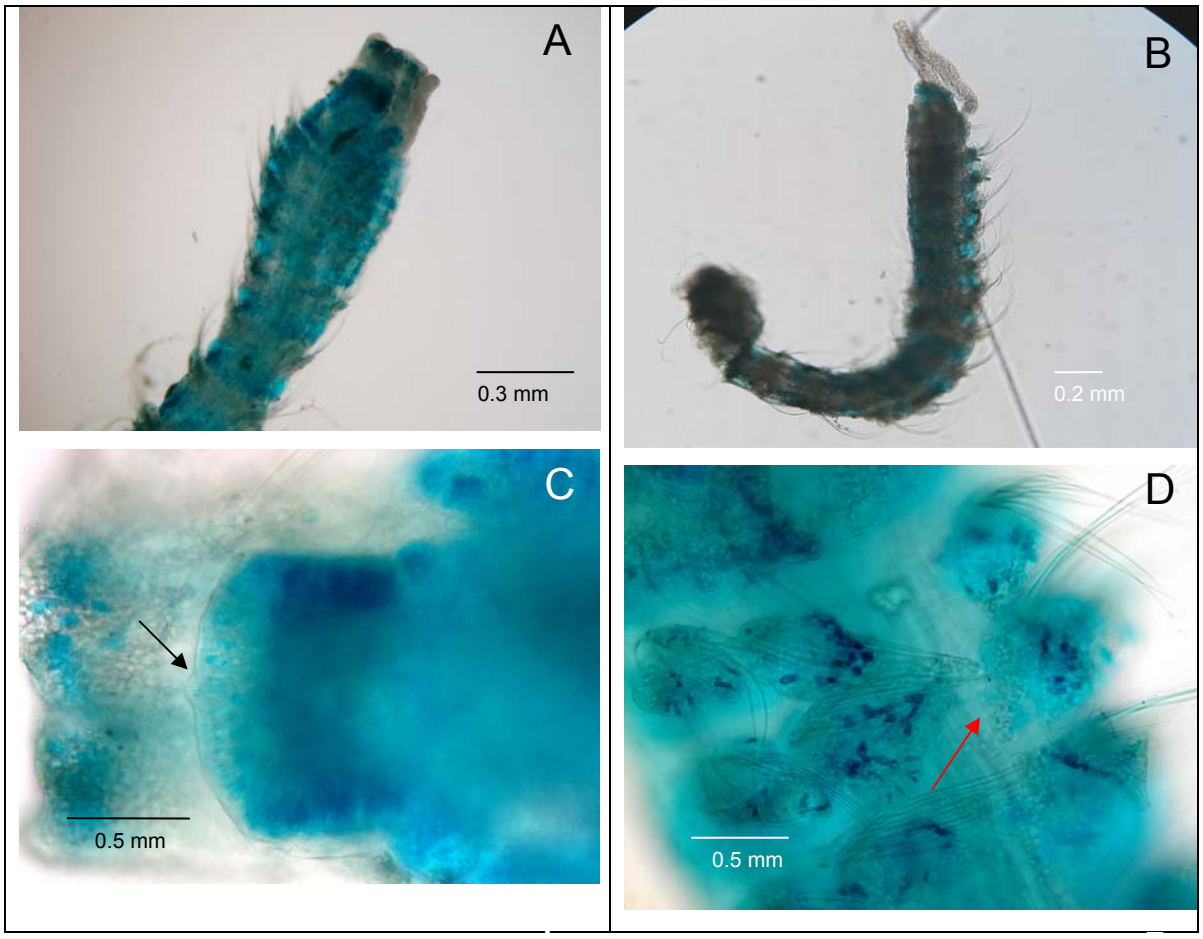
ramus accompanied by capillaries and granulated sabre chaetae which appear from chaetiger 10-11. There is no secondary hook. Pygidium with three anal cirri of variable length.

Methyl green staining: Prostomium and peristomium strongly stained. Anterior dorsal lamellae.

Remarks: The specimens share the majority of the characters with *Aurospio dibranchiata,* which mainly are the presence of short and cirriform two pairs of branchiae on chaetigers 3-4 and sabre chaetae always starting from chaetiger 10-11. *Aurospio dibranchiata* was described by Maciolek in 1981, who also observed specimens from northeast Atlantic Ocean (Rockall Trough and Ireland, Woods Hole).

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.



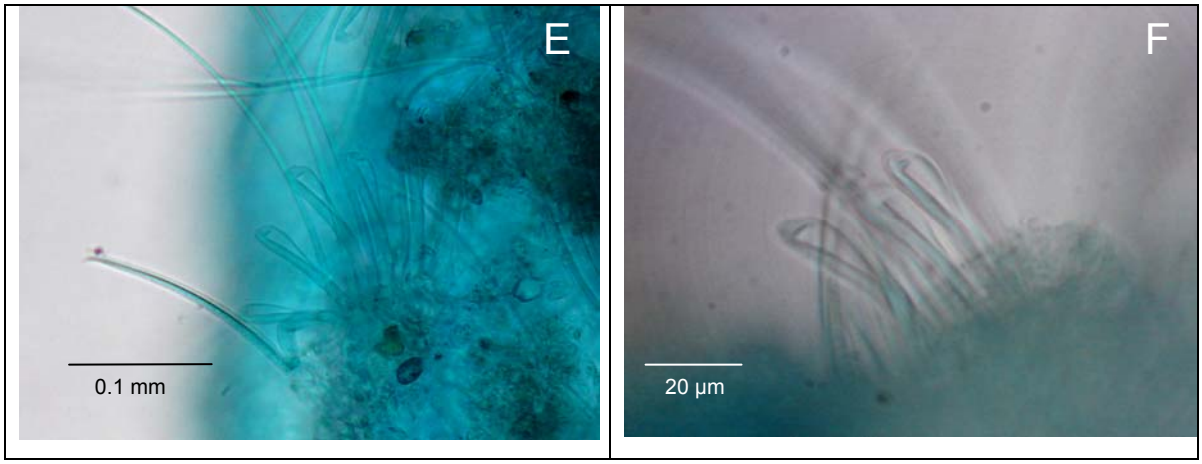


Figure 3.20. *Aurospio dibranchiata* a) anterior end dorsal view 10x b) incomplete body lateral view 10x c) prostomium detail 40x d) branchiae anterior end 40x, e) hooded hooks and sabre chaetae, dorsal view 40x and f) hooded hooks 100x.
The black arrow shows a medial peak on the prostomium and the red arrow shows the cirriform branchiae.

***Prionospio* complex Foster, 1971**

Genus: *Prionospio sensu stricto*. Malmgren, 1867

***Prionospio* sp. 81**

137 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79 May 1991 1 individual; RRS *Challenger* 111, April 1994 13 individuals; RRS *Discovery* 222, September 1996 25 individuals; RRS *Discovery* 226, March 1997 32 individuals; RRS *Discovery* 229, July 1997 35 individuals; RRS *Discovery* 231, March 1998 20 individuals and RRS *Discovery* 237, September 1998 11 individuals).

Description: The longest specimen with incomplete body, 5 mm long and 0.3 mm wide for 31 chaetigers. Prostomium rounded anteriorly, wider in posterior end, tapering to narrow caruncle. Peristomium partially fused with chaetiger 1. Lateral wings not observed. Eyes absent. Nuchal organ extending posteriorly. Anterior segment chaetigers crowded. Long and strong palps observed in some specimens. Interparapodial genital pouches and dorsal crests absent.

Branchiae present on chaetigers 2-4; short and cirriform on chaetiger 2-3; pinnate on chaetiger 4. Notopodial postchaetal lamellae of subtriangular and rounded shape. Posterior notopodial lamellae reduced. Neuropodial postchaetal lamellae small and digitiform

Notochaetal and neurochaetal capillaries granulated and long appearing from well developed parapodia; long capillaries chaetae on posterior chaetigers; neuropodial hooded hooks tridentate from chaetiger 15, 5-6 per ramus accompanied by non-granulated capillaries and sabre chaetae which appear from chaetiger 8. Pygidium not observed.

Methyl green staining: Uniform and diffused. Prostomium not stained

Remarks: The combination of pinnate and cirriform branchiae that were observed suggests that examined specimens lie within the genus *Prionospio*. Taxonomic characters such as the kind and number of pairs of branchiae, prostomium shape, anterior body shape and starting position of hooded hooks differentiates it from known *Prionospio* species.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

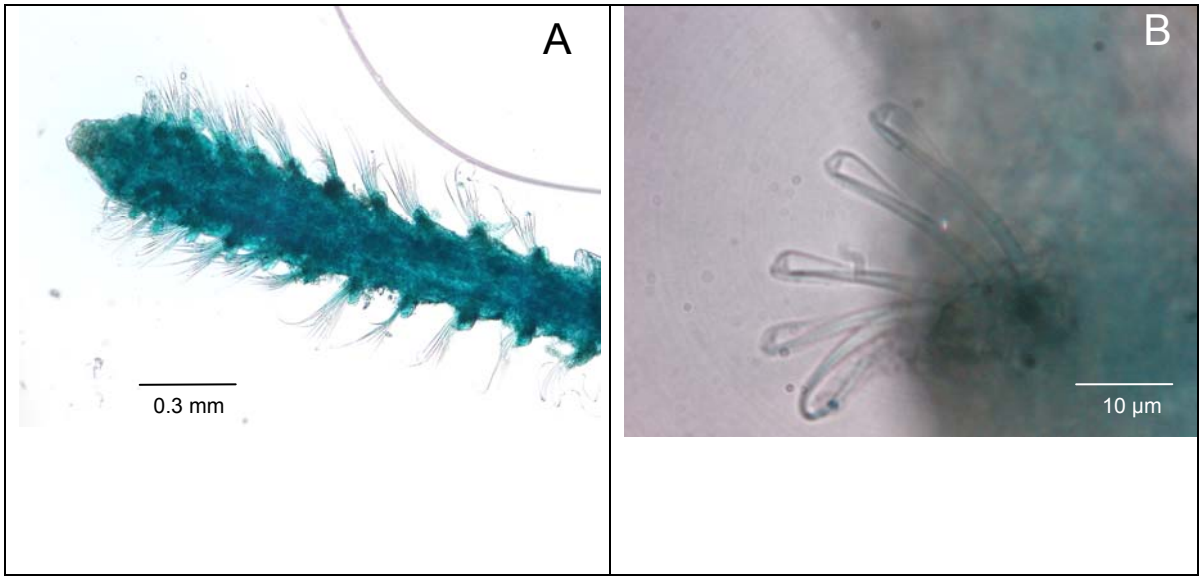


Figure 3.21. *Prionospio* sp. 81 a) anterior end, dorsal view 10x and b) hooded hooks, chaetiger 29 100x

***Prionospio* sp. 613**

84 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79 May 1991 13 individuals; RRS *Challenger* 111, April 1994 5 individuals; RRS *Discovery* 222, September 1996 5 individuals; RRS *Discovery* 226, March 1997 10 individuals; RRS *Discovery* 229, July 1997 37 individuals; RRS *Discovery* 231, March 1998 6 individuals and RRS *Discovery* 237, September 1998 8 individuals).

Description: The longest specimen with incomplete body, 5 mm long and 0.7mm wide for 32 chaetigers. Prostomium long rounded anteriorly tapering posteriorly with narrow and long caruncle. Peristomium not fused with chaetiger 1. Eyes absent. Nuchal organ not observed. Lateral wings observed

Branchiae pinnate and long on chaetigers 2 and 5; branchiae short and cirriform on chaetigers 3 and 4. Notopodial postchaetal lamellae on chaetiger 2-4 subtriangular shape changing to wide, rounded and leaf-like on following segments. On chaetiger 1 very small, short and rounded. Lamellae from chaetigers 3, 4 and 5 bigger than chaetigers 2 and 6. Neuropodial postchaetal lamellae rounded. Dorsal crests observed from chaetiger 6

Simple capillaries non granulated and no dense in neurochaetae and notochaetae; neuropodial hooded hooks tri-quadridentate from chaetiger 18-19, 6-8 per ramus, accompanied by non-granulated capillaries and sabre chaetae. Notopodial hooded hooks from chaetiger 21. Sabre chaetae from chaetiger 18, double on chaetigers 19, 21 and 22. Pygidium not observed.

Methyl green staining: Prostomium edges staining intensely. Lateral wings and peristomium; branchiaes, dorsal and ventral lamellae edges and dorsal crests.

Remarks: This species differs mainly from *Prionospio* sp. 81 in prostomium shape, number and kind of branchiae, starting position of hooded hooks and methyl green staining pattern. According to observed branchial pattern this species belongs to genus *Prionospio sensu stricto*.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

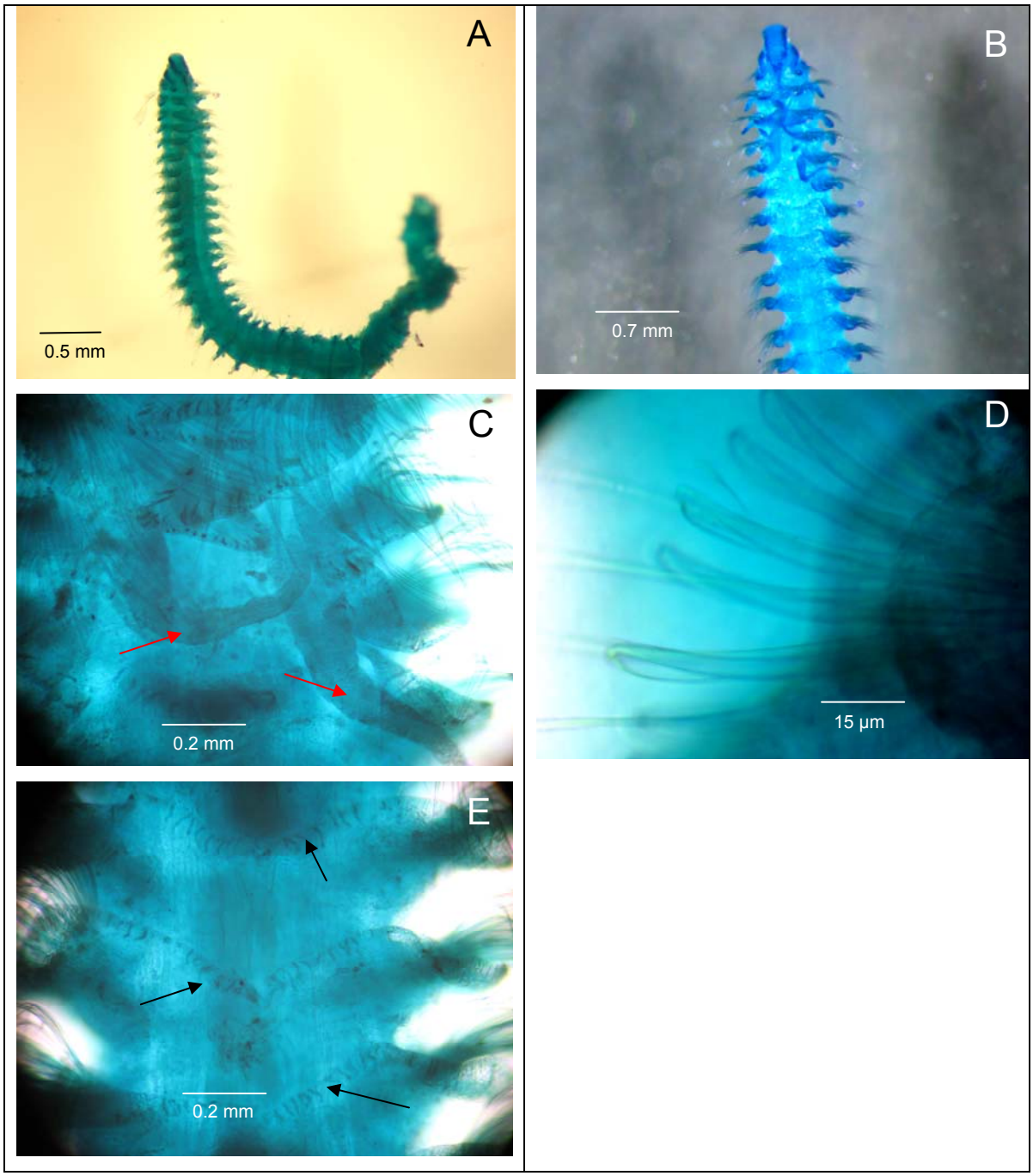


Figure 3.22. *Prionospio* sp. 613 a) incomplete body dorsal view 3x, b) anterior end dorsal view 4x, c) branchiae and lamellae details 10x, d) hooded hooks 40x and e) dorsal crests 10x. The red arrows show the long branchiae and the black arrows show the dorsal crests.

Subgenus: *Aquilaspio*. Foster, 1971

***Aquilaspio* sp. 1**

14 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 4 individuals; RRS *Discovery* 226, March 1997 2 individuals; RRS *Discovery* 229, July 1997 5 individuals and RRS *Discovery* 231, March 1998 2 individuals).

Description: The longest specimen with incomplete body, 5 mm long and 0.8 mm wide for 30 chaetigers. Prostomium long and thin rounded anteriorly tapering posteriorly with short and narrow caruncle. Eyes absent. Peristomium fused to chaetiger 1. Lateral wings observed. Body swollen in anterior region from lateral view. Parapodia well developed. Dorsal crests from chaetiger 6. Pharynx everted observed in some specimens. Genital pouches absent.

Branchiae observed just on chaetigers 3 and 4, pinnate. Branchiae on chaetiger 2 were not observed, possible they were missing. Notopodial and neuropodial postchaetal lamellae reduced on chaetiger 1; subtriangular notopodial lamellae on chaetigers 2. On chaetigers 3 and 4 notopodial lamellaes crowded and bigger than the rest, following neuropodial lamellae short and rounded decreasing in size posteriorly and varying to leaf-like.

Chaetae capillaries very dense in neuro and notopodia; neuropodial tridentate hooded hooks from chaetiger 19, 4-9 per ramus accompanied by capillaries and double sabre chaetae which appear from chaetiger 17. Double sabre chaetae just present in some posterior chaetigers. Pygidium not observed.

Methyl green staining: Transversal bands across the body on ventral region; prostomium, peristomium and lamellae edges staining intensely. Dorsal crests.

Remarks: The number (2 pairs) and kind of branchiae (pinnate) would indicate that the specimens belong to the subgenus *Aquilaspio*. This species mainly differs from other species within the *Prionospio* complex in characteristic staining pattern, type of and branchiae distribution and the high number of hooded hooks per ramus.

Habitat: This species was found within the sediment at a depth of 1-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

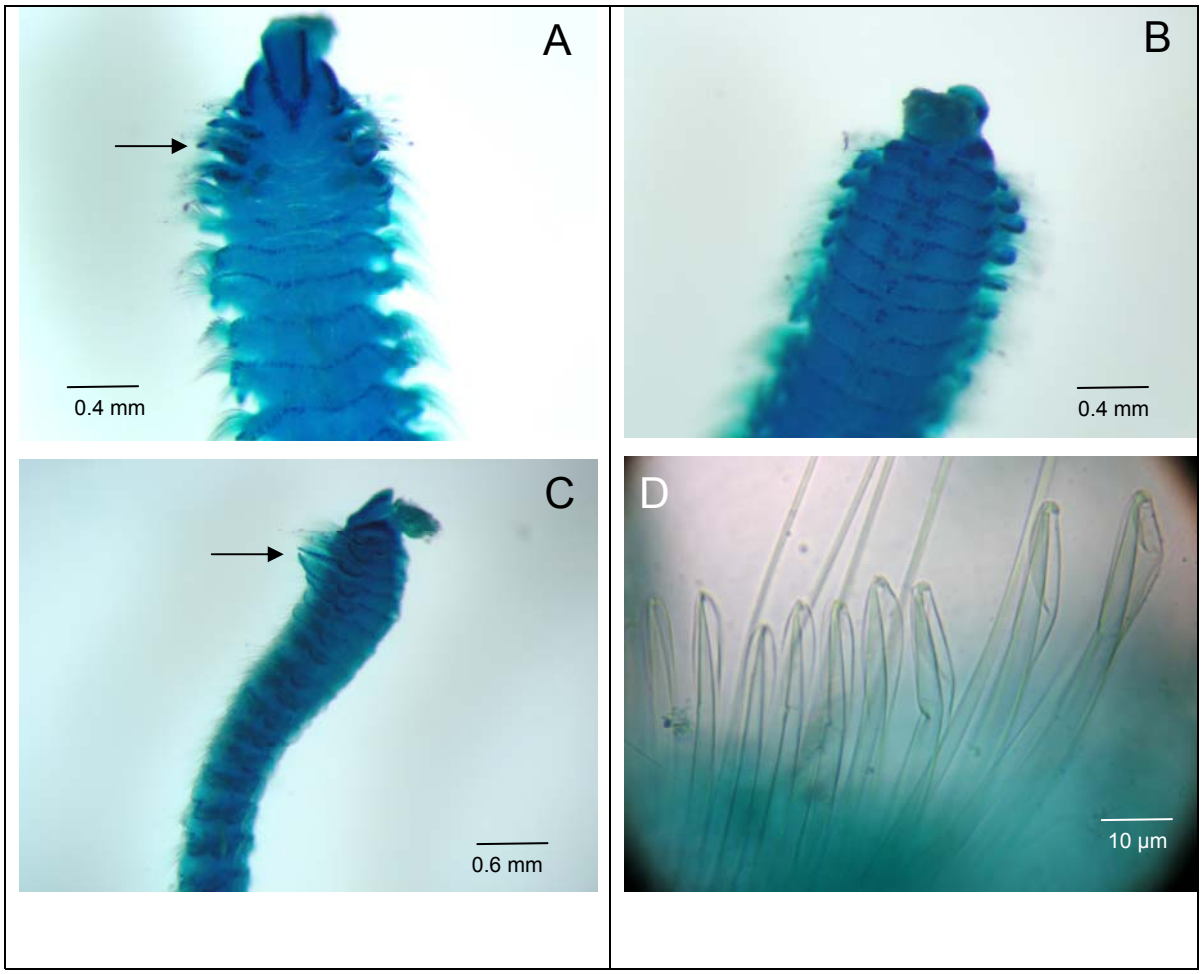


Figure 3.23. *Aquilaspio* sp. 1 a) anterior end dorsal view 4x, b) anterior end ventral view 4x, c) anterior end lateral view 4x and d) hooded hooks and capillaries chaetiger 27 40x. The black arrows show the big notopodial lamellaes.

Subgenus: *Minuspio*. Foster, 1971

***Minuspio* sp. 2**

90 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79 May 1991 8 individuals; RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 24 individuals; RRS *Discovery* 226, March 1997 18 individuals; RRS *Discovery* 229, July 1997 27 individuals; RRS *Discovery* 231, March 1998 5 individuals and RRS *Discovery* 237, September 1998 7 individuals).

Description: The longest specimen incomplete, 3.0 mm long and 0.2 mm wide for 47-48 chaetigers. Prostomium subtriangular rounded anteriorly with apical peaks; tapering posteriorly, caruncle ending rounded at anterior edge of chaetiger 1. Pair of eyes present. Peristomium dorsally fused to chaetiger 1, lateral wings absent.

Branchiae from chaetiger 2; 6 pairs on chaetigers 2-7, each separated from the dorsal lamellae and extending over 2 chaetigers. All pairs cirriform varying from thin and cylindrical to thick and slightly triangular-shape. Chaetiger 1 reduced, notopodial lamellae triangular and leaf-like. Neuropodial lamellae rounded and digitiform varying to thin and short posteriorly. Dorsal crests between chaetigers 8-15. Interparapodial genital pouches absent.

Anterior capillaries in neuro and notopodia, non-granulated; neuropodial quadridentate and bidentate hooded hooks from chaetiger 16, 5 per ramus; notopodial hooks from chaetiger 27, 3 per ramus, accompanied by capillaries and long and thin sabre chaetae which appear from chaetiger 15. Pygidium not observed.

Methyl green staining: Prostomium strongly stained; ventral and dorsal crests, dorsal lamellae and peristomium.

Remarks: The presence of only cirriform branchiae in examined individuals would indicate that the specimens belong to the subgenus *Minuspio*. The presence of six pairs of branchiae, apical peaks on prostomium (prostomium shape) and dorsal crests would be good characters to separate them from other *Minuspio* species.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

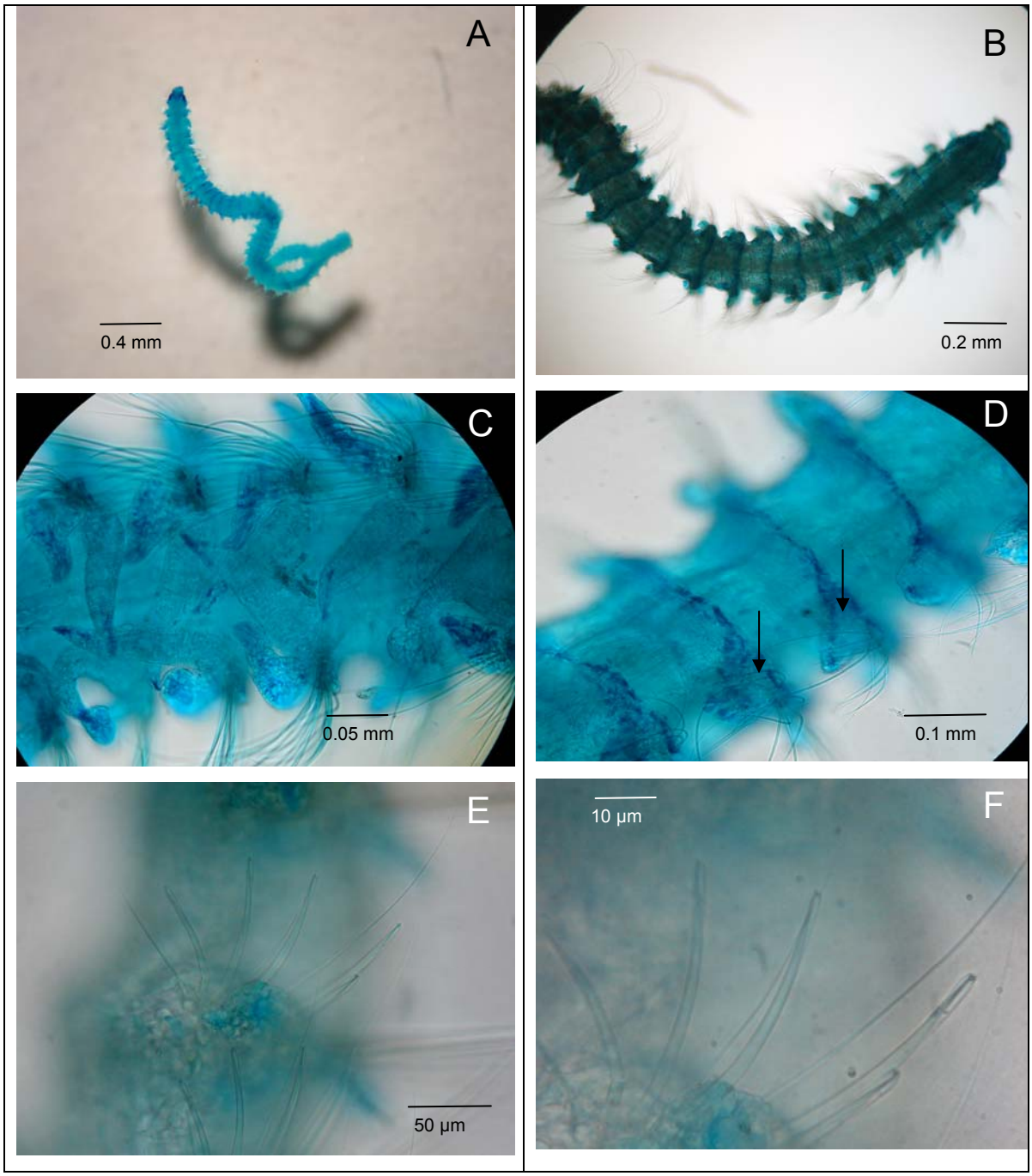


Figure 3.24. *Minuspio* sp. 2 a) incomplete body dorsal view 32x, b) anterior end ventral view 10x, c) anterior end branchiae and lamellae details 40x, d) dorsal crests (black arrows) 40x, e) hooded hooks posterior end ventral view 40x and f) hooded hooks detail ventral view 100x

***Minuspio* sp. 4**

159 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 185, August 1989 3 individuals; RRS *Challenger* 79 May 1991 20 individuals; RRS *Challenger* 111, April 1994 6 individuals; RRS *Discovery* 222, September 1996 26 individuals; RRS *Discovery* 226, March 1997 44 individuals; RRS *Discovery* 229, July 1997 36 individuals; RRS *Discovery* 231, March 1998 12 individuals and RRS *Discovery* 237, September 1998 12 individuals).

Description: The longest specimen with incomplete body, 4.5 mm long and 0.15 mm wide for 35 chaetigers. Body swollen in anterior region. Prostomium long; wide and rounded anteriorly, slightly incised, tapering to posterior end; narrow caruncle. Pair of eyes present. Peristomium dorsally not fused to chaetiger 1, lateral wings absent. Long palps present on some individuals.

Branchiae on chaetigers 2-5; first pair cirriform (wrinkled) and short; pairs 2 and 3 subequal in length and cirriform; pair 4 cirriform, thinner and 3 times as long as before branchiaes. Parapodia of chaetiger 1 smaller than subsequent parapodia, with well developed triangular notopodial lamellae varying to leaf-like and rounded shape. Neuropodial lamellae small, short and digitiform shape. Dorsal crests and interparapodial pouches absent.

Chaetae capillaries slightly granulated in neuro and notopodia; neuropodial tri and quadridentate hooded hooks from chaetiger 11, 6-7 per ramus accompanied by capillaries and neuropodial sabre chaetae which appear from chaetiger 10. Pygidium with 1 long ventral cirri.

Methyl green staining: Uniform

Remarks: The only presence of cirriform branchiae in examined specimens would indicate that it is *Minuspio* Foster, 1971. This species mainly differs from *Minuspio* sp. 2 in the presence of very long cirriform branchiae on chaetiger 5; prostomium length and starting position of hooded hooks.

Habitat: This species was found within the sediment at a depth of 0-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

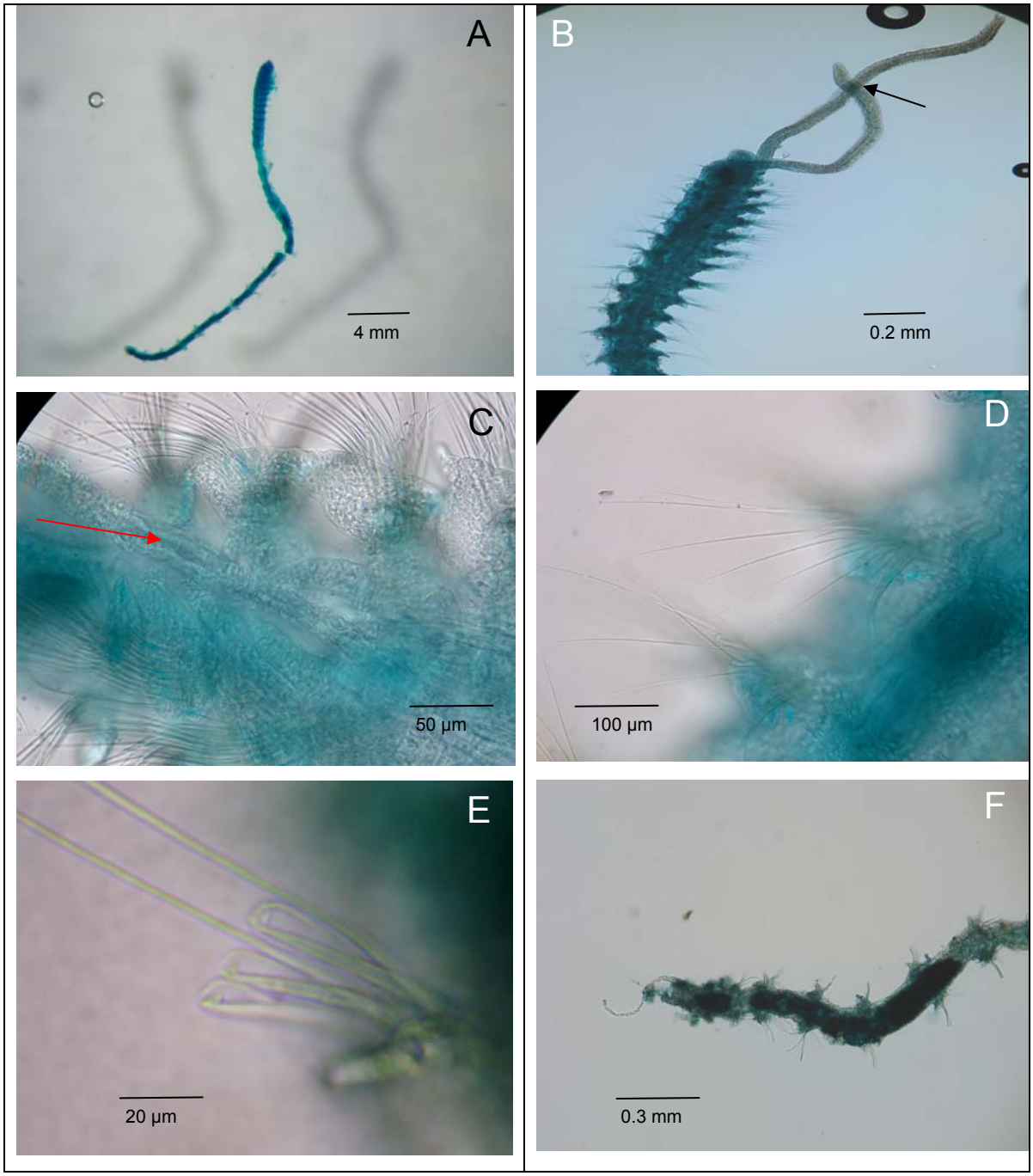


Figure 3.25. *Minuspio* sp. 4 a) complete body lateral view 32x, b) anterior end dorsal view 10x, c) anterior end, branchiae detail 40x, d) sabre chaetae and hooded hooks 40x, e) hooded hooks 100x and f) posterior end 10x.
The black arrow shows the long palps and the red arrow shows the long branchiae

***Minuspio* sp. 5**

9 individuals examined. Porcupine Abyssal Plain (RRS *Discovery* 222, September 1996 2 individuals; RRS *Discovery* 226, March 1997 2 individuals and RRS *Discovery* 229, July 1997 5 individuals).

Description: The longest specimen with incomplete body, 2.5 mm long and 0.1mm wide for 27 chaetigers. Prostomium long, wider and rounded anteriorly, tapering posteriorly. Nearly right angle in dorsal view though pointed in lateral view. Peristomium not fused with chaetiger 1. Eyes and nuchal organ not observed.

Branchiae short and cirriform from chaetiger 2-5, 4 pairs. Notopodial postchaetal lamellae varying from digitiform to rounded shape. Neuropodial postchaetal lamellae short and rounded. Interparapodial pouches and dorsal crests absent.

Notochaetal and neurochaetal capillaries granulated and not dense; neuropodial hooded hooks bi-tridentate from chaetiger 16-17, 1-3 per ramus changing to 5 per ramus on posterior region, accompanied by non-granulated capillaries and sabre chaetae. Notopodial hooks not observed. Ventral sabre chaetae from chaetiger 14-15, double in posterior region. Pygidium not observed.

Methyl green staining: Uniform. Prostomium ventrally stained.

Remarks: This species differs from *Minuspio* sp. 2 and *Minuspio* sp. 4 species in prostomium and branchiae shape and starting position of sabre chaetae.

Habitat: This species was found within the sediment at a depth of 1-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

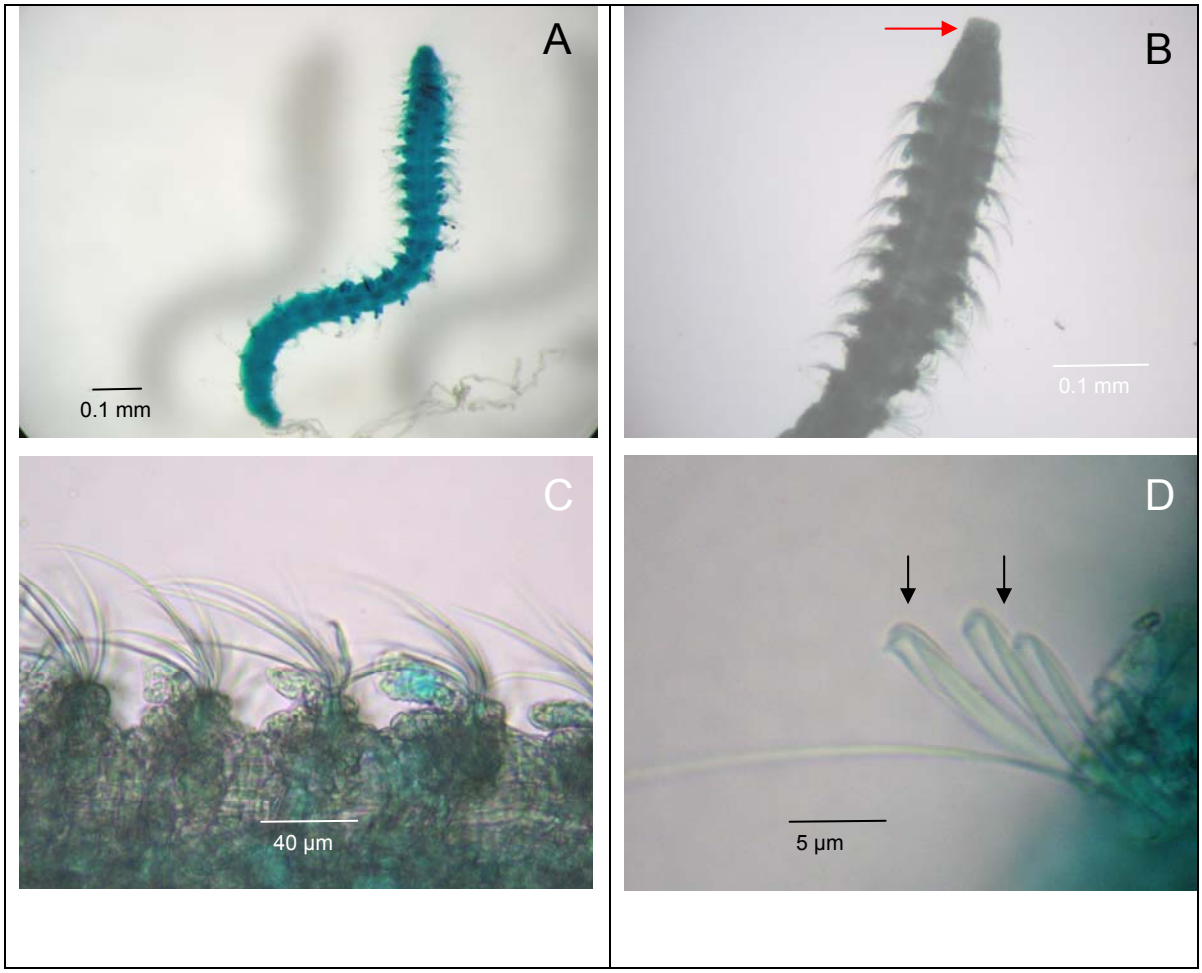


Figure 3.26. *Minuspio* sp. 5 a) incomplete body dorsal view 32x, b) anterior end dorsal view 10x, c) branchiae anterior end 10x and d) hooded hooks posterior region 40x.
The red arrow shows the prostomium and the black arrows show the hooks.

Species	Branchiae		Hooded hooks		Sabre chaetae start	Dorsal crests start
	Kind and start	*No.of pairs*	*Neuro start/ max no.*	*No. small teeth*		
***Prionospio* sp. 81**	Short and cirriform ch2-3, pinnate ch4	3	ch15/5-6	3	ch8	No
***Prionospio* sp.613**	Pinnate and long ch2-5; short and cirriform ch3-4	4	ch18-19/6-8	3-4	ch18	ch6
***Aquilaspio* sp. 1**	Pinnate ch3-4	2	ch19/4-9	3	ch17	ch6
***Minuspio* sp. 2**	Cirriform ch2-7. Cylindrical and triangular	6	ch16/5	2-4	ch15	ch8
***Minuspio* sp. 4**	Cirriform ch2-5. Wrinkled, short and long.	4	ch11/6-7	3-4	ch10	No
***Minuspio* sp. 5**	Short and cirriform ch2-5	4	ch16-17/1-5	2-3	ch14-15	No
A. dibranchiata	Short and cirriform ch3-4	2	ch10/6	4	ch10-11	Variable

Table 3.6. Taxonomic characters of *Prionospio* complex species. ch: chaetiger

Indeterminate spionids

Spionidae sp. 10

12 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 111, April 1994 1 individual; RRS *Discovery* 222, September 1996 2 individuals; RRS *Discovery* 226, March 1997 2 individuals; RRS *Discovery* 229, July 1997 1 individual; RRS *Discovery* 231, March 1998 1 individual and RRS *Discovery* 237, September 1998 5 individuals).

Description: Longest specimen with incomplete body 4.2 mm long and 0.6 mm wide for 26 chaetigers. Prostomium small rounded anteriorly with narrow caruncle; eyes not observed. Peristomium not fused to chaetiger 1. Nuchal organs not developed. Interparapodial pouches from chaetiger 15.

Branchiae very small observed on chaetigers 3, 4 and 5. Notopodial and neuropodial postchaetal lamellae very small or nearly not developed. Only on chaetiger 1, very small and rounded lamellae. Parapodia slightly developed.

Notochaetae and neurochaetae without dense capillaries; capillaries slightly granulated. Neuropodial bi and tridentate hooded hooks from chaetigers 17-18, 5-6 per ramus accompanied by thin capillaries and granulated sabre chaetae. Ventral sabre chaetae from chaetiger 5-7, double on chaetiger 8 and 9. Pygidium not observed.

Methyl green staining: Prostomium and peristomium strongly stained on ventral position. Four rectangular sidelines lied on peristomium from dorsal position. Lines across body in ventral anterior end

Remarks: Differs mainly from other PAP Spionidae species in the poor development of postchaetal lamellae, the kind of Methyl green staining pattern (MGSP) and the presence of double sabre chaetae on chaetigers 8 and 9. Branchiae observed from chaetiger 3 until chaetiger 5, however this character is not enough to assign genera. This species could be belongs to *Prionospio* complex, however further observations are required

Habitat: This species was found within the sediment at a depth of 1-5 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

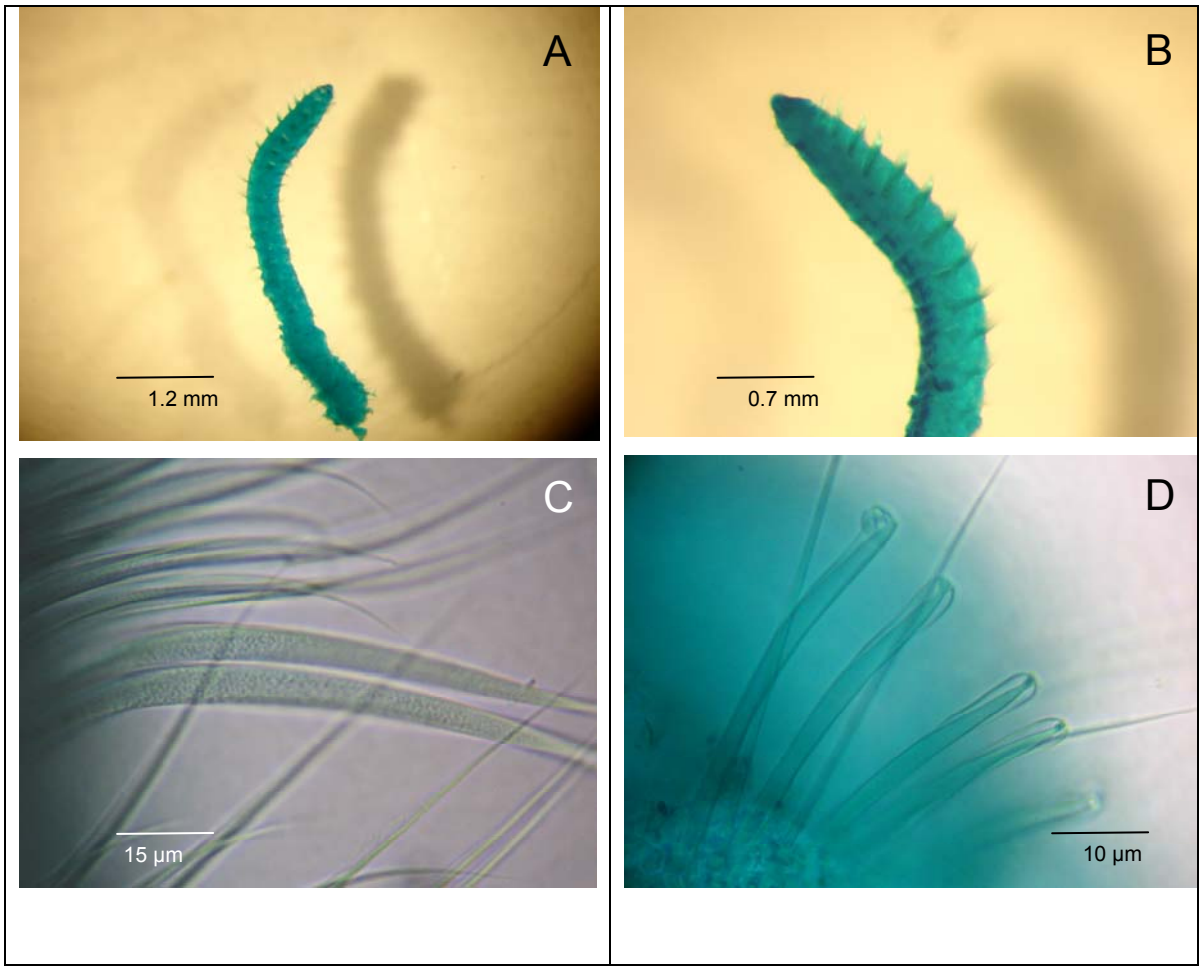


Figure 3.27. Spionidae sp. 10 a) incomplete body lateral view 24x, b) incomplete body ventral view 50x, c) double sabre chaetae 40x and d) hooded hooks, posterior region 40x

Spionidae sp. 6A

15 individuals examined. Porcupine Abyssal Plain (RRS *Challenger* 79 May 1991 6 individuals; RRS *Challenger* 111, April 1994 2 individuals; RRS *Discovery* 222, September 1996 5 individuals; RRS *Discovery* 226, March 1997 1 individual and RRS *Discovery* 229, July 1997 1 individual).

Description: The longest specimen with incomplete body, 2.5 mm long and 0.2 mm wide for 24 chaetigers. Prostomium long and thin; rounded anteriorly, with two small marginal peaks, tapering posteriorly. Eyes present. Peristomium dorsally fused to chaetiger 1, forming a neck around prostomium. Palps not observed. Nuchal organ as longitudinal ciliate until chaetiger 9.

Branchiae cirriform observed in only one specimen on chaetiger 3. Neuropodial lamellae short and digitiform; on chaetiger 3 it is bigger than the rest. Notopodial lamellae leaf-like and subtriangular; on chaetiger 3 it is bigger than the rest. Dorsal crests from chaetiger 8-9 until chaetiger 15.

Chaetae capillaries long from chaetiger 2 not granulated in neuro and notopodia; neuropodial hooded hooks from chaetiger 13, 3-7 per ramus accompanied by capillaries; ventral sabre chaetae from chaetiger 12. Pygidium not observed.

Methyl green staining: Prostomium, peristomium, branchiae on chaetiger 3 and dorsal crests strongly stained.

Remarks: This species differs from other described PAP spionids in prostomium and peristomium shape, branchiae number, starting position of hooded hooks and kind of capillaries. Unfortunately the observed specimens did not allow a good identification. A greater number of specimens are needed to get a better description. The presence of anterior marginal peaks on prostomium and branchiae absence could be useful character in later identifications.

Habitat: This species was found within the sediment at a depth of 1-3 cm.

Distribution: North-east Atlantic Ocean, Porcupine Abyssal Plain at 4835 m 48º N 16º W.

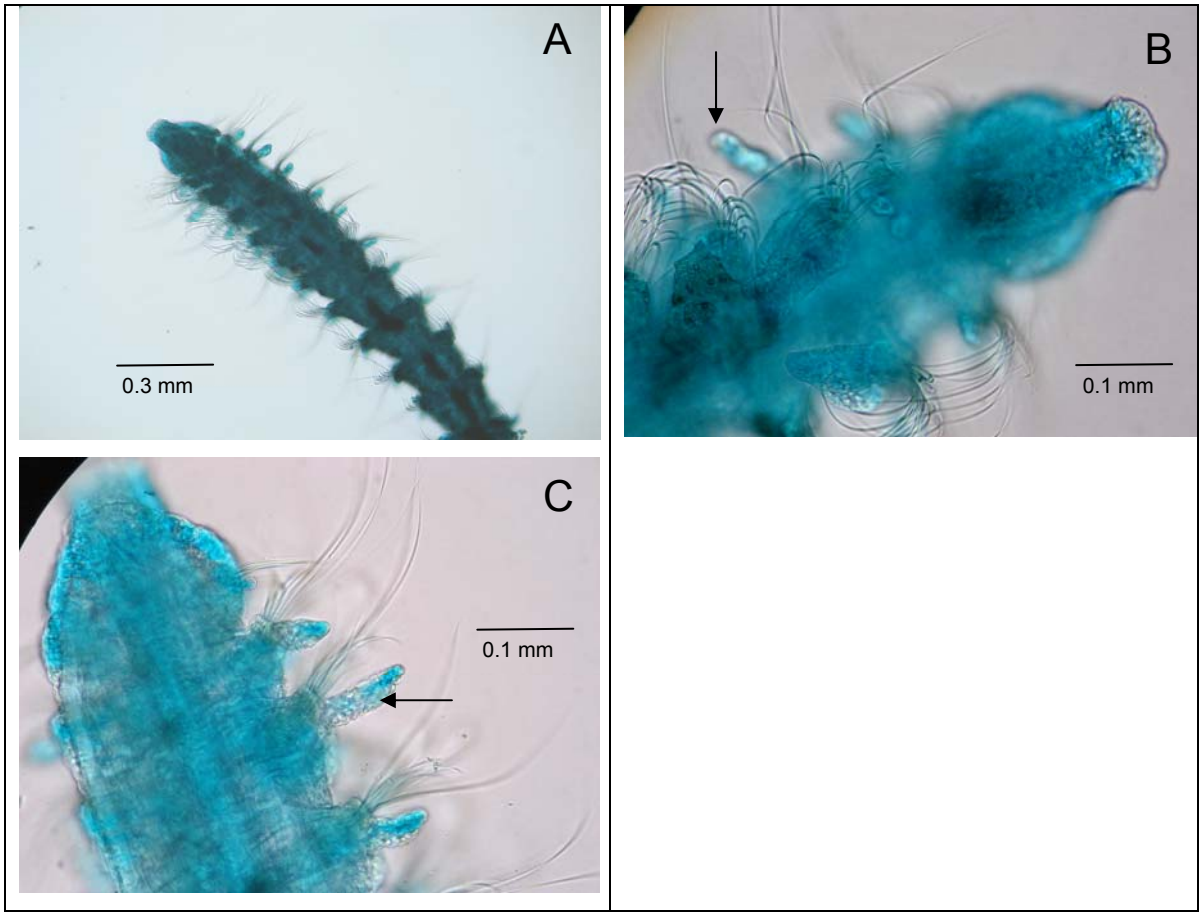


Figure 3.28. Spionidae sp. 6A a) incomplete body dorsal view 10x, b) anterior end dorsal view 40x and c) anterior end lateral view 40x.
The black arrows show the big lamellae.

3.2.3. Discussion

3.2.3.1. Introduction

The systematic of the Spionidae has undergone a number of major revisions since the family was established by Grube in 1850. In 1896 Mesnil divided the family into two groups using characters such as shape and presence of horns on the prostomium, distribution of branchiae, form of anal cirri, occurrence of dorsal hooded hooks, and presence of capillaries in segments with hooded hooks. Söderström (1920) created a classification based on the sexual reproductive patterns observed. He incorporated information on segmental organ structure, eggs membranes, sperm shape and larval development in erecting Nerinae, Laonicinae and Spioninae. Maciolek-Blake (1983), in her doctoral work made a comprehensive study of the systematics of Atlantic Spionidae with special reference to deep-water species. More recent studies on spionid phylogenetic relationships have been made by Mackie (1996), Sigvaldadóttir *et al*., (1997) and Blake and Arnofsky (1999). Recent local and geographic studies have been carried out by Imajima (1990, 1991) from Japan, Blake (1983) from South America, Antarctica and adjacent seas and islands, Blake (1996a) from California, Wilson (1990) from Australia; Meißner & Hutchings (2003) from eastern Australia, Ward (1981) from Hawaii and Maciolek (1984, 1985, 1987, 1990 and 2000) from north western Atlantic Ocean.

Recent revisions of some of the larger groups include Radashevsky (1993) on *Polydora*, Blake (1996b) of the genera and species from California, Sigvaldadóttir's (1998) cladistic study on *Prionospio*, Rice and Levin's (1998) analysis of *Streblospio* and Meißner & Hutchings (2003) and Meißner (2005) of the genus *Spiophanes*.

The Spionidae represents one of the large and most common polychaete families found in benthic infaunal communities. Spionids occur in a wide variety of habitats from the intertidal to the deep sea. They are readily recognized by their anterior ends which carry a pair of long prehensile palps (Blake, 1996b). The Spionidae is one of the most diverse and abundant families in deep-sea environments (Blake & Narayanaswamy, 2004; Cosson-Sarradin *et al.,* 1998; Glover *et al.,* 2001; Hilbig & Blake, 2006; Paterson *et al*., 1998 and Pérez-Mendoza *et al.,* 2003), with the exception of the Antarctica (Hilbig, 2004). Though Mincks *et al*. (2008), found a new species of *Aurospio* (*Aurospio* sp. nov) highly abundant and dominant in shelf-depths sites in the Bellingshausen Sea (over 70% of the polychaete community in some

instances). However the taxonomic studies of abyssal species under 2000 m depth are very scarce with few species being described in the last decades. From the first deep-sea Spionidae descriptions made by Grube (1860) of *Spiophanes kroeyeri*, Hartman (1943) of *Polydora websteri* and Hartman (1960) of *Spiophanes anoculata*, not many species descriptions have been developed in the last years. Maciolek (1981a), described *Aurospio dibranchiata*, a new genus and species of spionid polychaete found from widespread areas in the north and south Atlantic, between 300 m to 3600 m depth. In 1985, Maciolek described new species from Atlantic waters related to '*Prionospio* complex'. They were *Prionospio (Prionospio) dubia* (from 85 to 2379 m depth) and *Prionospio (Minuspio) fauchaldi* (from 530 to 4950 m depth). The same author in 2000 described to *Laonice magnacristata* and *Spiophanes abyssalis* from shelf and slope depths (from 1000 to 3356 m depth) of the east and western north Atlantic. Meißner (2005) from a revision of the genus *Spiophanes* described *Spiophanes longisetus* which was found in great depths between 3753-4680 m in western north Atlantic.

Results form several deep-sea programmes should change this situation increasing the record of already known species as well as the description of new species; such as for example ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns (ANDEEP) in the Southern Ocean and Antarctica; CROZet natural iron bloom and EXport experiment (CROZEX) in the Southern Indian Ocean; Latitudinal Gradients in Biodiversity in the deep Atlantic (DIVA) in Angolan waters; Study of the benthic communities in the deep sea influenced by the Zaire canyon (BIOZAIRE) off the Congo margin; Project on biodiversity, species ranges, and gene flow in the abyssal Pacific nodule province: predicting and managing the impacts of deep seabed mining (KAPLAN); NODINAUT in manganese nodule zones of the Central Equatorial Pacific; long-term monitoring of the San Francisco Deep Ocean Dredged Material Disposal Site (SF-DODS) off Northern California; the Atlantic Continental Slope and Rise Programme (ACSAR); Deep-sea & Extreme Environments, Patterns of Species and Ecosystem Time-Series (DEEPSETS) in the NE Atlantic and LEvantine Basin Biodiversity VARiability (LEVAR) in the Mediterranean sea.

New taxa from deep-sea hydrothermal vents in the eastern Pacific have been reported by Maciolek (1981b), Blake & Maciolek (1992), Sigvaldadóttir & Desbruyères (2003); additional genera and species remain to be described.

In the current investigation, thirteen species of Spionidae were described with *Aurospio dibranchiata* being the only one species previously recorded. This species was the second most abundant spionid in the study. In addition, two species of the genus *Laonice*, two species of the genus *Spiophanes*, three species of the subgenus *Minuspio*, two species of the subgenus *Prionospio* and one species of the subgenus *Aquilaspio* together two species of Spionidae indeterminate were recorded.

Morphotypes description was characterized by the high variability of forms among individuals of the same species, the small size of specimens and problems related to samples preservation. Deep-sea polychaetes show a trend of character loss (Glover, 2000). Therefore, the major taxonomic difficulties were the absence and poor condition of the branchiae and missing posterior end and pygidium. Also due to specimen preservation important characters such as occipital antenna, nuchal organ, branchiae, dorsal crests, genital pouches, sabre chaetae and hooks were not always present or well defined. Although the presence of palps is an important familial taxonomic character, they were found missing in the majority of specimens examined.

3.2.3.2. *Laonice*

The two species of *Laonice* described in this work did not show high abundance in comparison with other spionids. Species of PAP *Laonice* were defined by the presence and shape of anterior notopodial postchaetal lamellae and occipital antenna. The first character presented a large, triangular and leaf-like overall shape, often surrounding chaetal fascicles and varying its shape to posterior segments. The second character was always present varying in size among species. The prostomium shape, the presence of genital pouches and the methyl green staining pattern also were taxonomic characters that allowed *Laonice* sp. 1 to be distinguished from *Laonice* sp. 640. Unfortunately, the posterior end and pygidium was missing in both species. Maciolek (2000), in her revision of *Laonice* species also consider some of these characters, but she include the number of eyes, caruncle length (chaetiger), starting position of lateral genital pouches, pairs of branchiae, starting position and teeth number of neuropodial hooks as important characters to separate species. The first occurrence of interparapodial genital pouches has been used by some authors as a specific character within *Laonice* not restricted to deep-sea environments (Söderström, 1920; Hartman, 1953; Banse & Hobson, 1968 and Blake & Kudenov, 1978). Sikorski *et al*., (1988) from an Artic Ocean *Laonice* collection concluded the

information on the size of the material examined is necessary to ensure that comparisons are being made between animals of similar age/sizes. Characters such as the caruncle, capillary chaetae, hooded hooks and parapodia are also important on species definition. *Laonice magnacristata* (Maciolek, 2000) and *Laonice antarcticae* (Hartman, 1953) which have been recorded for North Atlantic Ocean at depths greater than 2800 m, mainly differ from *Laonice* sp. 1 and *Laonice* sp. 640 in prostomium shape, starting position of genital pouches, hooded hooks and ventral sabre chaetae. The PAP *Laonice* species described in the current study could be new to science, increasing the record of new descriptions for the genus in deep-sea waters and improving the knowledge of the northeast Atlantic Ocean polychaete fauna. However, more observations including full bodies are necessary to develop detailed descriptions. Blake (*unpublished*) thinks that a similar situation could occur for three species of *Laonice* from the continental slope off northern California.

3.2.3.3. *Spiophanes*

Two species belong to *Spiophanes* were found and described in the current investigation. Both species *Spiophanes* sp. 1 and *Spiophanes* sp. 619 recorded low abundances in comparison with the most abundant spionid species. The main taxonomic characters that define the genus were the total absence of branchiae and the presence of one large curved neuropodial hook (curved spine) in addition to normal capillaries in chaetiger. Both characters coincide with the original description established by Grube in 1860 for the genus. Most of the examined specimens were not in good condition, however the observation and analyses of the body allowed a consistent description of the morphotypes. Due to same reason some characters mainly from abdominal region were not detailed on descriptions. The main different taxonomic characters between PAP *Spiophanes* species were prostomium shape, methyl green staining pattern, presence of bacillary chaetae, nuchal organ shape and lamellae shape. Blake (1996) also considers these characters to distinguish between species but he also add the presence of long frontal horns in the prostomium, the nuchal organ length, the number of hooded hooks teeth, the presence of interparapodial pouches and ciliated dorsal ridges and the absence/presence of occipital antenna. Maciolek (2000) in her description of *Spiophanes abyssalis* separates this species from other *Spiophanes* adding to characters already mentioned the degree of crook chaetae granulation and the presence/absence of hooded hooks.

Meißner (2005) described the openings of glandular organs in parapodia of the middle region and the occurrence of pigmented cells associated with the parapodial glands as a new diagnostic characters. Most of the diagnostic characters before mentioned were not observed in deep-sea species. However, the appearance of these new characters in PAP *Spiophanes* species would improve the descriptions and would probably increase the number of morphotypes found.

Spiophanes kroeyeri Grube, 1860 has a widespread distribution in the northern hemisphere and has been recorded at depths to 3500 m. This species shares some similarities with PAP species, however differs from *Spiophanes* sp.1 and *Spiophanes* sp. 619 in nuchal organ length, presence/absence of eyes and bacillary chaetae, lamellae shape and number of hooks per fascicle. *Spiophanes anoculata* Hartman, 1960 has been recorded in California at depths of 2400 m. This species differs from PAP species in the presence of long frontal horns in the prostomium, absence of occipital antenna, number of teeth, nuchal organ length and number of curved spines on chaetiger 1. *Spiophanes abyssalis* Maciolek, 2000 is recorded in the North Atlantic at depths between 1922-2356 m and differs mainly from PAP species in the prostomium, nuchal organ and notopodial lamellae shape, and starting position of bacillary chaetae. *Spiophanes longisetus* Meißner, 2005 was found in great depths between 3753-4680 m in the North Atlantic Ocean. The shape of prostomium and occipital antenna, the length of nuchal organs and the presence of very long and granulated notochaetae in parapodia of posterior chaetigers were the main characters different to PAP *Spiophanes* species. According with comparisons made and taxonomic characters presented on descriptions *Spiophanes* sp. 1 and *Spiophanes* sp. 619 would be new deep-sea species of the Spionidae family. More detailed descriptions of these species including new characters will allow more comprehensive diagnosis.

3.2.3.4. *Prionospio* complex

Six species of the *Prionospio* complex were described in the current study: Three species of *Minuspio*, two species of *Prionospio* and one species of *Aquilaspio*. *Minuspio* sp. 4 was the most abundant species belonging to Spionidae family. The members of the *Prionospio*-complex are mainly characterised by the form and arrangement of their branchiae (Worsaae, 2003). However, Blake (1996b) referred to this group including spionids that have (1) slender, cylindrical bodies, (2) relatively

simple prostomium, without frontal horns and occipital antenna, and usually red eyes, (3) bi-to multidentate hooded hooks in both noto- and neuropodia, (4) well- developed anterior parapodial lamellae, and (5) hard-membraned eggs, in addition to branchiae of various forms first present from chaetiger 1-3 and limited to the anterior part of the body. Several genera have been referred to this complex: *Apoprionospio* Foster, 1969; *Aurospio* Maciolek, 1981; *Laubieriellus* Maciolek, 1981; *Orthoprionospio* Blake & Kudenov, 1978; *Paraprionospio* Caullery, 1914; *Prionospio* Malmgren, 1867; *Streblospio* Webster, 1879, *Minuspio* Foster, 1971 and *Aquilaspio* Foster, 1971 (Blake & Kudenov, 1978; Maciolek, 1985; Blake, 1996b; Sigvaldadóttir, 1998). Cladistic analyses of Spionidae and the *Prionospio*-complex generally support the monophyly of this group (Sigvaldadóttir *et al*. 1997; Sigvaldadóttir, 1998; Blake & Arnofsky, 1999). In this work the classification made by Foster (1971) is considered to include the genus *Aurospio* within the group.

3.2.3.5. *Prionospio* (*Minuspio)*

According to Foster (1971), *Minuspio* species have cirriform branchiae (apinnate) from chaetiger 2, with between 4-40 pairs. However, two species have short, apinnate branchiae beginning on chaetiger 3: *Minuspio banyulensis* Laubier, 1968 and *Minuspio pilkena* Wilson, 1990. PAP *Minuspio* species showed this taxonomic character but differ between them in the shape of the branchiae, number of pairs, starting position of hooded hooks, sabre chaetae and dorsal crests. *Minuspio* sp.4 showed wrinkled branchiae and the absence of dorsal crests, while *Minuspio* sp.2 showed apical peaks on prostomium and six pairs of branchiae. *Minuspio* sp. 5 showed a different overall shape of the prostomium. Blake (1996b) though considers *Minuspio* as subgenus and recognize similar characters to separate species, adding the absence of eyes, prostomial peaks development and variations in methyl green staining pattern. These differences are not restricted for the genus. Maciolek (1985) observed that the development and morphology of pinnules on the branchiae especially from several new deep-sea species, was more complicated than previously understood. She noted that branchiae could be entirely smooth (apinnate), weakly sculptured or wrinkled, have a variable number of digitiform pinnules, or have more elaborate platelike pinnules. The same author separated some *Minuspio* species using another characters such as dorsal crests shape and the presence and absence of lateral pouches. *Minuspio fauchaldi* Maciolek, 1985 has been recorded at depths

down to 4950 m in the Atlantic Ocean. Its main character is the presence of wrinkled branchiae on chaetiger 1 and 4. *Minuspio* sp. 4 only has wrinkled branchiae on the first pair. *Minuspio cirrifera* Wiren, 1883, recorded at depth until 2900 m readily differs from PAP *Minuspio* species in the presence of interparapodial pouches. *Minuspio delta* Hartman, 1965 has been recorded at depths to 2200 m. This specie mainly differs from PAP *Minuspio* species in the complete fusion of peristomium and chaetiger 1, starting position of neuropodial hooded hooks and sabre chaetae and the presence of very long and thin cirriform branchiae. *Minuspio sandersi* Maciolek, 1981 from Galapagos Rift geothermal vent, 2447 m depth, differs from other *Minuspio* species including PAP species in pygidium shape and the presence of 9 wide, wrinkled-appearing pairs of branchiae. PAP *Minuspio* species would be new deep-sea taxa to science, however further observations would allow knowing better their morphology. Therefore, new morphotypes could be found.

3.2.3.6. *Prionospio sensu stricto*

Prionospio Malmgren, 1867, *sensu stricto* has branchiae from chaetiger 2, with a combination of pinnate and cirriform branchiae (Foster, 1971). Two species of *Prionospio*, *Prionospio* sp. 81 and *Prionospio* sp. 613 were recorded and described in the current investigation. *Prionospio* sp. 81 was the third most abundant Spionidae species in the study. They showed the branchial pattern related to the genus however this character was not easy to recognize in several specimens due to missing and branchiae conditions. Also this character showed high variability in terms of width and length. Branchial pairs are apparently lost very easily; this condition is routinely seen in deep-sea specimens of *Prionospio* (Maciolek, 1981a). From *Prionospio* sp. 81 samples three pairs of branchiae were recognized: branchiae short and cirriform on chaetigers 2 and 3, while pinnate on chaetiger 4. In *Prionospio* sp. 613 four pairs of branchiae were observed: pinnate and long on chaetigers 2 and 5; short and cirriform on chaetigers 3 and 4. Differences in both starting position of hooded hooks and sabre chaetae, presence of dorsal crests, methyl green staining pattern and prostomium shape also were observed between them. The prostomium shape even showed high variability of forms between samples of the same species. Blake (1996b) considered many of the characters before mentioned to separate *Prionospio* species as well as the length of the branchiae and starting position of dorsal crests. This author, from a key to species of *Prionospio* from California, considered the presence of lateral

interparapodial pouches to separate two groups of *Prionospio* species. Maciolek (1985) in her revision of the genus concluded that the most common arrangement of pinnate/apinnate branchiae is pairs 1 and 4 pinnate, pairs 2 and 3 apinnate. Other species with three apinnate pairs followed by a pinnate pair are further distinguished by having a reduced number of apical teeth on the hooded hooks. Other characters have been considered to separate *Prionospio* species. Sigvaldadóttir & Desbruyères (2003) described *Prionospio unilamellata* from Mid-Atlantic Ridge hydrothermal vent which differs in the form of anterior notopodial lamellae. Worsaae (2003) found differences in the palps morphology (transverse cilia) in two species of *Prionospio*. This character may be useful in elucidating the phylogeny of the *Prionospio*-complex genera. There have been no deep-sea *Prionospio* species described in the last few years, so comparison with PAP specimens are needed to establish that *Prionospio* sp. 81 and *Prionospio* sp. 613 are truly new to science. The only one deep-sea species described in the last years has been *Prionospio* sp. PIP#2 from Central Pacific Abyssal Plain found at 4076 m depth (Altamira, *unpublished*). This species is distinguished from PAP *Prionospio* by the arrangement and appearance of branchiae, dorsal lamellae shape and starting position of hooded hooks. However, this species would belong to subgenus *Minuspio* because the presence of three apinnate pairs of branchiae.

3.2.3.7. *Prionospio* (*Aquilaspio)*

The subgenus *Aquilaspio* (Foster, 1971) has branchiae from chaetiger 2, 2-4 pairs all of them pinnate. Blake & Kudenov (1978), Mackie (1984), Maciolek (1985), Imajima (1990) and Blake (1996b) considered *Aquilaspio* as subgenus within *Prionospio*, while Sigvaldadóttir (1998) synonymized the genus with *Prionospio*. *Aquilaspio* sp. 1 differed from other PAP *Prionospio*-complex species in the presence of two pinnate pairs of branchiae on chaetigers 2 and 3, staining pattern, starting position and number of hooded hooks per ramus, starting position of sabre chaetae and the anterior notopodial lamellae size and shape. The most remarkably taxonomic character recorded in this species was the strong methyl green staining pattern observed in the anterior end. Transversal bands across the body on ventral region; prostomium, peristomium and lamellae edges were intensely stained observing a clear bottle-shape of the prostomium.

3.2.3.8. *Aurospio*

The genus *Aurospio* was erected by Maciolek in 1981. The new species of the deep-sea spionid with cirriform branchiae appearing on the third chaetiger, *Aurospio dibranchiata*, was described from the north and south Atlantic, and with close affinities to the genus *Prionospio*. Taxonomic and morphological characters of several PAP specimens examined belonging to genus *Aurospio* were compared with the description made by Maciolek, concluding that the species found for current study was *Aurospio dibranchiata*. Some minor differences in both prostomium shape, lamellae shape and capillaries length were observed between Maciolek's description and PAP samples, however they were not enough to change the species definition. *A. dibranchiata* was the second most abundant spionid species found in the PAP sediments. PAP *Aurospio dibranchiata* specimens mainly differ from *Aurospio* sp. nov. (Mincks *et al*. submitted) from Antarctica, depths between 550 m to 4817 m, in that the latter species has only one branchial pair starting from chaetiger 3. Further differences include the more elongated prostomium, the more pointed notopodial lamellae on chaetiger 3 and the starting position of the hooded hooks. PAP *A. dibranchiata* specimens differ from *Prionospio banyulensis,* which is now referred to *Aurospio* (Sigvaldadóttir, 1998) in that the latter species has three branchial pairs starting on chaetiger 3. Further observations from PAP *Aurospio* samples could derive on discovering of new morphotypes of *Aurospio* in northeast Atlantic sediments.

CHAPTER 4

4. FAMILY LEVEL RESPONSE

4.1. Results

4.1.1. Mean abundance

4.1.1.1. Long-term change in mean number of individuals

A total of 3245 polychaetes were recorded during the eight cruises carried out between August 1989 and September 1998. Mean abundance varied with cruise; greatest density was recorded during March 1998 with 144±121 specimens per 0.25 m^2. The lowest mean abundance was 53 specimens per 0.25 m^2 from a single sample taken in August 1989. From September 1996 there was a significant increase in the mean abundance of polychaetes which persisted until March 1998. Mean abundance was slightly lower in September 1998 (Fig. 4.1.). Analysis of Variance (ANOVA) made on total number of individuals (log transformed data) of cruises with 3 or more samples demonstrated significant differences between different cruises, i.e. with time (P<0.001). A non-parametric Kruskal-Wallis test also demonstrated significant differences between the abundance from different cruises (P<0.01). Post-hoc test indicated that differences were produced by the high value recorded in July 1997 about the low values observed in May 1991 and April 1994 cruises. The other stations did not show any difference. The differences observed between cruises were still more evident between periods. A *t*-Test carried out on same data demonstrated there were significant changes between pre-'*Amperima* Event' samples (1989-1994) and *'Amperima* Event' samples (1996-1998), P<0.001, indicating that abundances recorded during pre-'*Amperima* Event' period were significantly lower than during the '*Amperima* Event'. A non-parametric Mann-Whitney U test also demonstrated that there were significant differences.

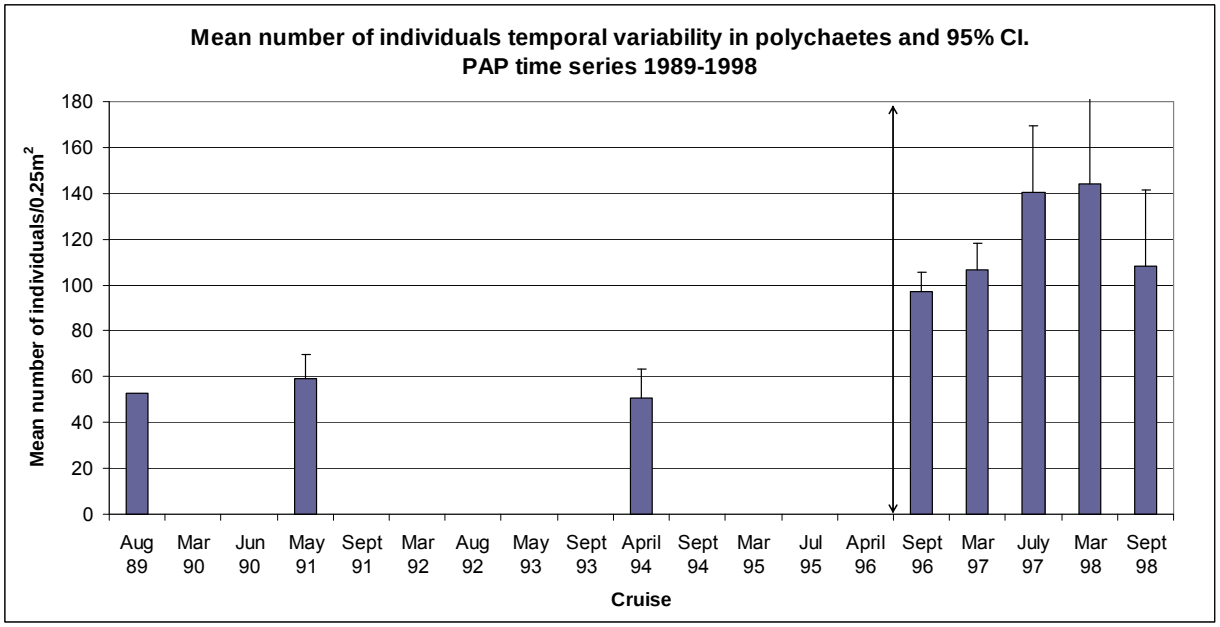


Figure 4.1. Temporal variability in mean abundance of polychaetes. The double headed arrow marks the start of the '*Amperima* Event'.

4.1.2. Sediment layers

4.1.2.1. Long-term change in mean number of individuals

Only results from the 0-1 cm, 1-3 cm and 3-5 cm sediment layers were analyzed because these were the only layers which were processed using 300 *μ*m sieve size. In total 2924 individuals were recorded in three layers. 1558 specimens (53% of polychaetes total number) were recorded from the 0 to 1 cm layer. 930 specimens were recorded from 1 to 3 cm (32% total numbers of individuals), while 436 specimens were recorded in the 3 to 5 cm sediment layer. They represented 15 % of total number of individuals (Fig. 1 Appendix 1). These data do not include any information from samples collected in September 1998 because no information was provided on the layers from which they were obtained.

In the upper layer (0 to 1 cm), the mean abundance varied between 27 and 81±106.1 individuals per 0.25 m^2 in August 1989 and May 1991, and March 1998 respectively. In the second layer (1 to 3 cm), mean abundance varied between 15±4.1 individuals per 0.25 m^2 in April 1994 and 52±7.9 individuals per 0.25 m^2 in July 1997. In the third layer (3-5 cm) abundance decreased one order of magnitude compared with the upper layers. Mean abundance varied between 5.5±0.6 and 23.2±14.7 individuals per 0.25 m^2, during April 1994 and July 1997 respectively. The highest abundances were

concentrated in the shallowest sediment layers (0 to 1 and 1 to 3 cm) and only a small proportion of polychaetes (15%) occurred in the 3-5 cm layer (Fig. 1 Appendix 1).

Mean abundance increased in the uppermost two layers, with the highest value occurring during July 1997 and March 1998. This trend was not as obvious in the 3 to 5 cm sediment layer, although there may have been a seasonal signal. Later September 1996 and July 1997 the abundance always decreased in March 1997 and March 1998 (Fig. 4.2.)

Analysis of variance and non-parametric Kruskal-Wallis tests showed significant differences in 0-1 cm sediment layer (P<0.05 and P<0.01) and 1-3 cm sediment layer (P<0.001 and P<0.005). No significant changes were recorded in 3-5 cm layer (P>0.05, ANOVA; P<0.02, Kruskal-Wallis). Post-hoc test indicated that differences in 0-1 cm sediment layer were due to particularly low densities during May 1991 and April 1994 cruises, while in 1-3 cm sediment layer differences were due to low density in April 1994 in comparison with the higher density in July 1997 cruise. *T*-tests made for 'pre-*Amperima*' and '*Amperima* Event' samples showed significant differences for each sediment layers analyzed with time. The upper sediment layer 0-1cm and the 1-3 cm sediment layer recorded highly significant changes between periods (P<0.001). The 3-5 cm sediment layer also recorded statistically significant differences (P<0.05) between sampling periods.

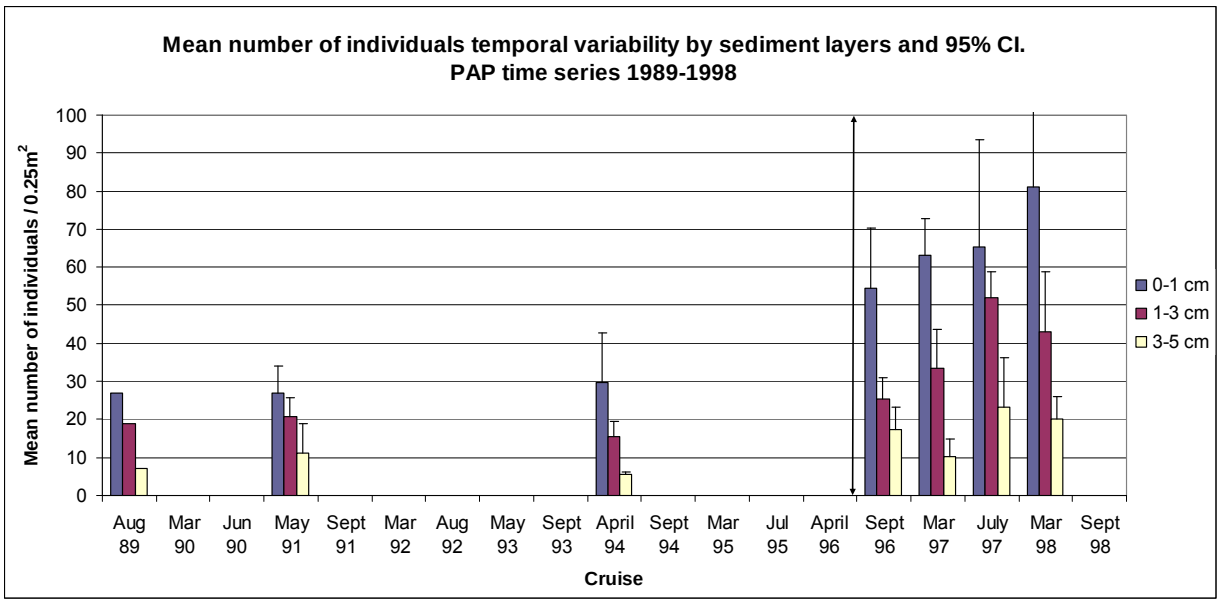


Figure 4.2. Temporal variability in mean abundance of polychaetes by sediment layers. The double headed arrow marks the start of the '*Amperima* Event'.

4.1.3. Family richness and faunal composition

4.1.3.1. Long-term change in number of families

A total of 42 polychaetes families were recorded from the eight cruises between August 1989 and September 1998. The lowest mean number of families (9) was recorded in April 1994, while the greatest mean number occurred in March 1998 with 20 families. Mean number of families per cruise was 15.7±5. The temporal pattern showed that the '*Amperima* Event' cruises recorded a geater mean number of families, almost two times, than the 'pre-*Amperima* Event' cruises (Fig. 4.3.).

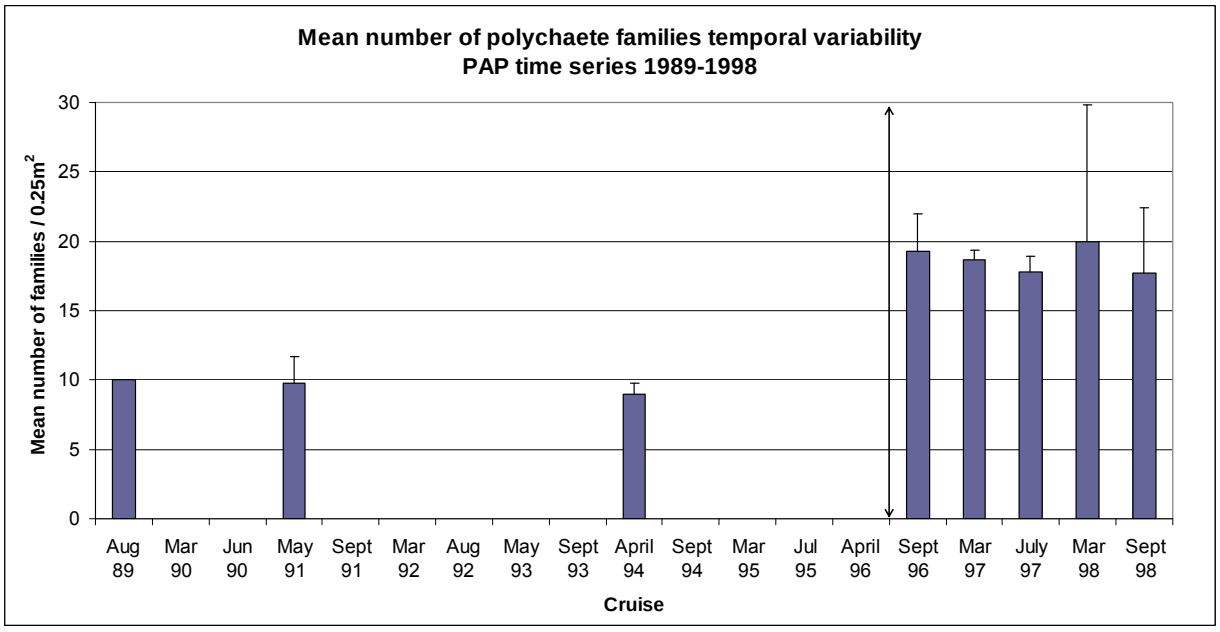


Figure 4.3. Temporal variability in mean number of polychaete families. The double headed arrow marks the start of the '*Amperima* Event'.

In terms of faunal composition, only the Ampharetidae, Chrysopetalidae, Cirratulidae, Paraonidae, Pilargidae, Sabellidae and Spionidae families were present during all cruises. These families, with the exception of the Chrysopetalidae and Paraonidae, increased significantly in abundance from the '*Amperima* Event'. The Chrysopetalidae did not changed in time, while the Paraonidae slightly decreased in time. The Hesionidae, Scalibregmatidae and Sphaerodoridae families showed the same pattern as the Paraonidae. However, they were not recorded in all cruises. The Capitellidae, Flabelligeridae, Glyceridae, Lumbrineridae, Opheliidae, Phyllodocidae, Sigalionidae and Syllidae families were not recorded in all pre-'*Amperima* Event' cruises but their abundance increased significantly during the post '*Amperima* Event' cruises. The Acrocirridae, Dorvilleidae, Goniadidae, Maldanidae, Owenidae and Polynoidae

families only occurred during the '*Amperima* Event' cruises with greatest abundances principally from September 1996 to July 1997. They were not recorded in the 'pre-*Amperima*' period. The Cossuridae, Fauveliopsidae and Orbiniidae showed a similar pattern to the previous group but were present during the pre-'*Amperima*' period albeit in small numbers. Finally, the rest of polychaete families did not show a defined pattern, recording low abundance and presence in 'pre-*Amperima*' and '*Amperima* Event' periods.

Analysis of variance and non-parametric Kruskal-Wallis tests showed significant differences in mean number of families between cruises (P<0.005). Post-hoc test showed that differences lay between the highest values sampled during '*Amperima* Event' cruises and the lowest values for pre-'*Amperima* Event' cruises. August 1989, May 1991 and April 1994 cruises showed significantly lower mean number of polychaete families than following cruises. Students *t*-test and Mann-Whitney U analysis also showed significant differences in number of families between 'pre-*Amperima*' and '*Amperima* Event' periods (P<0.005). Multivariate analysis, such as NMDS, showed a clear distinction between 'pre-*Amperima*' and '*Amperima* Event' periods: stress: 0.19, model occurred 6 times. The separation of the two data sets was evident in the corresponding ordination (Fig. 4.4. and 4.5.). The 'pre-*Amperima*' and '*Amperima* Event' samples did not overlap in ordination space. ANOSIM non-parametric test indicated that this separation was significant (R=0.82 p=0). Changes in polychaete faunal composition between periods were supported by the NMDS ordination. The similarity within groups and dissimilarity among groups were defined by the polychaete families that recorded the greatest number of individuals. Similarity index was used and data was not transformed. The SIMPER analysis showed the families with the greatest contribution were Cirratulidae (18.4) and Spionidae (15.5). The analyses indicate that the dissimilarity is most influenced by changes in abundance rather than changes in family composition. They also were supported with Cluster analyses (Bray Curtis Similarity Index) for abundance of polychaete families and sampled (Fig. 4.6. and 4.7.).

NMDS

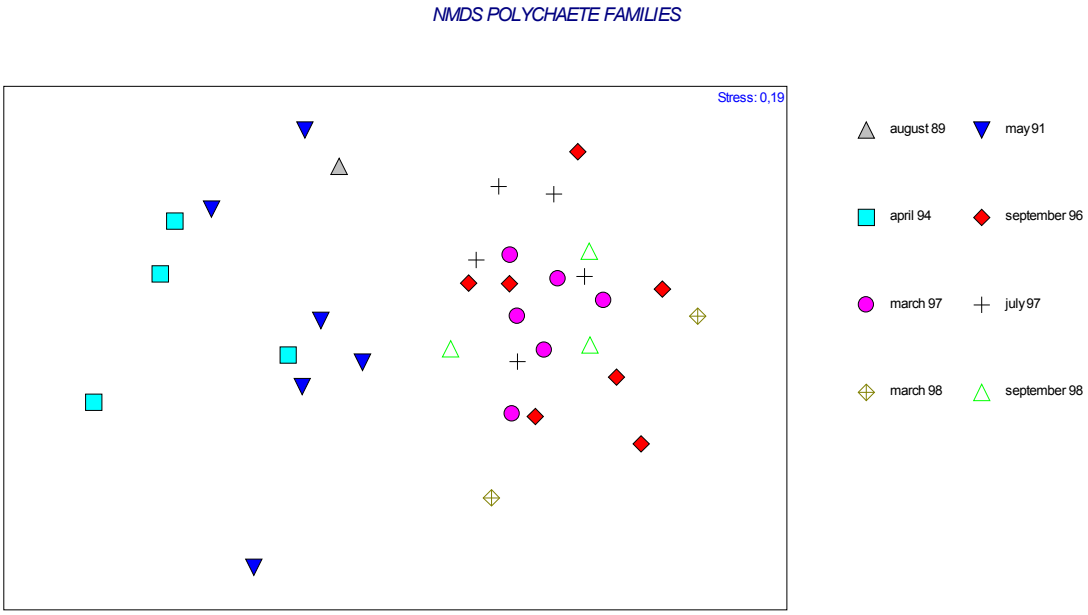


Figure 4.4. Non-metric multidimensional scaling ordination of family total abundance. Samples are coded by date cruises.

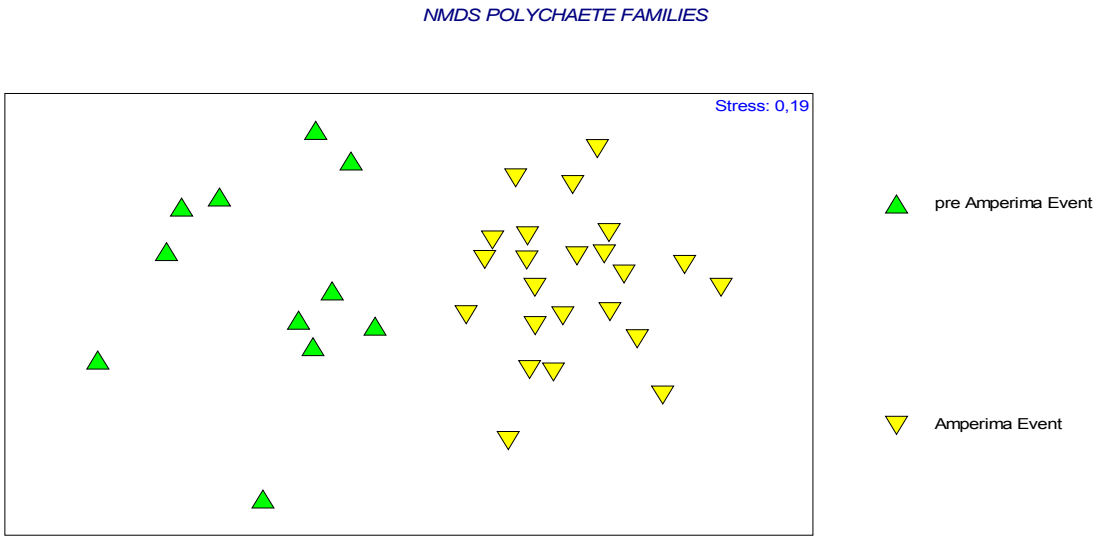


Figure 4.5. Non-metric multidimensional scaling ordination of family total abundance. Samples are coded by pre-'*Amperima* Event' (green triangles) and '*Amperima* Event' (yellow triangles).

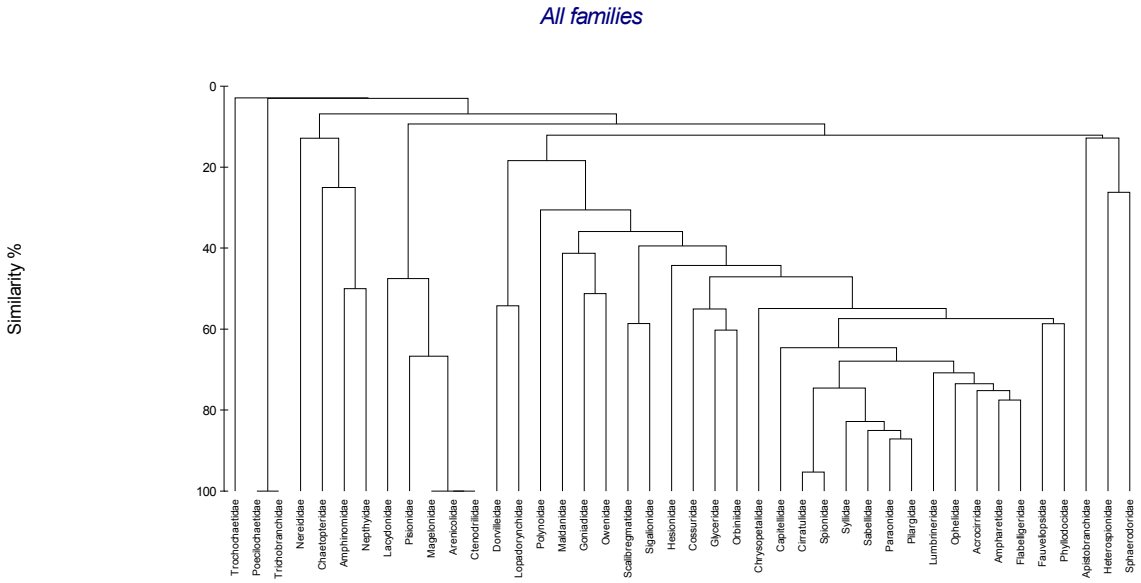


Figure 4.6. Dendrogram produced by Cluster analyses of the abundance of polychaete families on the Porcupine Abyssal Plain.

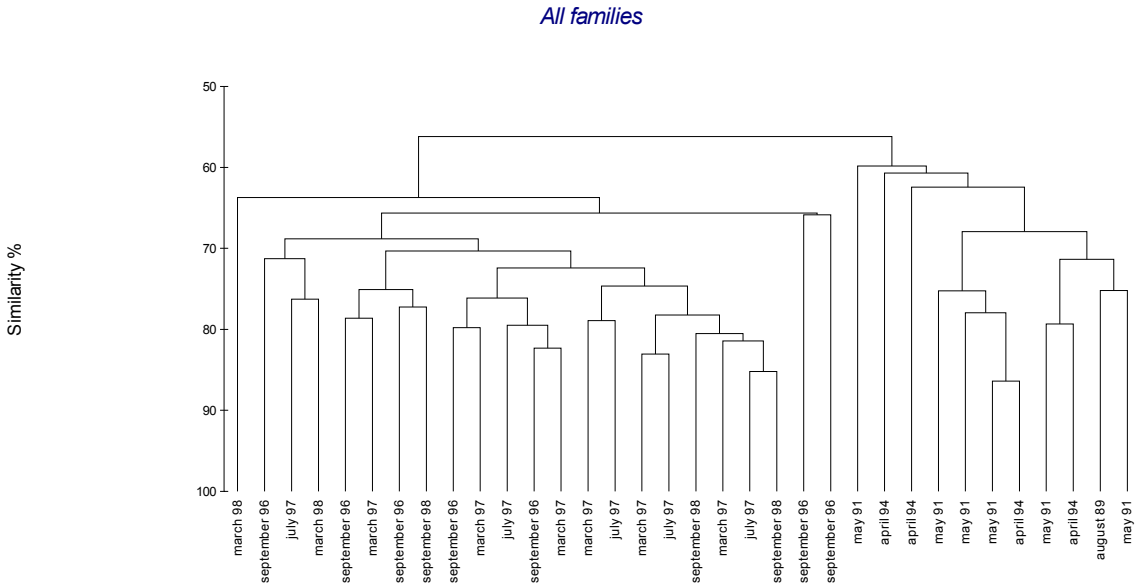


Figure 4.7. Dendrogram produced by Cluster analyses of the abundance (samples) on the Porcupine Abyssal Plain.

4.1.4. Main families

4.1.4.1. Long-term change in mean number of individuals

The study of the main families considered the four most abundant families: Cirratulidae, Spionidae, Opheliidae and Paraonidae.

The family Cirratulidae was the most abundant (28.8%). Mean abundance varied between 15 individuals per 0.25 m^2 in August 1989 and 37.6±8.7 individuals per 0.25 m^2 in July 1997. Spionidae accounted for 23%. Mean abundance varied between 12.3±5.1 individuals per 0.25 m^2 in April 1994 and 39.2±7.3 individuals per 0.25 m^2 during July 1997. Paraonidae and Opheliidae accounted for 7.3% and 5.7% respectively. Mean abundance of Paraonidae varied between 5±2.6 and 11 individuals per 0.25 m^2 in September 1998 and August 1989 respectively, while in the Opheliidae the mean abundance varied between 0 and 16.5±19.1 individuals per 0.25 m^2 in May 1991 and March 1998, respectively. Temporal fluctuations were observed in four families. Three families showed increasing temporal trends with maximum values during July 1997 (Cirratulidae and Spionidae) and March 1998 (Opheliidae). By contrast the Paraonidae did not show a positive temporal trend. Temporal changes in this family were minor between cruises, so effectively fairly consistent abundance was observed with time. The maximum value was recorded at the beginning of the study (August 1989), which is not very representative because there was only one sample (Fig. 4.8.).

Analysis of Variance conducted on log(x+1) transformed sample abundance data showed significant differences with time for the Cirratulidae, Spionidae and Opheliidae families ($P<0.05$). These differences were not observed for the Paraonidae ($P>0.5$). Non-parametric Kruskal-Wallis tests confirmed the observed changes. Post hoc tests showed for Cirratulidae that the highest values in July 1997 cruise differed significantly from May 1991 cruise; in Spionidae the highest value of July 1997 differed significantly from May 1991 and April 1994 cruises, while in Opheliidae the highest values in July 1997 and September 1998 differed significantly from May 1991, April 1994 even September 1996. *T*-tests carried out between 'pre-*Amperima*' and '*Amperima* Event' samples showed highly significant differences in Opheliidae ($P<0.001$), while significant changes were evident in Cirratulidae ($P<0.001$) and Spionidae ($P<0.05$). These differences were not observed in Paraonidae ($P>0.1$). Non-parametric Mann-Whitney U tests also showed similar results.

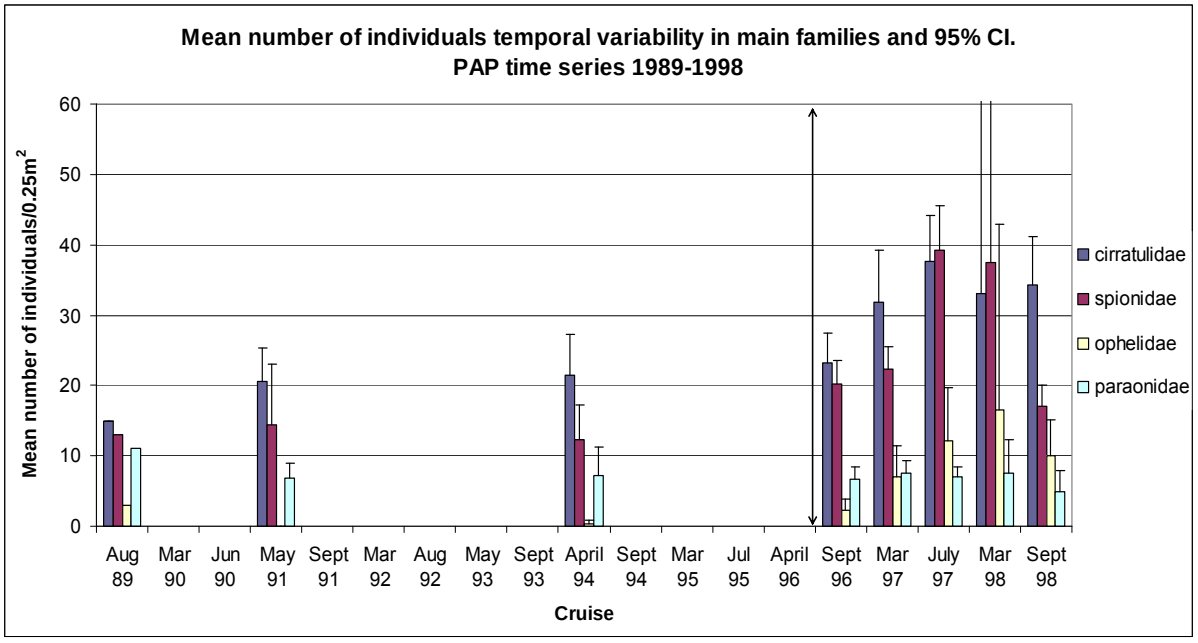


Figure 4.8. Temporal variability in mean abundance of main polychaete families. The double headed arrow marks the start of the '*Amperima* Event'.

4.1.5. Trophic groups

4.1.5.1. Long-term change in mean number of individuals

Surface deposit-feeders, predators and burrowers (subsurface deposit-feeders) were the main trophic groups recorded in this research. Although some families include more than one feeding strategy, species in this study have been assigned to the most common or dominant trophic group (Table 5, Appendix 1).

Surface deposit-feeder polychaetes were the dominant trophic group (73.3%), owing to the high abundance of the families Cirratulidae and Spionidae. Burrowers had 13.5% of individuals, with opheliid and capitellid polychaete abundances recorded during the '*Amperima* Event', making up a large proportion of this total. Predators (omnivore and carnivore polychaetes considered as one group) accounted for 13.2%, with the Syllidae and Pilargidae families as the most abundant within this group (Fig. 2 Appendix 1). However, the number of predator families often was greater than the number of surface deposit-feeder and burrower families during cruises.

Although there was a clear dominance in the number of individuals of surface deposit-feeder polychaetes in all cruises, the number of polychaete families belong to predator and burrower trophic groups was greater than those belong to surface deposit-feeder group in all cruises with the exception of August 1989.

Temporal variability was evident in all trophic groups. A pattern of increasing abundance was evident. Maximum values (mean number of individuals) were recorded in March 1998 for predators (23±18) and burrowers (28±25). In surface deposit-feeders the peak was observed in July 1997 with 104.8±24 individuals per 0.25 m^2. Minimum values were recorded during August 1989 and April 1994 for surface deposit-feeders (45 and 45±14, respectively), burrowers (1.3±1) and predators (4.5±2) (Fig. 4.9.).

Analysis of variance showed highly significant differences between cruises for all trophic groups (P<0.001). Non-parametric Kruskal-Wallis tests made for all trophic groups also showed significant differences. Post-hoc testing indicated for surface deposit feeders that differences occurred between the cruise July 1997 with the highest mean abundance and the cruises with the lowest abundance -May 1991 and April 1994; in predators these differences are mainly due to a low abundance during April 1994, while in burrowers differences are due to a low abundance in April 1994 and the highest abundance in September 1998. *T*-tests made on 'pre-*Amperima*' and '*Amperima* Event' samples showed significant differences between both periods for burrowers, surface deposit-feeders and predators (P<0.001). The Mann-Whitney U tests confirmed these differences (P<0.005).

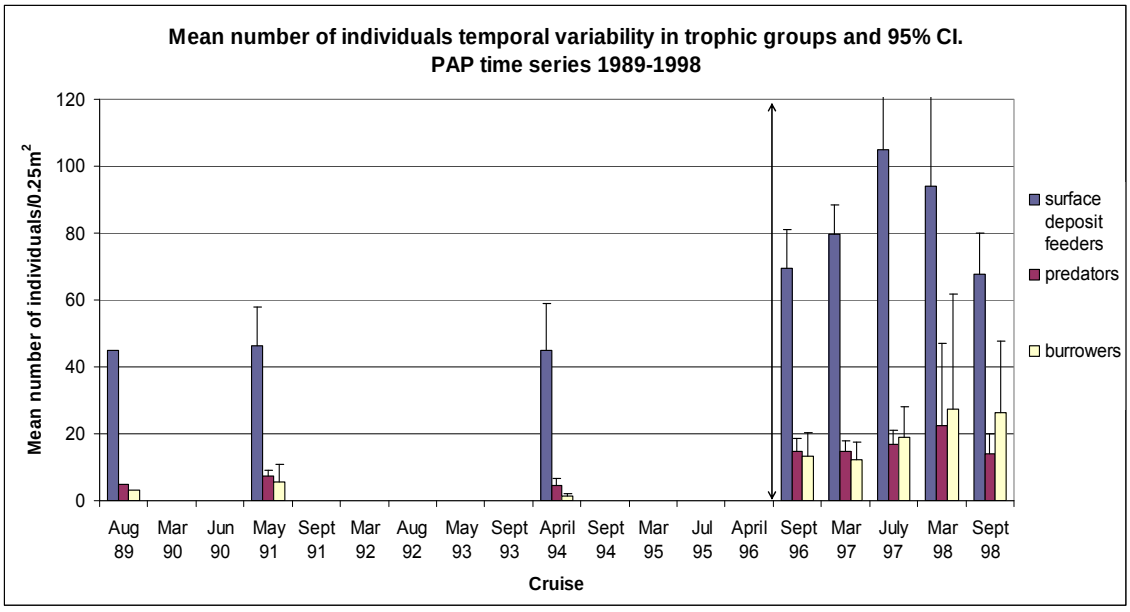


Figure 4.9. Temporal variability in mean abundance of polychaete trophic groups. The double headed arrow marks the start of the '*Amperima* Event'.

4.2. Discussion

4.2.1. Abundance

Table 4.1. compares the abundance of abyssal polychaetes recorded in other studies with previous and current data from the Porcupine Abyssal Plain (PAP). The PAP data generated by this study are split into two periods, one before the '*Amperima* Event' (1989-1994) and the other during the event (1996-1998). While the mean abundance of polychaetes recorded in this study before the '*Amperima* Event' was lower that reported by Glover *et al.,* (2001) and Galéron *et al.,* (2001) for the same site, this was because these other studies included data on all sieve sizes and not just the 300-500 *μ*m fraction as in this study. The increase in abundance from September 1996 with peaks in July 1997 and March 1998 was also recorded for opheliid polychaetes (Vanreusel *et al.,* 2001) and macrofaunal polychaetes (Galéron *et al*., 2001). Polychaete abundance showed a significant increase during the '*Amperima* Event'. The magnitude of the increase in abundance was, however, less than observed for the holothurian megafauna species, being just two to three times the abundance of 'pre-*Amperima'* samples, compared with a difference of two orders of magnitude for the megafauna. Polychaete abundances before the '*Amperima* Event' were comparable to abundances determined for other abyssal localities lying under eutrophic and seasonally productive surface waters including Antarctic deep-sea sites. However, polychaete abundances at the PAP during the '*Amperima* Event' were much greater than any other abyssal region measured previously highlighting that there has been a response to a changing nutrient regime. Only the abundance recorded at shallower depths in the Rockall Trough, Permanent Station was slightly greater (Paterson & Lambshead, 1995), (Table 4.1.).

Polychaetes were not the only infaunal group to show an increase in abundance during the '*Amperima* Event'. Galéron *et al*., 2001 noted that infaunal bivalves also increased during this period. Within the meiofauna, Gooday *et al*., (submitted) reported a similar response in protozoan meiofauna, while Kalageropoulou *et al*., (submitted) observed increases in abundance with metazoan harpacticoid copepods and nematodes. However these increases in the infaunal elements were again considerably less that observed for the megafauna (Billett *et al.*, 2001 and *submitted*; Bett *et al*., 2001). These results suggest that whatever the process was which resulted in the increase in abundance of the megafauna, also affected the infauna. The

reduced magnitude of the response of the infauna in comparison with the surface-dwelling megafauna points to some mediation or amelioration of the effects. In other words while there may have been an increase in nutrient flux to the ocean floor a smaller proportion of it appears to have been available to the infauna.

The '*Amperima* Event' may be a response to increases in the flux of organic matter to the seabed. Water column fluxes in total organic carbon and total nitrogen (Kiriakoulakis *et al.,* 2001), phytopigments (Fabiano *et al.,* 2001) and biogenic silica (Lampitt *et al.*, 2001) were greatest during the July 1997 and September 1998 periods. In sediments, bacterial carbon production (Eardly *et al.,* 2001), phytopigments (Witbaard *et al.,* 2001), lipid compounds (Galéron *et al.,* 2001) and biogenic silica components (Ragueneau *et al*., 2001) were greatest in September 1996 (Table 4.2.). These values coincide with first increase in abundance in the polychaete assemblages.

Unfortunately, there were no sediment trap data available just prior to the '*Amperima* Event' (Lampitt *et al*., 2001), but subsequent work has shown that fluxes at this site can change by an order magnitude from year to year (Lampitt *et al.,* 2008). It is possible, therefore, that enhanced organic matter inputs to the deep-sea floor have caused changes in the meiofaunal, macrofaunal and megafaunal size fractions of the benthic community (Billett et *al*., 2001; Gooday, 2002). For other sites, especially at lower continental slope and abyssal plain depths, the most successful taxa appear to be those that can adapt quickly to changing ecological parameters, such as a seasonal or otherwise oscillating food supply (Hilbig & Blake, 2006). In areas where the nutritional pulses can be very high, deep-burrowing polychaetes such as maldanids may be more successful than the deposit feeders that live close to the sediment water interface, such as spionids and paraonids (Witte, 2000: Arabian Sea). The area off the Farallon Islands in the north Pacific is characterized by high phytodetrital flux that can be related to very slow grazing of zooplankton on phytoplankton in the oxygen minimum zone (Blake *et al*., 1992). These environmental conditions may allow the cossurids to reach much farther down off the Farallones than off Cape Hatteras on the U.S. Atlantic slope. The depth zonation of the infauna is most likely a result of the predominantly downslope transport of sediments (Hilbig & Blake, 2006).

Different nutrient regimes with areas experiencing seasonal input of phytodetritus, aseasonal nutrient input and no phytodetritus input may determine differences in body

size of abyssal polychaetes (Paterson *et al*., 2006). A linear relationship has been revealed between the food supply of abyssal regions and the abundance of macrofauna (Cosson *et al*., 1997). Mesotrophic conditions of the overlying water body resulting in a highly food limited benthic community at the PAP could be a possible explanation when low macrofauna densities are observed (Iken *et al.,* 2001).

In considering the response of polychaete assemblages, two potential factors must be considered. First, an increase in the nutrient flux to the abyssal ocean floor and, second the effect of the massive increase in surface-feeding megafauna, particularly holothurians, which may have acted as competitors for this influx. Holothurians are not considered to be potential consumers of the polychaete infauna because many species appear to be quite restricted in the size of particles they can select (Hudson *et al.,* 2003). However, ophiuroids may predate upon small juveniles and settling larvae and ophiuroids increased significantly in abundance during the '*Amperima* Event' (Bett *et al*., 2001). In addition, the megafauna are likely to repackage the phytodetritus into faecal material with a reduced and potentially different particle size structure, which may influence the availability of organic material to certain polychaete species. Holothurian assimilation efficiencies are estimated to be around 30% when phytodetritus is present, but is reduced when it is absent (Ginger *et al.,* 2001; Sibuet, 1988). Therefore, a high level of organic matter may be available still to infauna given the assimilation efficiencies of the holothurians, but the organic matter will be of reduced 'quality' (e.g. key sterols will have been removed or reduced).

Two further aspects of megafaunal feeding need to be considered. First, the assimilation rates of ophiuroids are unknown. They are likely to be less selective and may be reducing available nutrients. Second, the rapidity with which mobile deposit-feeding megafauna rework the sediment surface may have an effect. So, while an assimilation efficiency of 30% would perhaps appear to leave a considerable amount of organic matter for infauna, it will have been processed a number of times and so the 'quality' of the organic matter will be much reduced. It is not possible, from the data available, to distinguish between the effects of organic matter input and faunal interactions in terms of species and family changes. However, both should have resulted in an increase in abundance and, in the case of nutrients being repackaged, a change in the composition of the polychaete fauna. Although changes in abundance were observed with time, a longer and more regular dataset would have improved the resolution and given greater confidence to the trends evident.

4.2.2. Abundance and vertical distribution within the sediment.

Polychaetes were most abundant in the top 1 cm layer of sediment confirming the PAP results of Galéron *et al.,* (2001) (62% of the polychaetes occurred in the top 1 cm layer of the sediment). This is similar to results reported from PAP and Madeira Abyssal Plain (MAP) (Glover *et al.,* 2002). By contrast results from the oligotrophic EUMELI site on the Cap Verde Abyssal Plain showed that the 0-1 cm layer contained >80% of the fauna and in the Pacific the top 0-1 cm layer contained 75% of the polychaete fauna (Paterson *et al*., 1998).

In this study temporal changes in abundance were significant in the 0-1 and 1-3 cm sediment layers, but not in deeper layers within the sediment. Downward and upward movements within the sediment were not evident in mean abundance following the '*Amperima* Event'. The overall proportions of polychaete abundance in the upper layers did not change substantially with time. So there was no evidence that the increase in abundance in the 0-1 and 1-3 cm layers was the result of migration from lower layers in the sediment. Rather there was a general increase in abundance within the 0-3 cm layers. There was a small variation in the proportion of individuals among the 0-1 and 1-3 cm sediment layers in July 1997. An increase in abundance of 1-3 cm sediment layer could indicate some downward movements from the top 0-1 cm sediment layer at that time. A similar situation was also observed in May 1991. This suggests that whatever the processes affecting polychaete abundance were operating primarily at the sediment surface and rather than within the sediment column as a whole.

In July 1997, Witbaard *et al*., (2000) found higher quantities of phytopigments in the 1-2 cm layer than in the 0-1cm layer of sediment. At the same time, nematodes, bivalves and tanaidaceans increased significantly in abundance in the 1-3 cm layer. It is likely these taxa moved deeper into the sediment because there was more food available in the subsurface layers (Galéron *et al.*, 2001). The nature of the response in polychaetes indicates that they were affected by the same process (es) which drove the '*Amperima* Event'. Similarly, temporal variations in the vertical distribution of the polychaete abundance within sediment layers in the Porcupine Abyssal Plain could support the hypothesis that the vertical distribution of macrofauna within the sediment is more likely to be related to total organic matter input rather than to seasonality in food supply, because food supply could be low and seasonal.

Glover (2000) has suggested that food availability might be related closely to patterns in polychaete body size and vertical distribution. This author demonstrated for Pacific sites that polychaete families were larger in the deeper layers of the sediment in areas where food supply was lower. In addition, species which were abundant throughout the sediment showed reduced size at the sediment surface. These observations might relate to metabolic efficiency because it would be more efficient to have larger body size in food poor deeper layers. In addition, greater bioturbation of the top layer of sediment, as a result of the increase in the populations of large deposit-feeders, may also have contributed to a downward movement of infaunal organisms seeking to avoid physical disturbances of their habitat (Thiel, 1983; Lambshead *et al.,* 1995). Feeding and locomotory activities by holothurians will have contributed to some churning up of the phytodetritus with the sediment (Bett *et al.*, 2001). Phytodetrital material may also have been subducted and mixed into subsurface layers of sediment by burrowers such as echiurans and sipunculids, which are found in deeper sediment layers (Bett & Rice, 1993). Macrofaunal polychaetes will also have contributed to the bioturbation of organic matter from surficial sediments into deeper sediments.

Similar patterns of vertical distribution and dominance were reported for harpacticoid copepods (>63%), bivalves (45-80%), tanaidaceans (~40%) and isopods (>60%) at the PAP (Galéron *et al.,* 2001). The abundances of all macrofauna including polychaetes declined significantly with depth in the sediment. This may be related to concentrations of phytopigments (Witbaard *et al.,* 2001) and lipids, where temporal changes in the vertical distributions of fatty acids, alkanes, alcohols and sterols were observed (Galéron *et al*., 2001) in surficial sediment at the PAP (Table 4.2.).

Studies point out the great importance of the uppermost sediment layers for macrofauna organisms (Aberle & Witte, 2003; Flach & Heip, 1996; Witte, 2000). Studies on macrofauna made by means of *in situ* pulse-chase experiments using ^{13}C-labelled phytodetritus at the PAP site (Aberle & Witte, 2003) have also studied the vertical distribution of communities within the sediment. These authors showed that 40% of all macrofauna were found in the uppermost cm of the sediment (0 to 1 cm). 80% of all crustaceans and polychaetes were found in the upper 5 cm of the sediment. 52% of the macrofauna were polychaetes. This study concurs with the current results where 85% of all polychaetes concentrated within the upper 3 cm of the sediment, therefore deeper layers showed much lower individuals number. However, the number of polychaetes was quite homogeneous between the surface and below 5 cm, which is

significantly different from the results presented here. Witte (2000) recorded a different vertical distribution in the Arabian Sea; >75% of polychaete abundance at three of four stations occurred below the upper sediment layer. At these three stations, polychaetes represented a constant 20% of total macrofauna. Moreover more than 50% of polychaete biomass was found below 5 cm. These stations experienced a highly seasonal food input and a greater number of deep-dwelling macrofauna populations. The sediment surface layer was numerically dominated by Crustacea, while that the deeper layers were numerically dominated by polychaetes. Species occur at different levels in the sediment corresponding to their morphologies and expected feeding strategies. Disturbance during coring or sample extraction might cause the animals to retract into their burrows and so occur deeper in the sediment (Blake, 1994).

Artificial disturbances of the seafloor such as from deep-sea mining could lead to changes in the biota-sediment processes. Possible effects are expected to involve biochemical changes resulting in biotic responses (Raghukumar *et al*., 2001) and direct impacts on organisms (Shirayama, 1999; Ingole *et al.*, 1999). Results post-disturbance obtained by Ingole *et al.,* (2001) in the deep Central Indian Basin indicated 63% reduction in the numerical count in the top 0-2 cm layer, high aggregation of polychaetes in deeper (2-5 cm and 5-10 cm) sediment layers and composition changes in the upper layers. The vertical distribution of organisms in the sediment column may be important for the transport of organic material into deeper layers. Some polychaetes collect food from surface sediments and store it beneath the surface layer out the reach of competitors (Jumars *et al*., 1990).

4.2.3. Faunal composition and family richness

Variability in faunal composition, diversity and family richness are evident in benthic deep-sea communities on a variety of spatial scales relating to water depth (Paterson & Lambshead, 1995; Hilbig & Blake, 2006), regional biogeography (Rex *et al*., 1993), and patchy distributions (Rice & Lambshead, 1994; Rice *et al*., 1994; Thurston *et al*., 1994). Changes in the faunal composition may also be caused by disturbance (Grassle & Morse-Porteous, 1987; Gage, 2003; Ingole *et al*., 2001, 2005), physical effects (Grassle & Maciolek, 1992), eurybathy (Arntz *et al*., 1994; Hilbig *et al*., 2006) and the physiological properties of the animals (Somero, 1990; Brey *et al*., 1996). Seasonal or interannual variability has been recorded only for a few deep-sea taxa

and at a limited number of localities (Billett *et al*., 2001). In the current study, an increase in the mean number of polychaete families was recorded from September 1996 which coincided with the '*Amperima* Event'. The increase was not directly correlated to sampling effort and so appeared to be the result of a general increase in the overall abundance of polychaetes. At the PAP 23 families were recorded prior to the '*Amperima* Event' and 43 families during the Event. The dominant families did not change during the study. Rather there was an increase of polychaetes generally. The overall increase in abundance led to a corresponding immigration at PAP of individuals from a greater range of families.

The families which showed the greatest response were those that dominated deep-sea polychaete infaunal assemblages even before the '*Amperima* Event' –the Spionidae, Cirratulidae and Paraonidae (Hilbig & Blake, 2006). Blake *et al.*, (2007) argue that the consistency of dominance by the Cirratulidae and Paraonidae in deep-sea sediments is a consistent global biodiversity pattern in bathyal and abyssal benthic infaunal communities. These families were described by Smith & Hessler (1987) as opportunists (species that wait for optimal conditions and respond quickly to high levels of organic enrichment to accumulate energy). Nowell *et al*., (1984) showed that some spionids change their feeding type from suspension to deposit-feeding when their food supply changed.

In this present study the Cirratulidae and Spionidae showed significant temporal variation, increasing in abundance at the time of the '*Amperima* Event'. In terms of abundance the Cirratulidae dominated the polychaete families in six of eight cruises. The Spionidae was only more abundant than Cirratulidae in July 1997 and March 1998 (Fig. 4.8.). By contrast the Paraonidae did not show any changes in total abundance. Both the Cirratulidae and Spionidae are thought to be surface deposit feeders, sessile or mobile without showing any burrowing activity (Fauchald & Jumars, 1979). Aberle & Witte (2003) using tracer uptake studies indicated that cirratulids play a key function in reworking freshly deposited material at the PAP. Downward transport of particles within sediment has been documented in cirratulids polychaetes (Shull & Yasuda, 2001). This kind of mechanism may play an important role in the burial and diagenesis of organic carbon (Blair *et al*., 1996) and in the organizing of soft-bottom benthic communities (Levin *et al.*, 1997).

One other family which notably increased in abundance was the Opheliidae. Opheliids are burrowers and appear to be non-selective subsurface deposit feeders. Studies

made by Hermans (1978) in shallow-water opheliids and Renaud *et al.*, (1999) on opheliids on the shelf off North Carolina suggested that opheliids are opportunistic polychaetes. Vanreusel *et al*., (2001) found a large influx of post-larval individuals of an unknown opheliid species at the PAP during the '*Amperima* Event' and suggested that this influx was an opportunistic response to an increase in nutrient flux. Therefore, these life history traits may explain the temporal variability noted for the PAP opheliids polychaetes.

The rise in overall abundance and the response of opportunistic polychaetes points to a quantitative change in organic matter input. In experiments using a variety of different substrates, early colonisers are usually from different families to those observed here, in particular members of the Dorvilleidae (Grassle & Morse-Porteous, 1987; Snelgrove *et al*., 1994). In the PAP samples there was not a major shift in the dominant families, although there was a large increase in the abundance of opheliids.

The families Acrocirridae, Cossuridae, Fauveliopsidae, Glyceridae, Goniadidae, Lumbrineridae, Maldanidae, Nepthyidae, Orbiniidae, Owenidae, Polynoidae, Scalibregmatidae and Sigalionidae showed major changes in the time series. The majority of these families were not present during pre-'*Amperima Event'* period and only appeared in September 1996 and in later cruises. Many of these families are predators and subsurface deposit-feeders. These families probably took advantage of greater food supply and the general increase in macrofauna and meiofauna. There was no evidence that any polychaete families present prior to the '*Amperima Event*' period disappeared after September 1996. Many of these families increased in abundance with time.

The causes generating changes and temporal variability in composition and richness of polychaete assemblages at family and species level are very diverse. The observed temporal variability could be explained by methodological reasons such as recorded samples number in each cruise, polychaetes total abundance or due to biogeochemical processes such as the increase of food supply to the seabed through the phytodetritus deposition from water column. Seasonal and interannual variations in the total organic matter flux to the seabed are likely to be the main reasons. Similar conclusions have been obtained by other authors (Cosson-Sarradin *et al*., 1998; Levin & Gage, 1998; Paterson *et al*., 1998; Witte, 2000; Glover *et al*., 2002). Multivariate analyses indicate that temporal changes in PAP polychaete assemblages during the study period (1989-1998) were mainly due to variations in abundance rather than

changes in faunal composition at the family level. Studies at species level will allow a more detailed appraisal as to whether specific taxa within families showed temporal variability.

4.2.4. Trophic groups

The nature of the polychaete response in the upper sediment layers suggests that trophic groups which exploit organic matter at the sediment surface should be favoured. At PAP, surface deposit-feeders polychaetes were the most important trophic group representing 73.3% of polychaete fauna and were concentrated principally in the sediment surface. Temporal variability in the abundance of surface deposit feeders showed an increasing pattern from September 1996. The enrichment of the sediment surface due to a summer pulse of organic supply to the seabed from September 1996 would explain this pattern (Lampitt *et al.,* 2001, 2008; Witbaard *et al.,* 2000). The peak in abundance of this trend was recorded in July 1997 coinciding with the higher abundance of holothurians. In addition, sediment trap data recorded a significant phytodetrital pulse in June-July 1997 (Lampitt *et al*., 2001). Later between March and September 1998 a decreasing in abundance was detected. A decrease of organic matter input to the seabed due to high consumption by megafauna could explain this decreasing pattern in surface deposit feeders. Although an increase in the abundance of burrowing polychaetes was recorded at the same time, there is no evidence that this increase may be related to surface deposit feeders decrease.

Coverage of the seabed with phytodetrital material might be associated with a shift in the composition of the benthic megafauna (Lampitt *et al*., 2001, Bett *et al*., 2001). Burrowing (subsurface deposit feeders) polychaetes represented 13.5% of total abundance. The observed increase in abundance was due partly to high number of opheliid polychaetes (juveniles) recorded from March 1997. Iken *et al.,* (2001) observed that in most surface deposit feeders and subsurface deposit feeders the proportion of phytodetritus in the guts was high in September 1996 and low in March and June 1997. Predators (carnivores and omnivores together) were a minor component of the polychaete community (13.2%), despite the number of predator families was higher than the number of deposit feeder families in several cruises. This trophic group showed a slight increasing temporal trend with time.

Deposit feeders are one of the most important consumers of the organic material flux, playing an important role in the removal, recycling and repackaging of nutrients,

especially organic carbon (Boudreau, 1994; Jumars & Self, 1986). Qualitative changes in the organic flux might regulate essential dietary compounds required by benthic populations (Ginger *et al.*, 2001) and changes in the composition of phytodetritus may drive changes in the composition of the benthic communities (Wigham *et al.*, 2003). However there were no obvious changes in the trophic composition of the polychaete trophic groups to support this. Once again it appears there was a general up-lift in surface deposit and burrowing deposit feeders, with the exception of the opportunistic occurrence of the opheliid deposit feeders. Temporal variability also showed changes in the abundances and the proportions of burrowing and predator polychaetes. From July 1997 the mean abundance of burrowers was greater than predators. This persisted until September 1998. At the same time surface deposit feeders decreased in abundance. The overall increase in abundance of some burrowing families such as Opheliidae, Capitellidae and Orbiniidae, and the overall increase of predator families such as Pilargidae, Syllidae and Chrysopetalidae in 1998 would explain the observed temporal changes between these two trophic groups. Densities recorded in opheliids by Vanreusel *et al*., (2001) for the same period of time would support these conclusions. In September 1996, the opheliids were too small to be retained in the >250 µm macrofaunal residues. From September 1996 to March 1997, they had grown (Vanreusel *et al.*, 2001) and so they appeared in macrofaunal samples in March 1997. This explains the observed increase in the density of burrowing polychaetes during this period. Other studies and experiments have demonstrated the opportunistic characteristics of Capitellidae (Snelgrove *et al*., 1994, 1996; Grassle & Morse-Porteous, 1987) and Opheliidae (Renaud *et al.*, 1999).

Sedimented POM is the major food source for the benthic community at PAP. On the seafloor, POM is mixed with the surficial sediment layer by benthic storms, tidal movements and bioturbation (Smith, 1992) and these become the principal food source for all surface deposit feeders. Depending on the amount of sedimented matter, sediment reworking by bioturbation and feeding activity of larger animals incorporates only a relatively small fraction of this material into deeper sediments, making it available to subsurface deposit feeders (Lisitsyn & Vinogradov, 1982). Predators may rely on either benthic food sources or, depending on their mobility, on abyssopelagic prey in the benthic boundary layer. Suspension feeders, mainly cnidarians, have a broad trophic spectrum through feeding on resuspended material as well as capturing pelagic prey. Their feeding strategies are assumed to be closely coupled to the seasonal input of POM. Because of

the restricted availability of fresh POM, deep-sea suspension feeders compete directly with the deposit feeders (surface and subsurface) intensifying the trophic competition. Most benthic cnidarians are considered to be opportunistic omnivores, containing high proportions of sediment and animal prey (mainly polychaetes and crustaceans) in their guts (Iken *et al.,* 2001). This could partially to explain the temporal variability observed by the polychaete deposit feeder trophic group. The conclusion is that there is strong competition for food in the abyssal benthic food-web, and therefore there is development of different feeding strategies. Highly specialized surface deposit-feeding organisms may compete with other feeding specialists, e.g. predators, suspension feeders and subsurface deposit feeders (Aberle & Witte, 2003).

Deposit feeders are the dominant trophic group in the deep sea (Dauer, 1983; Jumars *et al.,* 1990). Studies made by different authors have recorded similar trophic groups composition and dominance. Glover *et al.,* (2001) found deposit-feeders dominance in PAP, EUMELI oligotrophic site (EOS) and MAP sites. Only at Tagus Abyssal Plain (TAP) did they find burrowers dominated (opheliid polychaetes). Similar results were found by Aberle & Witte (2003) during May and June 2000 from PAP; Paterson & Lambshead (1995) in the Rockall Trough; Hilbig & Blake (2006) at 2400-3000 m depth in the northeast Pacific; Glover *et al*., (2002) in the central Equatorial Pacific site (EqPac), Hawaii Ocean Time Series site (HOT) and Clarion-Clipperton fracture zone sites (CCFZ), central Pacific; Blake & Narayanaswamy (2004) in Antarctic waters between 1110-6319 m depth; Pérez-Mendoza *et al*., (2003) from Gulf of Mexico and at the Climax II, ECHO 1, Preservational Reserve Area (PRA) and Deep Ocean Mining Environmental Study sites (Domes) in the Pacific Ocean (Hessler & Jumars, 1974; Paterson *et al.,* 1998). Different trophic group dominance was recorded by Hilbig *et al.*, (2006) in Antarctic waters for deep-sea stations between 1000 to 2500 m depth. Here, carnivores and surface deposit feeders were the most abundant. Temporal variability in PAP trophic groups did not show significant changes in terms of dominant group composition, as observed in the Atlantic, Pacific and Southern Oceans. This is irrespective of organic enrichment conditions and nutrients regime and could show that the functional structure is very similar and dominated by surface deposit feeding polychaetes.

Site	Depth (m)	Sieve fraction size	No. of box cores	Abundance per 0.25m^2 (SE)	No of species	Reference
JGOFS Equatorial Pacific Study 0º N	4300	300*µm*	3	84 (27.9)	73	Glover *et al*. 2002
JGOFS Equatorial Pacific Study 2º N	4400	300*µm*	4	60 (6.4)	82	Glover *et al*. 2002
JGOFS Equatorial Pacific Study 5º N	4400	300*µm*	3	80 (19.1)	76	Glover *et al*. 2002
JGOFS Equatorial Pacific Study 9º N	4900	300*µm*	3	13 (2.3)	23	Glover *et al*. 2002
Hawaii Ocean Time Series 23º N	4800	300*µm*	4	9 (1.7)	14	Glover *et al*. 2002
Deep Ocean Mining Environmental Study A	5100	300*µm*	47	16 (0.8)	104	Glover *et al*. 2002 Paterson *et al*. 1998
Preservation Reserve Area	4800	300*µm*	16	65 (16.8)	100	Glover *et al*. 2002
ECHO 1	4500	300*µm*	15	42 (5.5)	113	Glover *et al*. 2002
CLIMAX II	5010	300*µm*	10	15.6 (1.7)	46	Hessler & Jumars, 1974
Cape Verde Abyssal Plain	4580-4647	250*µm*	5	37.8	39	Cosson-Sarradin *et al*. 1998
Cape Verde Abyssal Plain	4600	1mm, 500*µm* and 250*µm*	8	35.8 (10)	75	Glover *et al*. 2001 Sibuet *et al*. 1993
Tagus Abyssal Plain	5035	300*µm*	Vegematic SBC (6) (0.09m^2)	64.5 (25.8)	57	Glover *et al*. 2001 Gage *et al*. 1995
Madeira Abyssal Plain	4900	1mm, 500*µm*, 300*µm* and 250*µm*	5	17.5 (7.8)	29	Glover *et al*. 2001 Paterson *et al*. 1994
Porcupine Abyssal Plain	4800	1mm, 500, 300 and 250*µm*	5	81 (20.25)	101	Glover *et al*. 2001 Paterson *et al*. 1994
Porcupine Abyssal Plain	4850	1mm, 500*µm*, 300*µm* and 250*µm*	23	252.00	No data	Galéron *et al*. 2001
Weddell Sea & Drake Passage	2400	500*µm*, 300*µm*	36	62.5	13	Hilbig, 2001
Antarctic Peninsula	1000-2500	500*µm*	42	107,5	80	Hilbig *et al*. 2006
Deep Weddell & Scotia seas	1138-5194	500*µm*, 300*µm*	16	33.6	90	Hilbig, 2004
Farallones, California	3100	300*µm*	3	~55 (at 3100m)	~40	Hilbig & Blake, 2006
CCZ (Central Pacific) site C	5050	300*µm*	6	20.8	36	Smith *et al*. 2008
Sigsbee Basin, Gulf of Mexico	3760	250 *µm*	1	49.3	10	Pérez-Mendoza *et al*. 2003
Rockall Trough, Northeast Atlantic	2875	420 *µm*	5	240(9)	40	Paterson & Lambshead, 1995
Arabian Sea (SAST station)	4424	500*µm*	21	~24	No data	Witte, 2000
Central Indian Basin	5300	No data	6	16 (39.2)	No data	Ingole *et al*. 2001
Venezuela Basin	3500-5050	300*µm*		36		Richardson & Young, 1987
This study (1989-1994)	4850	300*µm*	11	54.4 (4.4)	23 (family)	Soto, this paper
This study (1996-1998)	4850	300*µm*	23	195.7 (7.8)	43 (family)	Soto, this paper

Table 4.1. Site, depth, sieve fraction size, number of USNEL spade box core samples, mean individuals number per 0.25m^2, number of species and references.

Parameter	Value/range
Nutrient regime	Seasonal phytoplankton bloom
Sedimentation accumulation rate[a]	3.5 cm ky^{-1}
Sediment median grain size[a]	8-8.6 μm (calcareous ooze)
TOC surface sediment[b]	0.35% - 0.45%
C:N ratio[c] C:N ratio [d]	4.8 – 7.8 7.6±1.6 (1989-2004)
POC flux [d]	10.6 mgC m^{-2} d^{-1} (average)
Carbohydrates and proteins (0-5mm)[e] TCHO TPRT	 1194 (July 97)-2210 (March 98) μg g^{-1} 614 (July 97)-1422 (Sept 96) μg g^{-1}
Sedimentary profiles (0cm, Sept 96-July 97)[b] O_2 NO_3	 ~290 μmol/l ~23 μmol/l
Biogenic silica (0-2.5cm)[f] Silicic acid (0-2.5cm) [f] Biogenic silica fluxes [d]	372.8 (spring 97)-412.5 (autumm 96) μmol Si cm^{-2} 0.354 (spring 98)-0.474 (summer 97) μmol Si cm^{-2} 19.6±18 mg SiO_2 $m^{-2}d^{-1}$ (April-October,1998-2005)
Ca CO_3 (%) (0-10mm)[g] Ca CO_3 (average flux)[d]	69.08-74.54 53±42 mg m^{-2} d^{-1} (April-October,1998-2005)
Al (%) (0-10mm) [g]	1.29-1.83
Fe (%) (0-10mm) [g]	0.97-1.24
Mn (mg/Kg) [g]	447-499
Mean Bacterial abundance (0-1cm)[h]	18.2 (Sept 98) – 34.8 (March 94) $x10^7 cm^3$
Integrated amino acids incorporation[h] Thymidine Leucine	 1.6 (March 98)- 4.4 (Sept 96) nmoles tracer m^2 day^{-1} 16 (March 97)- 25 (March 98) nmoles tracer m^2 day^{-1}
Carbon production (1994)[h] Carbon production (1996-1998)	0.4-2.5 ngC cm^{-3} day^{-1} 2-12 ngC cm^{-3} day^{-1}
Lipids compounds (mean) 0-1cm[i] Fatty acids Alkanes Alcohols Sterols	 496.9 (Oct 97)-2719.3 (Sept 96) ng/g 113.4 (Oct 97)-946.9 (Sept 96) ng/g 33.5 (March 98)-529 (Sept 96) ng/g 344.6 (March 98)- 1580.3 (March 97) ng/g
Seabed phytodetritus cover[j] Phytodetritus (%) Total megabenthos tracking	 ~3 (April 97-Feb 99)- ~96 (April 94-Jul 94) ~10 (May 91-April 92, April 94-Jul 94)- ~360 (March 98-Feb 99) $cm^2/m^2/d$
Nucleic-acids (mean values)[k] RNA DNA	 3.5 (March 97)- 13 (Sept 96) ųg g^{-1} 21 (March 97)- 29 (July 97) ųg g^{-1}
Amino acid fluxes AA (average)[l] Hexosamine fluxes HA(average) Glycine composition (average) Alanine composition (average) Threonine composition (average)	2.5±3.5 mg m^2 d^{-1} (1998-2004) 0.18±0.27 mg m^2 d^{-1} (1998-2004) 16.4±3.5 mol% (1998-2004) 16.1±1.4 mol% (1998-2004) 9.5±1 mol% (1998-2004)
Phytopigments[k] Chlorophyll-a Phaephorbides	 3 (Sept 98, 1cm)-15 (Sept 96, 1mm) ng cm^{-3} 40 (March 97, 1cm)- 180 (Jul 97, 1mm) ng cm^{-3}

Table 4.2. Main biogeochemical characteristics measured at PAP

[a]Rice *et al*., (1991); [b] Rabouille *et al*.,(2001); [c] Santos *et al*., (1994); [d] Lampitt *et al*., (2008).
[e] Fabiano *et al*.,(2001), [f] Ragueneau *et al.,* (2001), [g] Varnavas *et al.,* (2001), [h] Eardly *et al*., (2001), [i] Galéron *et al*., (2001), [j] Bett *et al*., (2001), [k] Witbaard *et al*., (2001), [l] Salter *et al.,* (2008).

CHAPTER 5

5. SPECIES LEVEL RESPONSE

5.1. Results

5.1.1. Cirratulidae

5.1.1.1. Changes in abundance of the dominant cirratulids species: *Aphelochaeta* sp. 13A, *Chaetozone* sp. 1, *Chaetozone* sp. 55A and *Aphelochaeta* sp. 647D

Table 5.1. shows temporal variability in the mean number of individuals of nineteen Cirratulidae species recorded between August 1989 and September 1998. Twelve species belonged to genus *Chaetozone*, six to *Aphelochaeta* and one to *Tharyx*. The species composition was dominated by *Chaetozone* and *Aphelochaeta* species, while temporal variability was evident with time.

Mean number of individuals increased by a factor of two, while species richness did not change between periods. The three most abundant species were *Aphelochaeta* sp. 13A, *Chaetozone* sp. 1 and *Chaetozone* sp. 55A. These three species made up 67% of the total numbers of cirratulid polychaetes.

The temporal variability observed for the most dominant species of Cirratulidae is shown in Figs. 5.1., 5.2., 5.3. and 5.4. Statistical analyses are presented in tables 12 and 13 (Appendix 2).

Species	Aug 89	May 91	April 94	Sept 96	March 97	July 97	March 98	Sept 98	Mean
***Aphelochaeta* sp 13A**	**5**	**7.7**	**7.0**	**7.0**	**7.8**	**9.4**	**9.0**	**9.3**	**7.9**
Chaetozone sp 685	0	0.7	0.3	0.9	0.8	0.8	0.0	0.0	0.6
***Chaetozone* sp 55A**	**3**	**5.7**	**0.3**	**3.4**	**4.8**	**4.2**	**3.5**	**3.0**	**3.8**
Aphelochaeta sp 643C	0	1.3	0.3	0.9	1.2	0.4	3.0	0.7	0.9
Chaetozone sp 657E	0	0.2	0.5	0.1	0.8	0.8	1.0	0.3	0.5
Chaetozone sp 605B	0	0.7	0.8	1.0	1.5	0.8	0.0	0.0	0.8
Aphelochaeta sp 7	0	0.0	0.3	0.4	0.5	0.4	0.0	0.3	0.3
***Chaetozone* sp 1**	**7**	**2.3**	**7.5**	**3.1**	**7.3**	**13.6**	**10.5**	**8.3**	**6.8**
Aphelochaeta sp 9	0	0.0	0.0	1.9	0.7	0.6	0.0	0.3	0.6
Chaetozone sp 10	0	0.0	0.5	0.4	1.5	0.2	0.0	1.3	0.6
Aphelochaeta sp 11	0	0.0	0.8	0.3	0.8	0.6	0.5	0.3	0.4
Chaetozone sp 12	0	0.0	0.8	0.4	0.0	0.2	0.0	0.3	0.2
***Aphelochaeta* sp 647D**	**0**	**0.2**	**2.3**	**2.6**	**2.8**	**4.2**	**5.5**	**9.0**	**3.1**
Tharyx sp 1	0	0.0	0.3	0.6	1.0	0.0	0.0	0.7	0.4
Chaetozone sp 2	0	0.3	0.3	0.3	0.2	1.4	0.0	0.3	0.4
Chaetozone sp 755I	0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chaetozone sp 698H	0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Chaetozone sp 625D	0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Chaetozone sp 677F	0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Total	**15**	**20.5**	**21.5**	**23.3**	**31.8**	**37.6**	**33.0**	**34.3**	**27.5**

Table 5.1. Mean number of individuals in Cirratulidae species recorded between August 1989 and September 1998. In bold the dominant species.

Aphelochaeta sp. 13A showed a weak increasing trend with time from a minimum of 5 individuals per 0.25 m^2 in August 1989 to a maximum of 9.4±3.8 individuals per 0.25 m^2 in July 1997, average abundance per cruise was 7.9±3.5 individuals per 0.25 m^2. No significant differences between cruises were detected (P>0.5). A comparison made between 'pre-*Amperima*' and '*Amperima* Event' samples also demonstrated that there was no significant differences between periods (P>0.1).

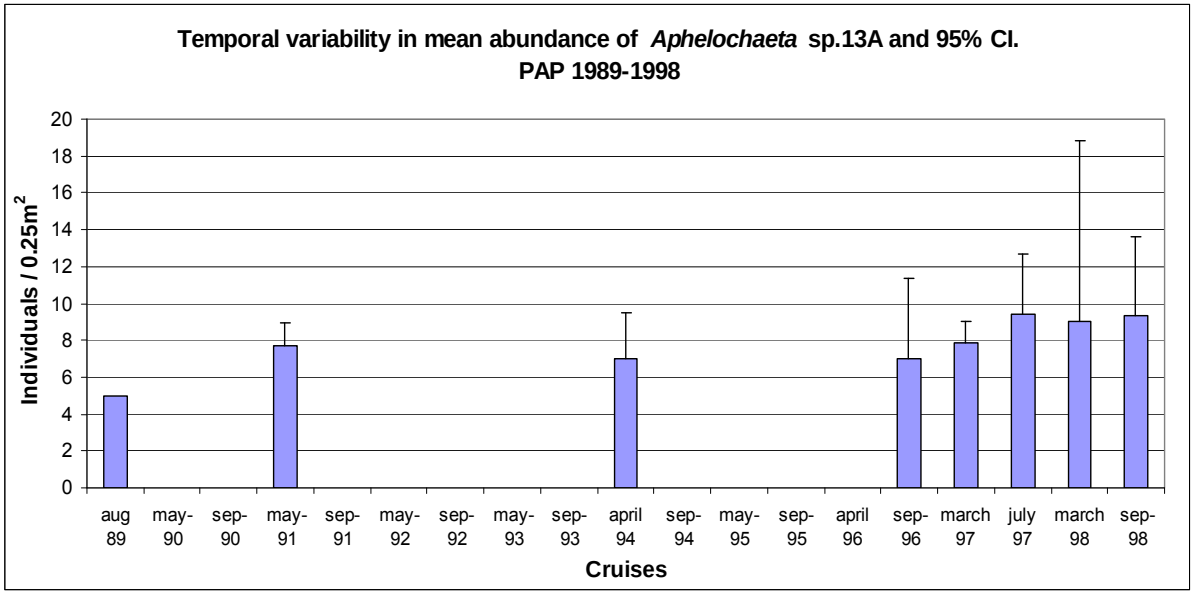


Figure 5.1. Mean number of individuals for *Aphelochaeta* sp.13A between 1989 and 1998. Mean and 95% confidence limit.

Chaetozone sp. 1 showed high variability between cruises without a clear temporal pattern and abundance values appeared to oscillate with time. The minimum value was 2.3 individuals per 0.25 m^2 (May 1991) and the maximum was 13.6 individuals per 0.25 m^2 (July 1997). Average abundance per cruise was 6.8±5 individuals per 0.25 m^2. Significant differences were observed between cruises (P<0.001). Post-hoc test showed that differences lay between the highest values sampled during July 1997 and low values during May 1991 and September 1996. However, differences in abundance were not detected between 'pre-*Amperima*' and '*Amperima* Event' periods (P>0.05).

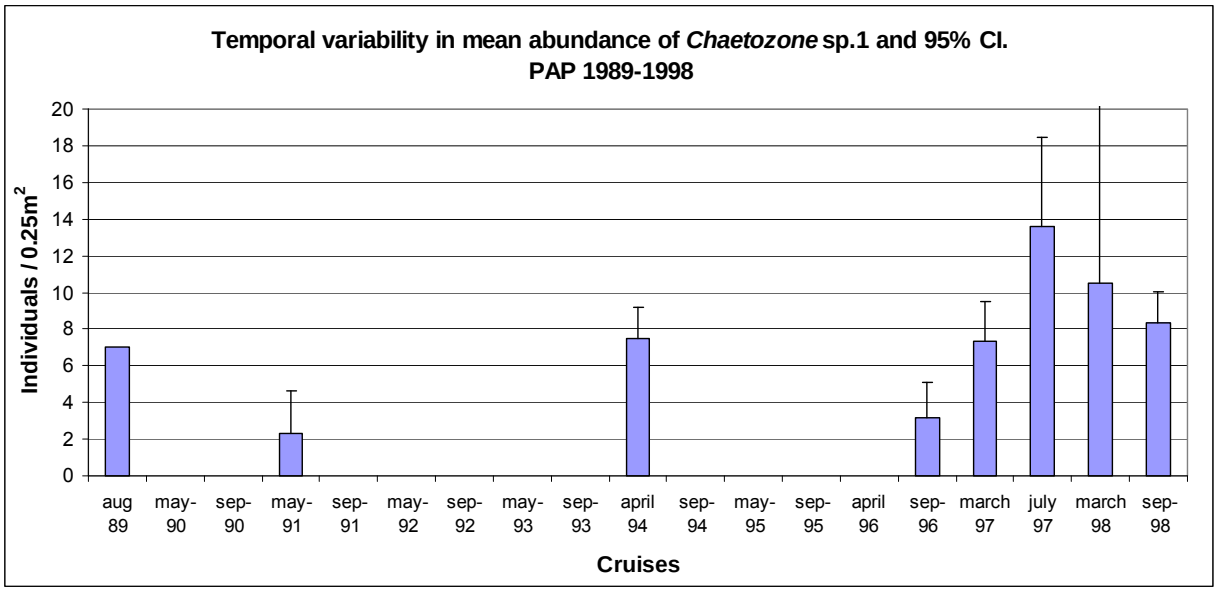


Figure 5.2. Mean number of individuals for *Chaetozone* sp. 1 between 1989 and 1998. Mean and 95% confidence limit.

Chaetozone sp. 55A did not show any pattern, with abundance great fluctuating on five first cruises (August 1989–March 1997) and then a decreasing pattern from March 1997 until September 1998. The peak was observed in May 1991 with 5.7 individuals per 0.25 m^2 and the lowest abundance was recorded in April 1994 with 0.3 individuals per 0.25 m^2. Average abundance per cruise was 3.8±3.1 individuals per 0.25 m^2. Analyses of variance showed significant differences between cruises (P<0.05). Post-hoc tests showed that the two highest values were recorded during the '*Amperima* Event', March 1997 and July 1997, and differed significantly from April 1994. However none of the values for abundance from the other cruises differed from one another significantly even

the values for May 1991 which were much lower than April 1994. There were no statistically significant differences in abundance between 'pre-*Amperima*' and '*Amperima* Event' periods (*P*>0.1).

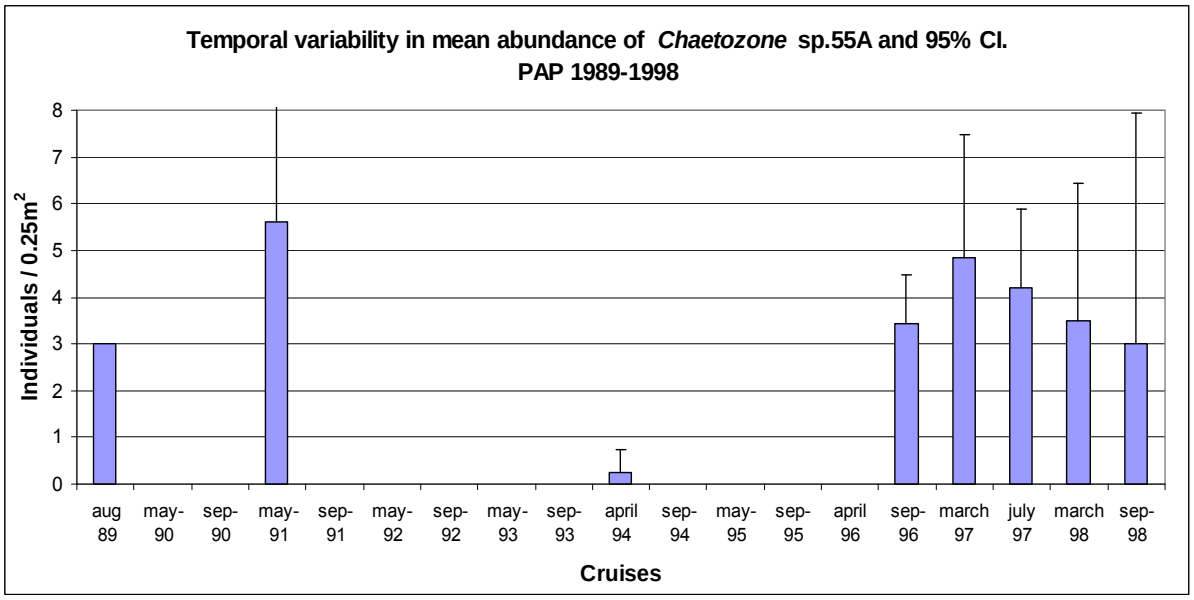


Figure 5.3. Mean number of individuals for *Chaetozone* sp. 55A between 1989 and 1998. Mean and 95% confidence limit.

The abundance of *Aphelochaeta* sp. 647D showed a clear increasing pattern through time. The species was not recorded in August 1989, while the greatest abundance was recorded in the last cruise in September 1998 with 9.0±4.6 individuals per 0.25 m^2. Average abundance per cruise was 3.1±3.5 individuals per 0.25 m^2.

Analyses of variance showed highly significant differences between cruises (*P*<0.005). Post-hoc testing indicated that this is due to differences between the most abundance cruises July 1997 and September 1998 and the cruise with the lowest abundance May 1991. *T*-tests indicated significant difference between the 'pre-*Amperima*' and '*Amperima* Event' samples (*P*<0.01) with the latter showing higher abundance than the 'pre-*Amperima*'.

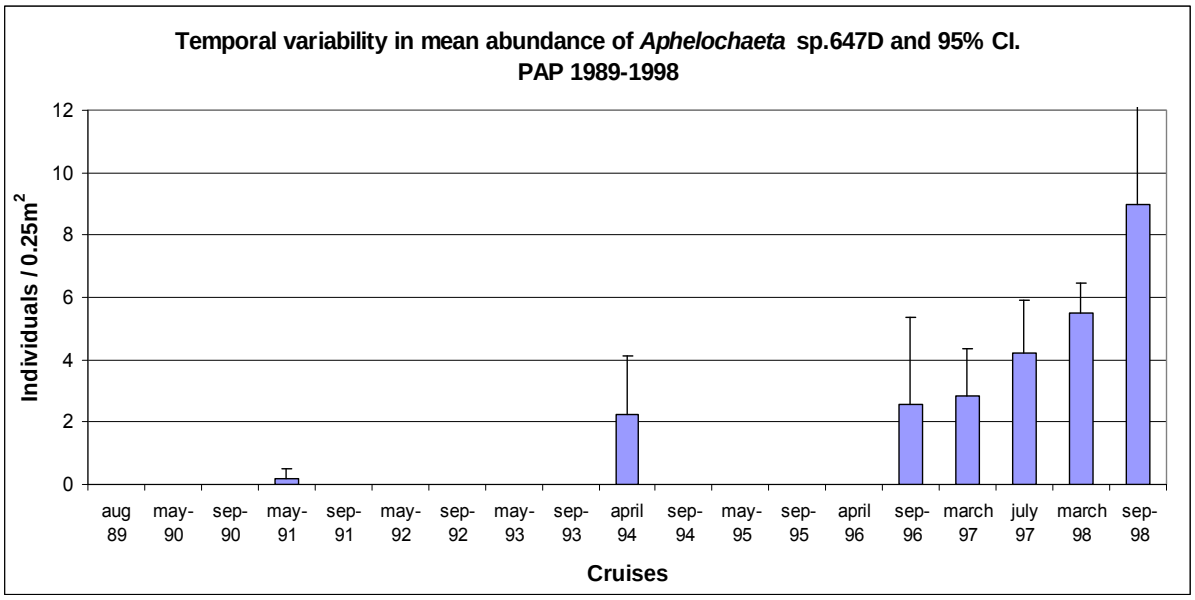
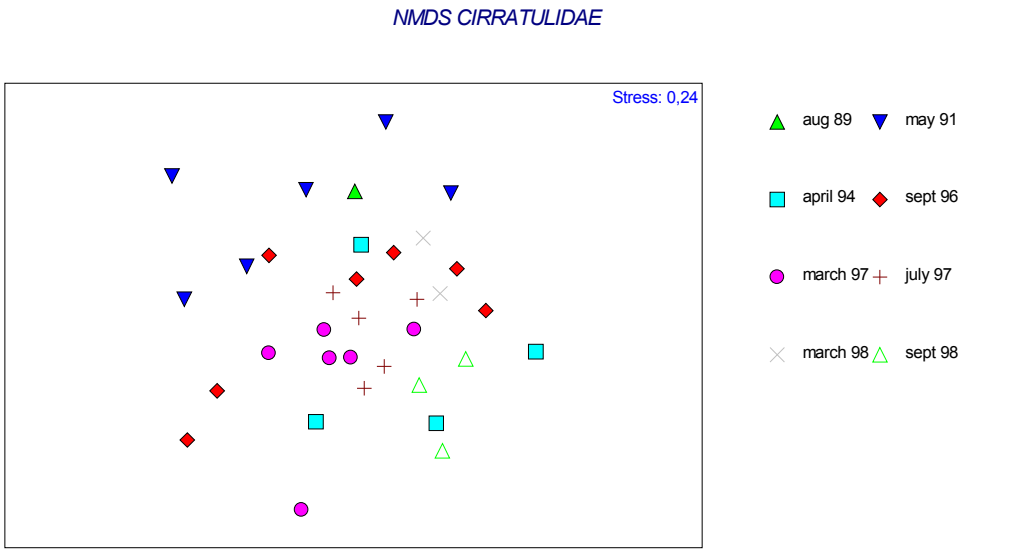


Figure 5.4. Mean number of individuals for *Aphelochaeta* sp. 647D between 1989 and 1998. Mean and 95% confidence limit.

5.1.1.2. Multivariate analyses

Multivariate analyses were carried out to determine whether changes between 'pre-*Amperima*' and '*Amperima* Event' periods are due to variations in abundance or species composition with time. They are shown in figure 5.5. Data was fourth root transformed and Bray Curtis Similarity Index was used. The non-metric multi-dimensional scaling ordination (NMDS) showed cruises coinciding with the '*Amperima* Event' do not overlap in ordination space with pre-'A*mperima* Event' cruises; stress: 0.24, model occurred 7 times. Samples from '*Amperima* Event' cruises are grouped together indicating there is a more consistent pattern. There is apparent division between pre-'*Amperima* Event' cruises indicating signals of variability and changes in species composition. Changes in faunal composition between periods were determined using the analyses of similarities procedure (ANOSIM) and similarities percentages of the different cruises (Table 14 Appendix 2). Analyses showed significant differences and the clear presence of two groups. Similarity and dissimilarity averages lay around 50%. Similar species composition defined these groups. These analyses would support the idea that changes between periods and cruises would be a consequence of variations in number of individuals rather than changes in the fauna composition.

NMDS



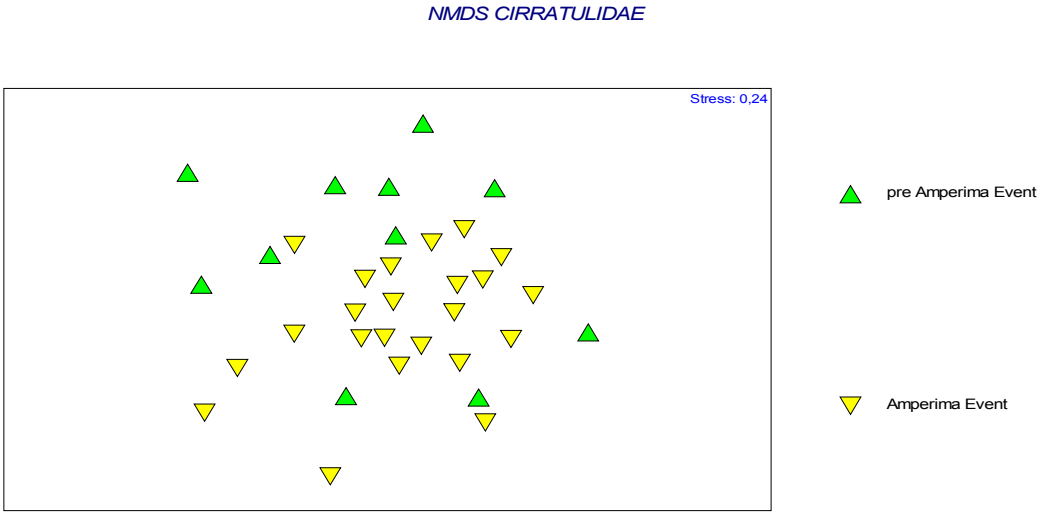


Figure 5.5. Non-metric multidimensional scaling in Cirratulidae (a) cruises (b) 'pre-*Amperima*' and '*Amperima* Event' periods.

5.1.2. Spionidae

5.1.2.1. Changes in abundance of the dominant spionids species: *Minuspio* sp. 4, *Aurospio dibranchiata*, *Prionospio* sp. 81 and *Prionospio* sp. 613

Table 5.2. shows temporal variability in the mean number of individuals of sixteen Spionidae species. Only one species, *Aurospio dibranchiata* Maciolek, 1981 belongs to taxa previously described. The rest of species are undescribed morphotypes and could be new. The diversity and species composition was characterized by great number of *Laonice* and *Prionospio* complex specimens. Four species belonged to *Laonice*, three to *Prionospio sensu stricto*, three to *Minuspio*, two to *Spiophanes*, one to *Aquilaspio* and *Aurospio* and two species were identified as Spionidae indeterminate.

The most abundant species were *Minuspio* sp. 4, *Aurospio dibranchiata* and *Prionospio* sp. 81. These species accounted for 59% of total number of spionids. High temporal variability was observed in these dominant species (Table 5.2.). Statistical analyses are shown in tables 15 and 16, Appendix 2.

Species	Aug 89	May 91	April 94	Sept 96	March 97	July 97	March 98	Sept 98	Mean
Laonice sp 1	0	0.0	0.3	0.6	0.3	0.8	2.0	0.0	0.4
A. dibranchiata	**6**	**4.8**	**4.0**	**4.3**	**0.8**	**6.8**	**10.5**	**3.7**	**4.5**
Minuspio sp 2	0	1.3	0.3	3.4	3.0	5.4	2.5	2.3	2.6
***Prionospio* sp 81**	**0**	**0.2**	**3.3**	**3.6**	**5.3**	**7.0**	**10.0**	**3.7**	**4.0**
Spiophanes sp 1	0	0.0	0.3	0.9	0.7	0.2	0.0	0.7	0.4
***Minuspio* sp 4**	**3**	**3.3**	**1.5**	**3.7**	**7.3**	**7.2**	**6.0**	**4.0**	**4.7**
Laonice sp 640	1	0.2	0.5	0.7	1.3	0.8	0.0	0.3	0.6
Minuspio sp 5	0	0.0	0.0	0.3	0.3	1.0	0.0	0.0	0.3
Spionidae indet. 1	0	0.0	0.3	0.3	0.3	0.2	0.5	1.7	0.4
Spiophanes sp 619	3	0.8	0.0	0.6	0.7	1.2	2.0	1.3	0.9
***Prionospio* sp 613**	**0**	**2.2**	**1.3**	**0.7**	**1.7**	**7.4**	**3.0**	**2.7**	**2.5**
Aquilaspio sp 1	0	0.0	0.3	0.6	0.3	1.0	1.0	0.0	0.4
Spionidae indet (6A)	0	1.0	0.5	0.7	0.2	0.2	0.0	0.0	0.4
Prionospio sp 679	0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Laonice juv sp 694	0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laonice sp 714	0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	**13**	**14.5**	**12.2**	**20.3**	**22.3**	**39.2**	**37.5**	**20.3**	**22.3**

Table 5.2. Mean number of individuals in Spionidae species recorded between August 1989 and September 1998. In bold the dominant species.

Minuspio sp. 4 showed fluctuations and low values during the first four cruises reaching a peak in March 1997, and decreasing in abundance later. The average abundance per cruise was 4.7±3.4 individuals per 0.25 m^2. Statistical analyses (ANOVA) showed significant differences between cruises (P<0.05). Tukey-Kramer post hoc test showed that no station was significantly different; although with a more relaxed post hoc test using Fisher's LSD March 1997 and July 1997 cruises showed significantly higher abundance that the other samples. Both these stations were during the '*Amperima* Event'. T–test P<0.02 showed significant differences between 'pre-*Amperima*' and '*Amperima* Event' samples with the post samples having higher abundances.

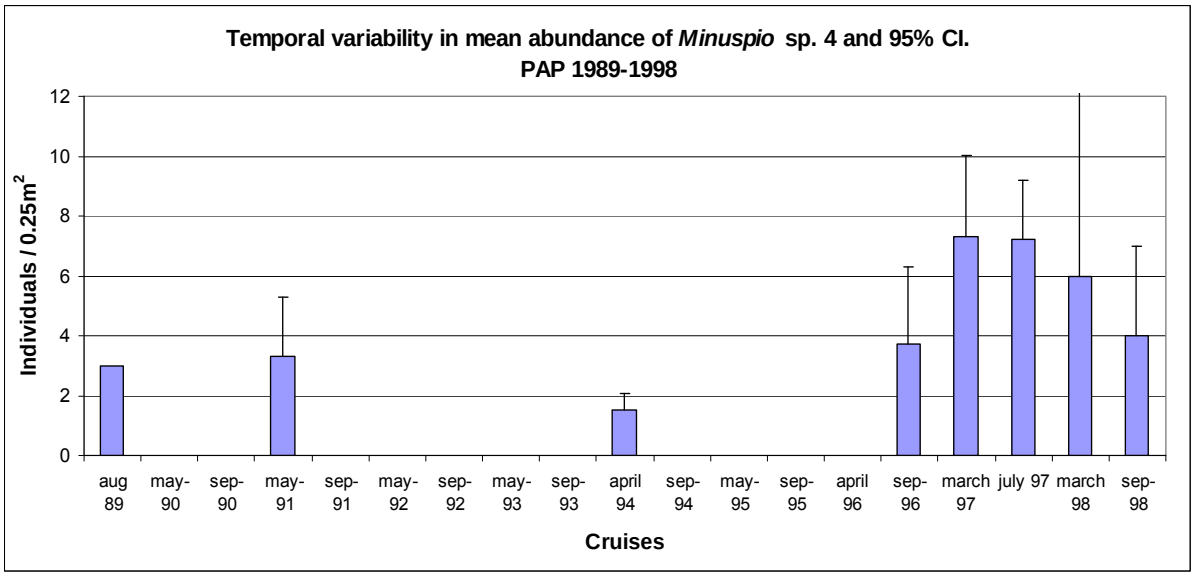


Figure 5.6. Mean number of individuals for *Minuspio* sp. 4 between 1989 and 1998. Mean and 95% confidence limit.

Aurospio dibranchiata showed a decreasing trend from August 1989 until March 1997, then mean abundance increased sharply reaching a maximum value 10.5 individuals per 0.25 m^2 in March 1998. The average abundance per cruise was 4.5±5 individuals per 0.25 m^2. No significant differences were detected between cruises and 'pre-*Amperima*' and '*Amperima* Event' periods for this species (P>0.1). Although Kruskal-Wallis post-hoc test confirmed the results obtained by ANOVA (P>0.1), observations showed that March 1997 is significantly lower than the mean abundance from the other cruises.

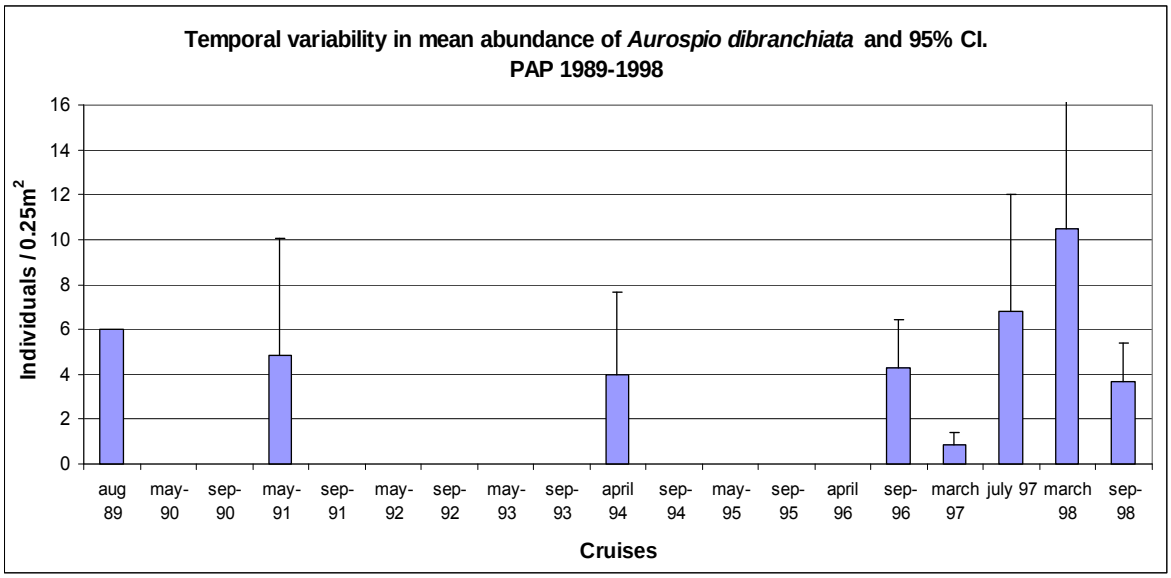


Figure 5.7. Mean number of individuals for *Aurospio dibranchiata* between 1989 and 1998. Mean and 95% confidence limit.

Prionospio sp. 81 showed an increase in mean abundance from May 1991 until March 1998 where the maximum value was recorded (10 individuals per 0.25 m^2) before decreasing during September 1998. The average abundance per cruise was 4.0±3.7 individuals per 0.25 m^2. ANOVA analyses indicated significant differences between cruises (P<0.01). Post hoc tests indicated that these differences are due to a low abundance during May 1991, the other sampling periods not show any major difference. T-test comparing 'pre-*Amperima*' and '*Amperima* Event' samples showed significantly higher post '*Amperima*' abundance (P<0.001).

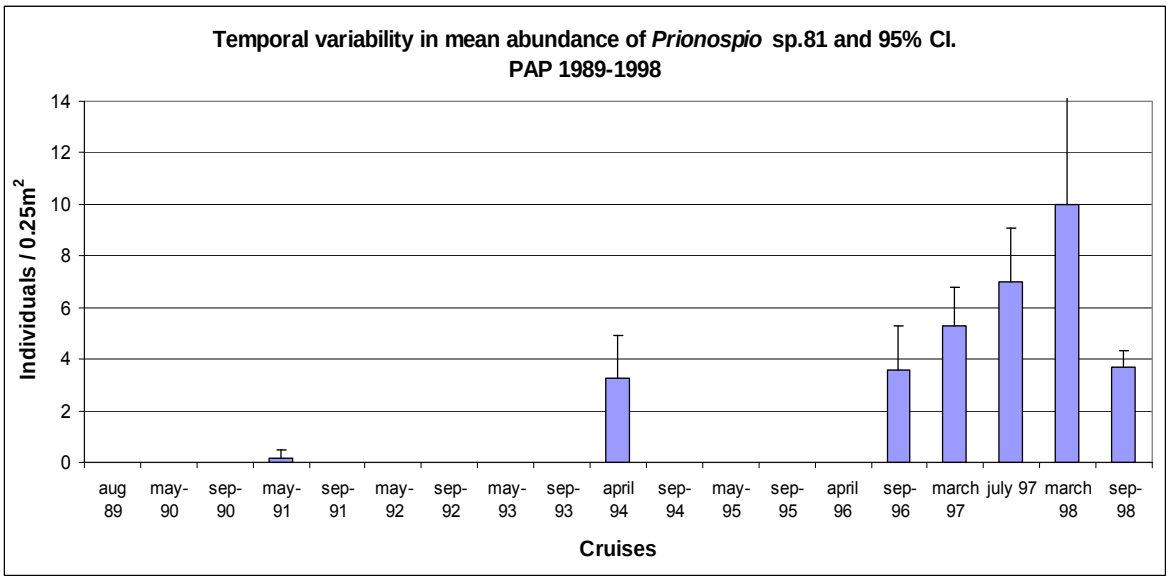


Figure 5.8. Mean number of individuals for *Prionospio* sp. 81 between 1989 and 1998. Mean and 95% confidence limit.

Prionospio sp. 613 showed a decreasing pattern from May 1991 until September 1996 when the minimum mean abundance was recorded (0.7 individuals per 0.25 m^2). There was increase from March 1997 until July 1997 with maximum value 7.4 individuals per 0.25 m^2 was observed. Then a decrease in abundance again was recorded. The average abundance per cruise was 2.5±2.7 individuals per 0.25 m^2. Analyses of variance showed significant differences between cruises (P<0.01). However post hoc analyses indicate that the difference can be attributed to a high value of July 1997 compared with the values from other cruises. This is the only indication of a major peak in abundance during the '*Amperima* Event'. T-test did not show any significant differences before or during '*Amperima* Event' periods (P>0.1).

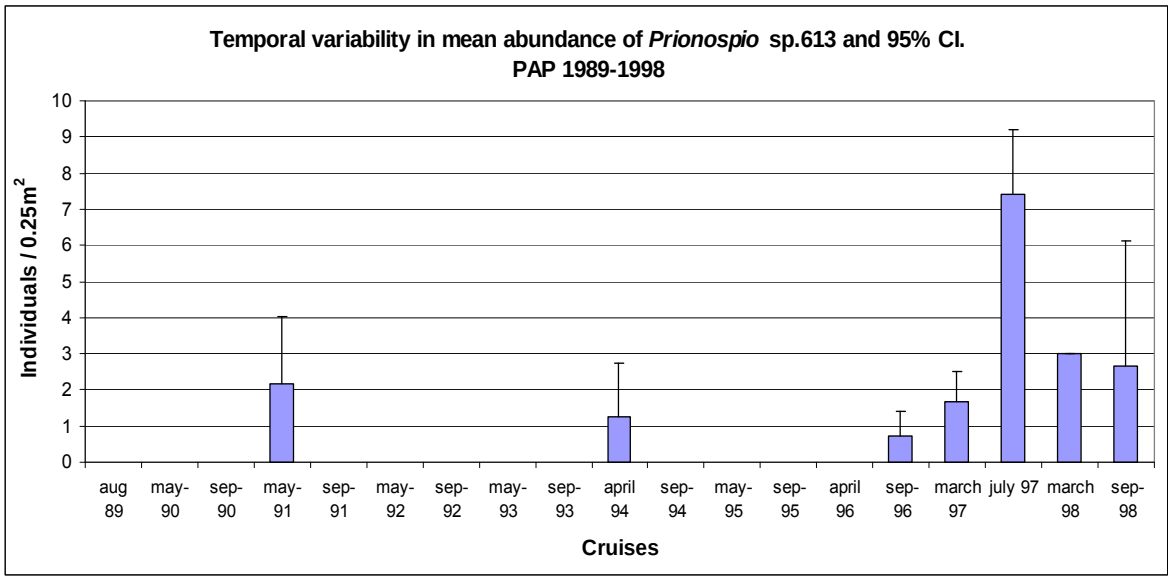
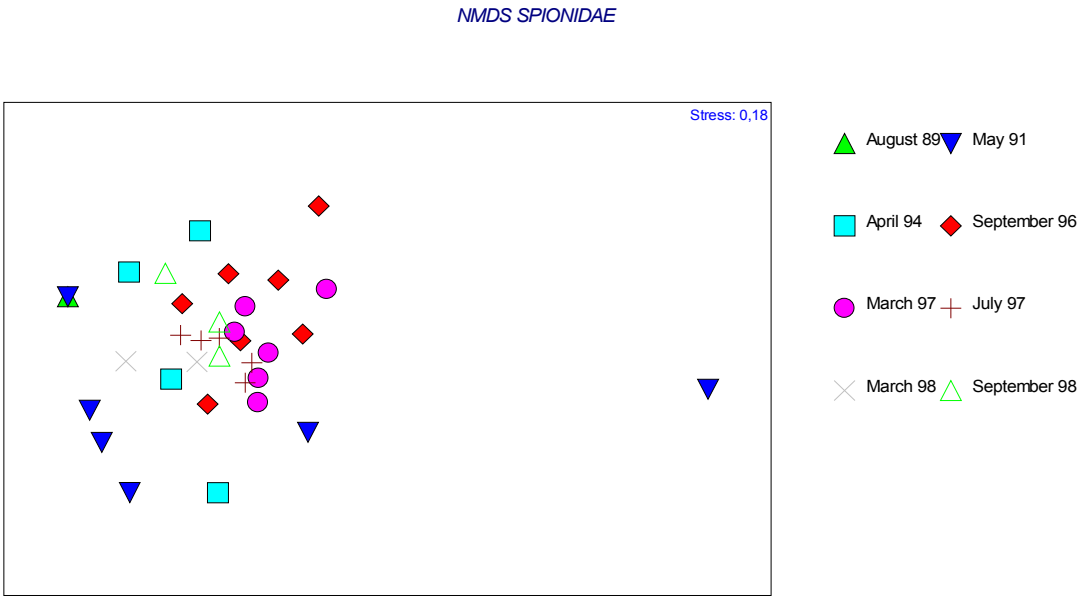


Figure 5.9. Mean number of individuals for *Prionospio* sp. 613 between 1989 and 1998. Mean and 95% confidence limit.

5.1.2.2. Multivariate analyses

Multivariate analyses (NMDS) are showed in Figure 5.10. and ANOSIM and SIMPER analyses in Table 17 (Appendix 2). Data was square root transformed and Bray Curtis Similarity Index was used. NMDS ordination does not show any overlap between samples from different cruises and periods. Two groups are clearly defined; stress: 0.18, model occurred 5 times (ANOSIM Global R=0.54; 0.0% significance level). Samples from pre-'*Amperima*' cruises showed a greater variation than '*Amperima* Event' samples, revealing differences in abundance and composition between cruises. The two groups were defined by the same dominant species so differences between periods are thought to be mainly caused by variations in species abundance.

NMDS



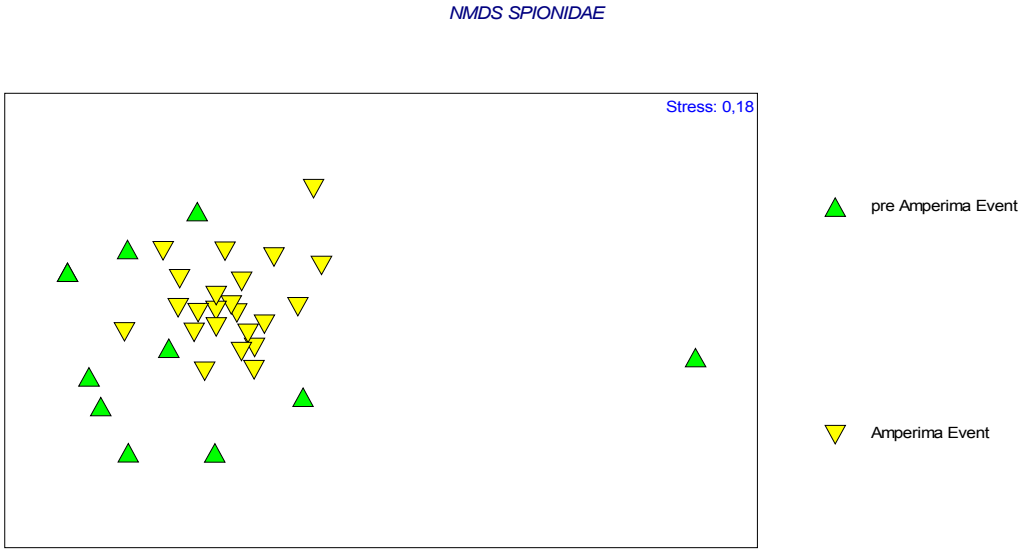


Figure 5.10. Non-metric multidimensional scaling in Spionidae (a) cruises (b) 'pre-*Amperima*' and '*Amperima* Event' periods.

5.1.3. Paraonidae

5.1.3.1. Changes in abundance of the dominant paraonids species:

***Aricidea* sp. 676, *Aricidea* sp. 36 and *Aricidea* sp. 678E**

Twenty four species of the Paraonidae family were identified in the study site between August 1989 and September 1998. Fourteen species belonged to *Aricidea.* Species of this genus were the most abundant. *Levinsenia* accounted for seven species and *Paradoneis* accounted for two species. Only one species of Paraonidae indeterminate was recorded. The species composition was characterized by the occurrence of *Aricidea* species. Four of them were dominant in terms of abundance and frequency of occurrence. The rest of *Levinsenia*, *Paradoneis* and *Aricidea* species recorded low abundance and frequency of occurrence with time. Only the species *Aricidea cf. neosuecica* had been described previously.

The three most abundant species were *Aricidea* sp. 676, *Aricidea* sp. 36 and *Aricidea* sp. 678E. They accounted for up to 45% of the total abundance of paraonids.

Species	Aug 89	May 91	April 94	Sept 96	March 97	July 97	March 98	Sept 98	Mean
Aricidea cf neosuecica	1	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.1
Aricidea sp 28	1	0.2	0.3	0.6	1.0	0.6	0.5	0.3	0.5
***Aricidea* sp 36**	**6**	**0.2**	**1.0**	**0.9**	**0.8**	**1.0**	**2.0**	**0.7**	**1.0**
Aricidea sp 11	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Paraonidae indet1	0	0.0	0.3	0.4	0.5	0.0	0.5	0.0	0.2
***Aricidea* sp 676**	**1**	**2.7**	**2.0**	**0.9**	**0.7**	**1.4**	**1.0**	**0.7**	**1.4**
Levinsenia sp 3	0	0.0	0.0	1.1	0.5	0.2	0.0	0.3	0.4
***Aricidea* sp 678E**	**0**	**0.3**	**1.0**	**0.9**	**1.2**	**1.0**	**2.0**	**0.3**	**0.9**
Aricidea sp 6	0	0.2	0.0	0.1	0.0	0.0	0.5	0.0	0.1
Aricidea sp700	0	0.7	0.8	0.4	0.5	0.6	0.5	0.0	0.5
Aricidea sp 7	0	0.5	0.3	0.0	0.2	0.2	0.0	0.3	0.2
Aricidea sp721	0	0.3	0.0	0.1	0.2	0.4	0.0	0.7	0.2
Aricidea sp 601	0	0.8	0.3	0.0	0.0	0.2	0.0	0.0	0.2
Aricidea sp 8	0	0.0	0.3	0.0	0.2	0.2	0.0	0.3	0.1
Levinsenia sp A	0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Aricidea sp 695F	0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Levinsenia sp Z	0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Levinsenia sp Y	0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Paradoneis sp 1	0	0.0	0.5	0.1	0.7	0.0	0.5	0.3	0.3
Paradoneis sp 2	0	0.0	0.0	0.1	0.3	0.2	0.0	0.0	0.1
Levinsenia sp 6	0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.1
Levinsenia sp 1	0	0.2	0.0	1.0	0.5	0.8	0.0	0.7	0.5
Levinsenia sp 5	0	0.0	0.0	0.0	0.2	0.0	0.0	0.3	0.1
Aricidea sp 12	0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	**11**	**6.8**	**7.2**	**6.7**	**7.5**	**7.0**	**7.5**	**5.0**	**7.0**

Table 5.3. Mean number of individuals in Paraonidae species recorded between August 1989 and September 1998. In bold the dominant species.

Aricidea sp. 676 showed a greater abundance during the 'pre-*Amperima'* period. More than 50% of total number of individuals collected occurred in two cruises (May 1991 and April 1994). The lowest mean abundance was recorded in March 1997 and September 1998 cruises both with 0.7 individuals per 0.25 m^2. The greatest mean abundance was recorded in May 1991 with 2.7 individuals per 0.25 m^2. The mean number per cruise was 1.4±1.4 individuals per 0.25 m^2. Significant differences were not observed between cruises (ANOVA *P*>0.1), however there were statistically significant differences between 'pre-*Amperima*' and '*Amperima* Event' periods (t-Test, *P*<0.05).

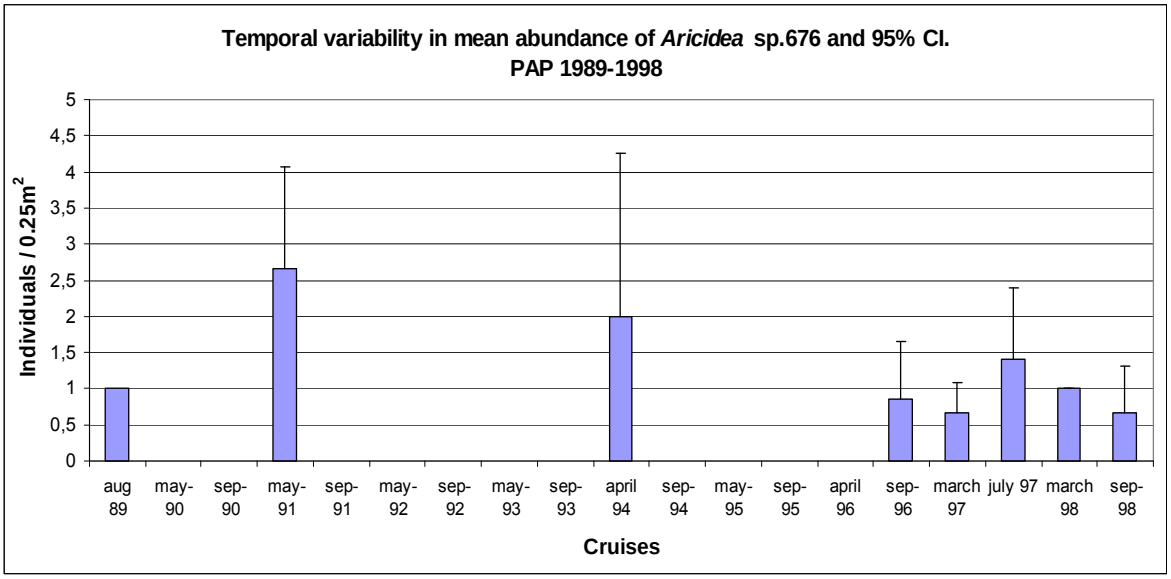


Figure 5.11. Mean number of individuals for *Aricidea* sp. 676 between 1989 and 1998. Mean and 95% confidence limit.

Aricidea sp. 36 showed a relatively consistent pattern with the exception of the August 1989 cruise. Remarkably the maximum value, 6 individuals per 0.25 m^2 was observed during 1989 (n=1). The minimum abundance was 0.2 individuals per 0.25 m^2 in May 1991. The mean number per cruise for this species was 0.9±1.4 individuals per 0.25 m^2. ANOVA indicated that there were no significant differences between cruises (*P*>0.5), and t-Test also showed no significant differences between 'pre-*Amperima*' and '*Amperima* Event' periods (*P*>0.1).

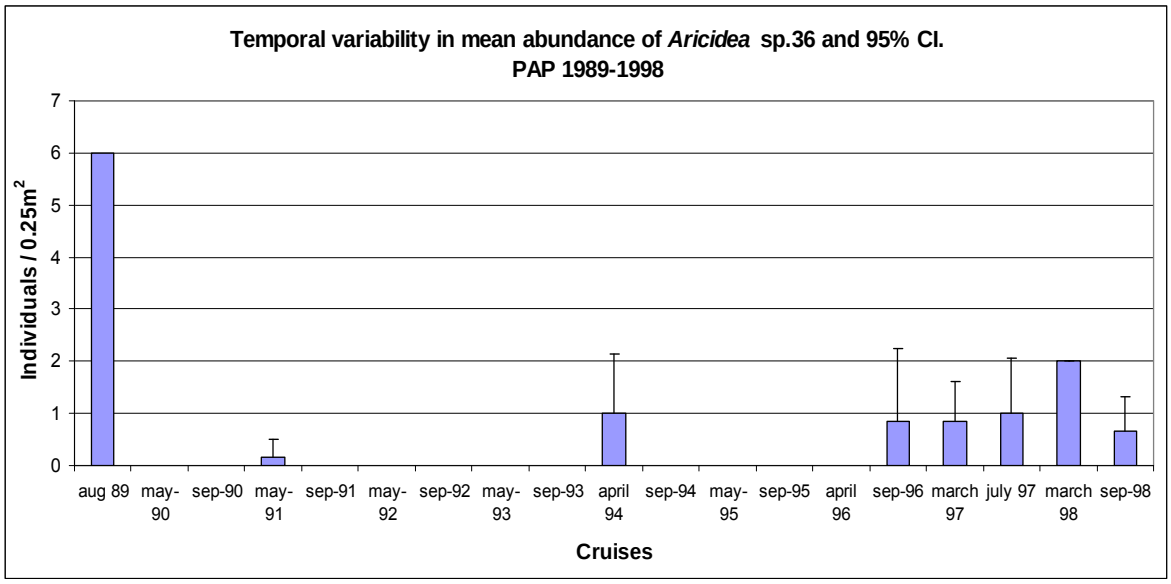


Figure 5.12. Mean number of individuals for *Aricidea* sp. 36 between 1989 and 1998. Mean and 95% confidence limit.

Aricidea sp. 678E showed a slight increase in March 1998. In September 1998 mean abundance fell sharply. No individuals were recorded in August 1989. The greatest mean abundance was observed in March 1998 with 2 individuals per 0.25 m^2. The mean number per cruise was 0.9±0.9 individuals per 0.25 m^2. Statistical analyses demonstrated that no significant differences were observed between cruises and 'pre-*Amperima*' and '*Amperima* Event' periods (ANOVA and t-Test P>0.1).

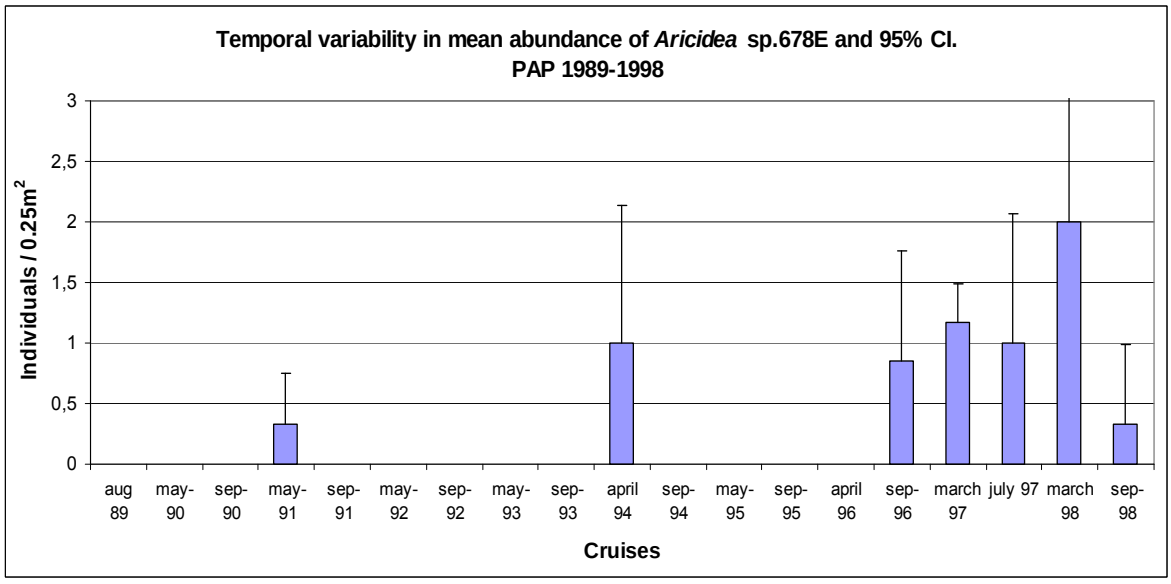
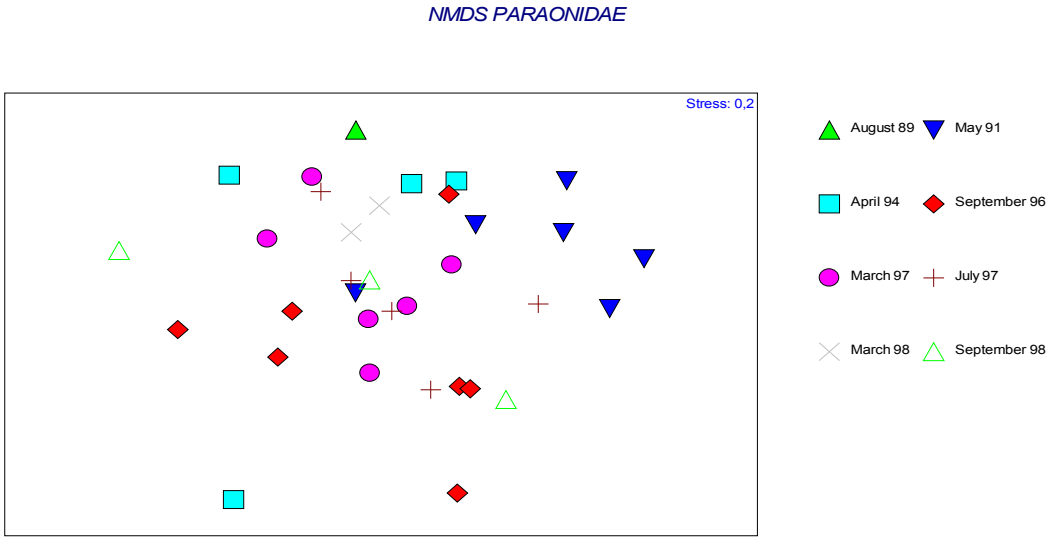


Figure 5.13. Mean number of individuals for *Aricidea* sp. 678E between 1989 and 1998. Mean and 95% confidence limit.

5.1.3.2. Multivariate analyses

The NMDS ordination does not show a clear separation in the two sets of samples, with some overlap in ordination space (Fig. 5.14.). Data was square root transformed and Bray Curtis Similarity Index was used. The high percentages of dissimilarity against the low percentages of similarity recorded (ANOSIM Global R=0.24; 0.1% significance level) indicate the presence of different groups; stress: 0.2, model occurred 4 times. This suggests that temporal variability is mainly due to changes in species composition but to a lesser extent by the number of individuals. Five species accounted for at least for 50% of dissimilarity observed between groups (Table 20, Appendix 2).

NMDS



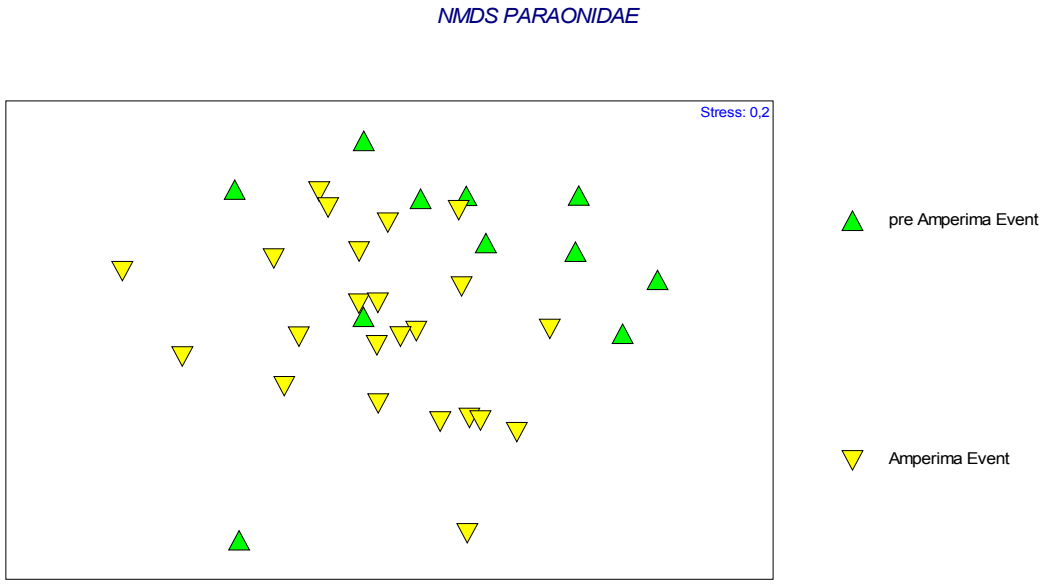


Figure 5.14. Non-metric multidimensional scaling in Paraonidae (a) cruises (b) 'pre-*Amperima*' and '*Amperima* Event' periods

5.1.4. Pilargidae

5.1.4.1. Changes in abundance of the dominant pilargids species: Pilargidae (all family) and *Sigambra magnuncus* (*Sigambra* sp. 1)

Table 5.4. shows temporal variability in the mean number of individuals of Pilargidae and the five recorded species from August 1989 and September 1998 in the study site. Three species belonged to *Sigambra* and one to *Ancistrosyllis*. One species was Pilargidae indeterminate. There was high dominance of *Sigambra magnuncus* (*Sigambra* sp. 1). The other species had very low mean abundances and frequency of occurrence. The total fauna of the Pilargidae accounted for 104 individuals, while the most abundant species, *Sigambra magnuncus*, recorded 94 individuals.

Species	Aug 89	May 91	April 94	Sept 96	March 97	July 97	March 98	Sept 98	Mean
***Sigambra magnuncus* (sp1)**	**1.0**	**1.8**	**1.8**	**3.1**	**4.0**	**2.2**	**4.0**	**3.3**	**2.8**
Sigambra sp 2	0.0	0.0	0.0	0.6	0.0	0.0	0.0	1.0	0.2
Sigambra sp 3	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Ancistrosyllis sp 1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Pilargidae indet.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Pilargidae (all family)	**1.0**	**1.8**	**1.7**	**3.8**	**4.2**	**2.4**	**4.0**	**4.3**	**3.1**

Table 5.4. Mean number of individuals in Pilargidae species recorded between August 1989 and September 1998. In bold *Sigambra magnuncus*.

In terms of mean number of individuals, the Pilargidae showed fluctuations between cruises but overall there was an increase in abundance with time. The mean abundance per cruise was 3.1±1.8 individuals per 0.25 m^2. *Sigambra magnuncus* showed a similar temporal pattern. This species accounted by 90% of total abundance. Only slight variations were observed in abundance during '*Amperima* Event' cruises (September 1996–September 1998). The mean abundance per cruise was 2.8±1.7 individuals per 0.25 m^2.

Analyses of variance showed significant differences between cruises for Pilargidae (P<0.05). However, these differences were not statistically significant for *Sigambra magnuncus* (P>0.1). In the Pilargidae Post-hoc analyses indicated that differences are due to higher values in March 1997 and September 1998 cruises compared to lower values of May 1991 and April 1994 cruises. The comparison carried out for 'pre-*Amperima*' and '*Amperima* Event' samples showed highly significant differences for

Pilargidae (*P*<0.01) and *Sigambra magnuncus* (t-Test *P*<0.03). Statistical analyses are presented in tables 21 and 22, Appendix 2.

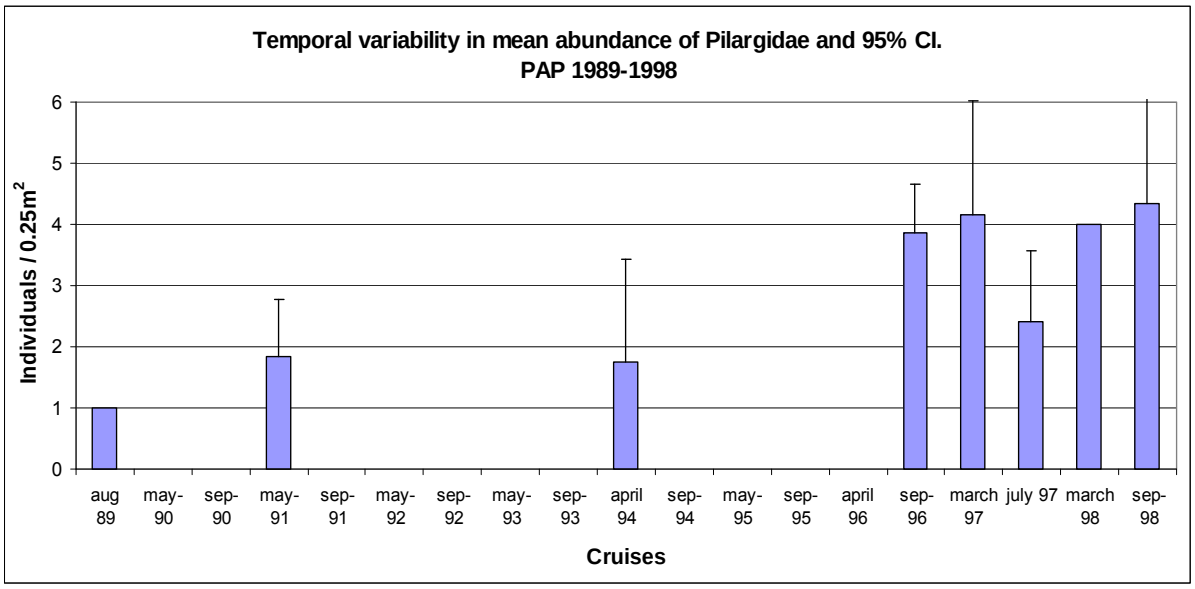


Figure 5.15. Mean number of individuals for Pilargidae between 1989 and 1998. Mean and 95% confidence limit.

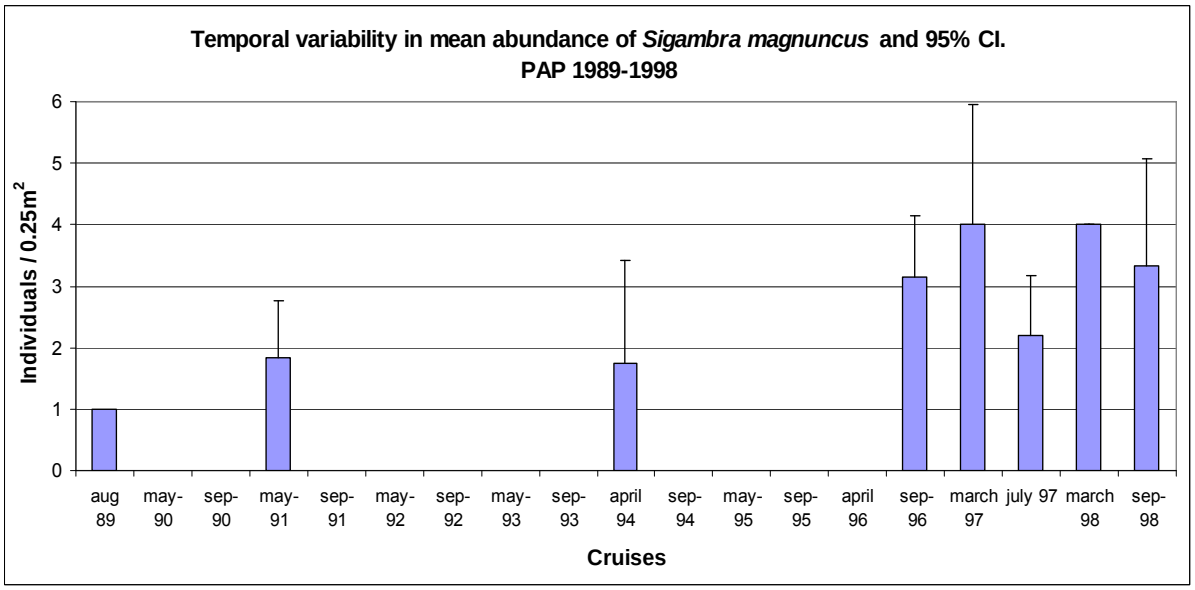
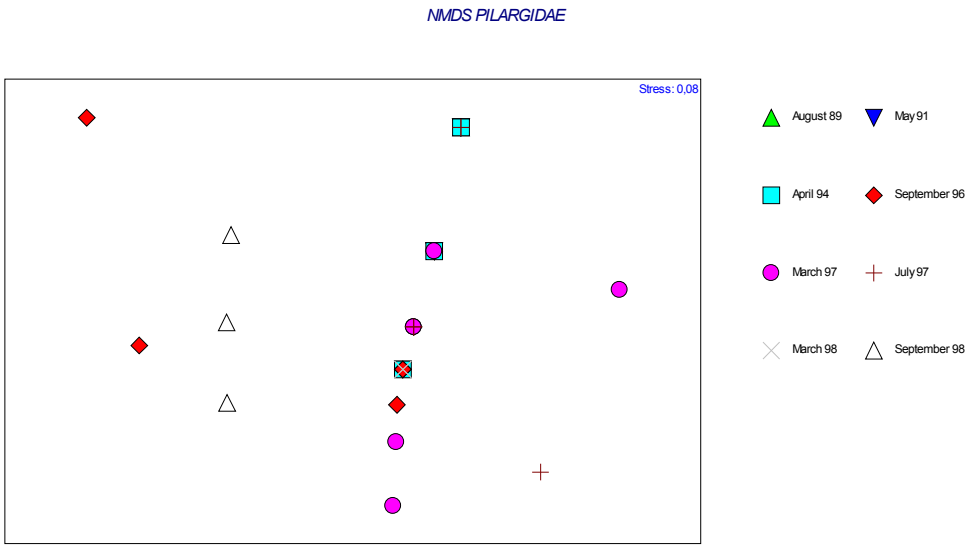


Figure 5.16. Mean number of individuals for *Sigambra magnuncus* between 1989 and 1998. Mean and 95% confidence limit.

5.1.4.2. Multivariate analyses

The non-metric multi-dimensional scaling ordination and analyses of similarities did not identify any clear trends on groups. Data was square root transformed and Bray Curtis Similarity Index was used. The apparent overlapping in ordination space between some 'pre-*Amperima*' and '*Amperima* Event' samples showed there is certain consistent temporal pattern; stress: 0.08, model occurred 5 times (Fig. 5.17.). Variations in time between samples were not significant (ANOSIM Global R=0.12; 7.6% significance level). Similarity and dissimilarity percentages were related to just one species (*Sigambra magnuncus*), which dominated Pilargid abundance in all cruises (Table 23, Appendix 2). The potential significance of these changes between cruises and periods would be related to an increase of the abundance with time.

NMDS



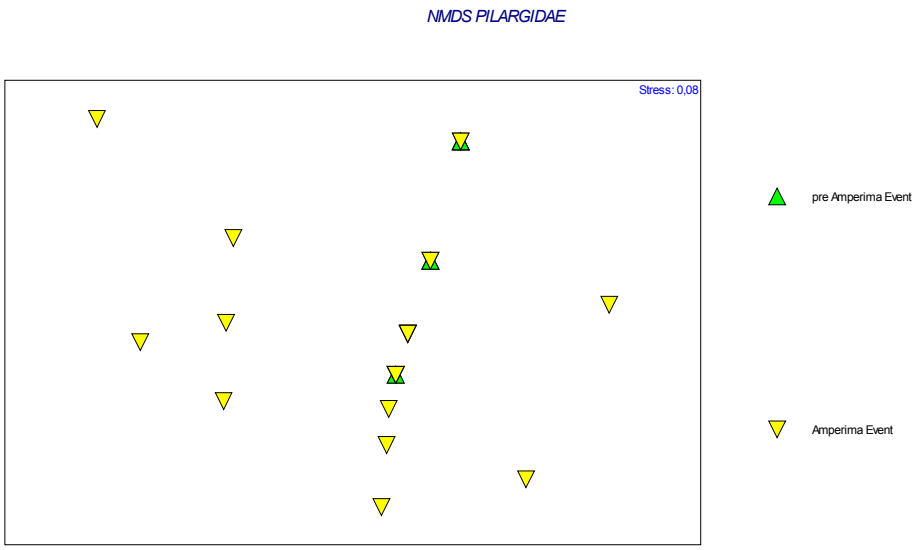


Figure 5.17. Non-metric multidimensional scaling in Pilargidae (a) cruises (b) 'pre-*Amperima*' and '*Amperima* Event' periods. A sample with value=0 was not considered

5.1.5. Glyceridae

5.1.5.1. Changes in abundance of the dominant glycerids species: Glyceridae (all family) and *Glycera* sp. 726

Table 5.5. shows temporal variability in the mean number of individuals of Glyceridae and five Glyceridae species between August 1989 and September 1998. Glyceridae were almost exclusively collected during the '*Amperima* Event' cruises. Only one species *Glycera* sp. 726 (Glyceridae sp. 1) was recorded in April 1994 cruise with one individual. Species richness was variable between cruises with no species and maximum of 4 species.

Species	Aug 89	May 91	April 94	Sept 96	March 97	July 97	March 98	Sept 98	Mean
***Glycera* sp726 (sp1)**	**0.0**	**0.0**	**0.3**	**0.4**	**0.3**	**0.4**	**0.0**	**0.3**	**0.3**
Glyceridae sp2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Glyceridae sp3	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.1
Glyceridae sp4	0.0	0.0	0.0	0.1	0.3	0.0	0.0	0.0	0.1
Glyceridae sp5	0.0	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.1
Glyceridae (all family)	**0.0**	**0.0**	**0.3**	**1.0**	**0.7**	**0.8**	**0.0**	**0.7**	**0.5**

Table 5.5. Mean number of individuals in Glyceridae species recorded between August 1989 and September 1998. In bold *Glycera* sp. 726

The temporal variability in both Glyceridae (Fig. 5.18.) and *Glycera* sp. 726 (Fig. 5.19.) showed a similar pattern The lowest mean abundance for Glyceridae and *Glycera* sp. 726 was 0 individuals recorded from several cruises. The greatest mean abundance for Glyceridae was 1 individual per 0.25 m^2 in September 1996 while for *Glycera* sp. 726 was 0.4 individuals per 0.25 m^2 also in September 1996.

The mean number per cruise was 0.5±0.8 individuals per 0.25 m^2 in Glyceridae and 0.3±0.5 individuals per 0.25 m^2 in *Glycera* sp. 726. This variability was characterized by the almost total absence of individuals during pre-'*Amperima*' cruises. Fluctuations and slight decreasing trend was observed to the end of time series in September 1998. Analyses of variance showed no significant changes in both Glyceridae and *Glycera* sp. 726 between cruises (*P*>0.3). By contrast, the '*Amperima* Event' comparison using the t-Test showed that significant difference was evident in Glyceridae taken as a whole (*P*<0.01) but not evident in the species *Glycera* sp. 726 (*P*>0.05). Statistical analyses in detail are shown in tables 24 and 25, Appendix 2.

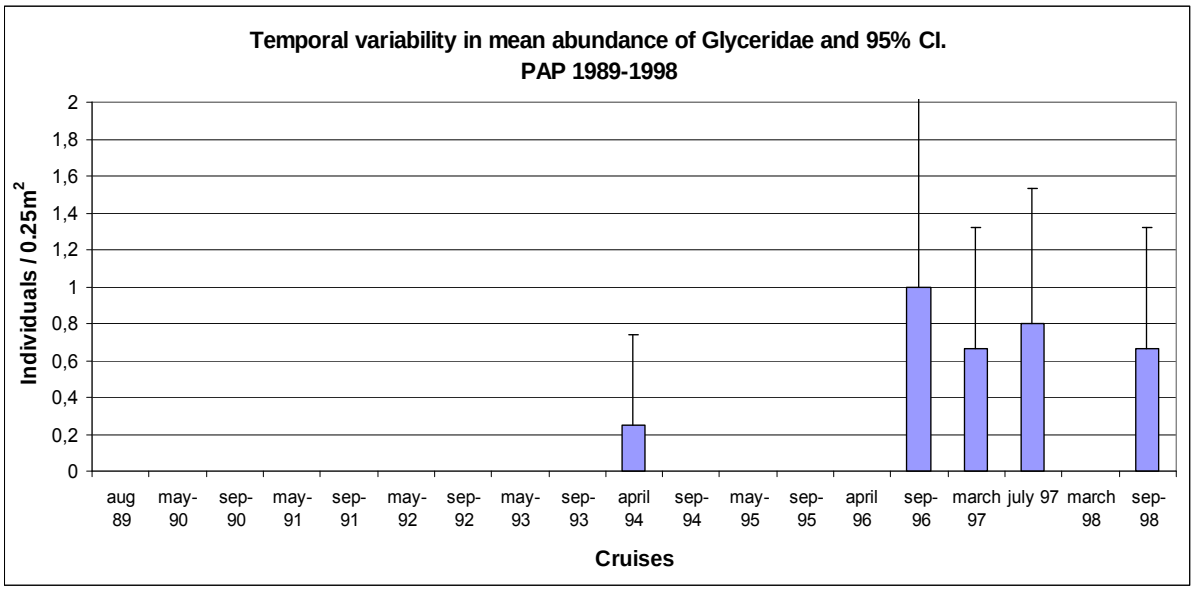


Figure 5.18. Mean number of individuals for Glyceridae between 1989 and 1998. Mean and 95% confidence limit.

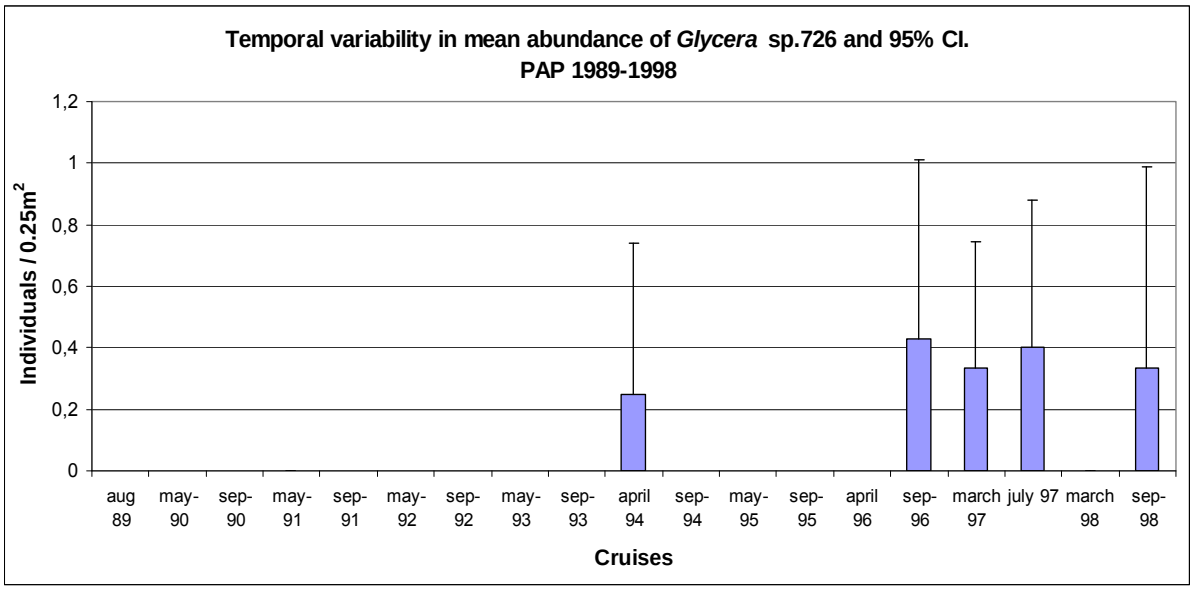


Figure 5.19. Mean number of individuals for *Glycera* sp. 726 between 1989 and 1998. Mean and 95% confidence limit.

5.1.5.2. Multivariate analyses

It was not appropriate to carry out this form of analyses when there were so few individuals and many sampling periods did not have any glycerids. However, NMDS ordination was made without consider samples with value= 0. Data was fourth root transformed and Bray Curtis Similarity Index was used. Also it was not possible to establish the groupings comparison (ANOSIM Global R=-0.28; 100% significance level) from the similarity percentages procedure (Table 26, Appendix 2).

The NMDS ordination did not find any major separations between periods; stress: 0.04, model occurred 3 times. The only one sample that recorded abundance during 'pre-*Amperima* Event' showed overlap with a sample from '*Amperima* Event' (Fig. 5.20.). The high separation in ordination space for the samples would indicate there is no a consistent temporal pattern. Therefore, there appears to be no major trends either interannual or between the 'pre-*Amperima*' and during '*Amperima* Event' in the abundance or composition of Glyceridae. However, four of the five species recorded (80%) only appeared from '*Amperima* Event' cruises or later.

NMDS

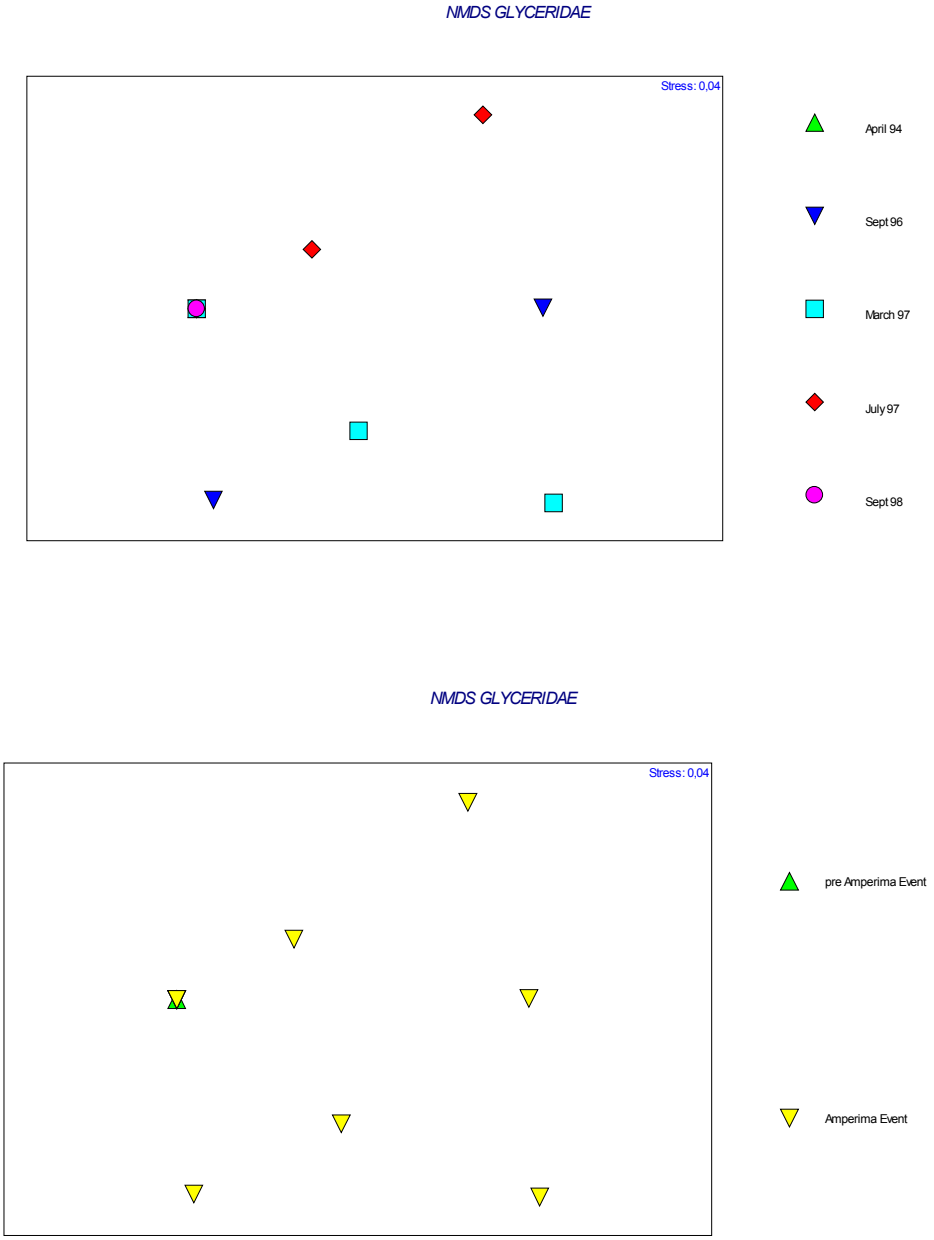


Figure 5.20. Non-metric multidimensional scaling in Glyceridae (a) cruises (b) 'pre-*Amperima*' and '*Amperima* Event' periods. Samples with value= 0 were not considered.

5.1.6. All species

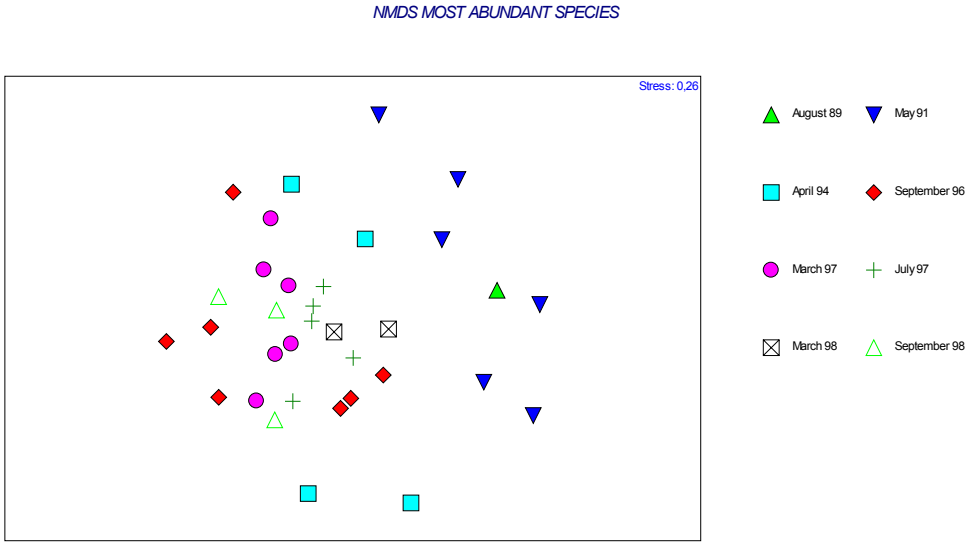
5.1.6.1. Multivariate analyses

A species/samples data matrix was created and multivariate analyses were undertaken to 1) explore what species are responsible by patterns observed, 2) answer the question is the fauna before the '*Amperima* Event' different to after, and 3) determine if the temporal variability is due to changes in species abundance or species composition.

Multivariate analyses such as NMDS showed a clear distinction between 'pre-*Amperima*' and '*Amperima* Event' periods. The separation of the two data sets was evident showing a good configuration, where the 'pre-*Amperima*' and '*Amperima* Event' samples do not overlap in ordination space; stress: 0.26, model occurred 5 times (Fig. 5.21.). Analyses results were validated through of the ANOSIM non-parametric test (R=0.59; significance level: 0.0%). (Table 27, Appendix 2). Temporal changes in abundance and polychaete faunal composition at species level could be supported by the NMDS ordination. The similarity within groups and dissimilarity among groups were defined by the species with the greatest abundances (contribution percentage). Data was fourth root transformed and Bray Curtis Similarity Index was used. The SIMPER analyses showed the species that principally contributed to similarity observed within groups were *Aphelochaeta* sp. 13A and *Chaetozone* sp. 1. The average dissimilarity between groups ('pre-*Amperima*' and '*Amperima* Event') was defined by species such as *Chaetozone* sp. 1, *Aurospio dibranchiata*, *Prionospio* sp. 81 and *Minuspio* sp. 4 which recorded low contribution percentages (Table 27, Appendix 2).

Analyses carried out above and observations from the original data matrix allow the conclusion that observed temporal variability in polychaete assemblages appear to be caused mainly by changes in species abundance but only to a minor degree by changes in species composition.

NMDS



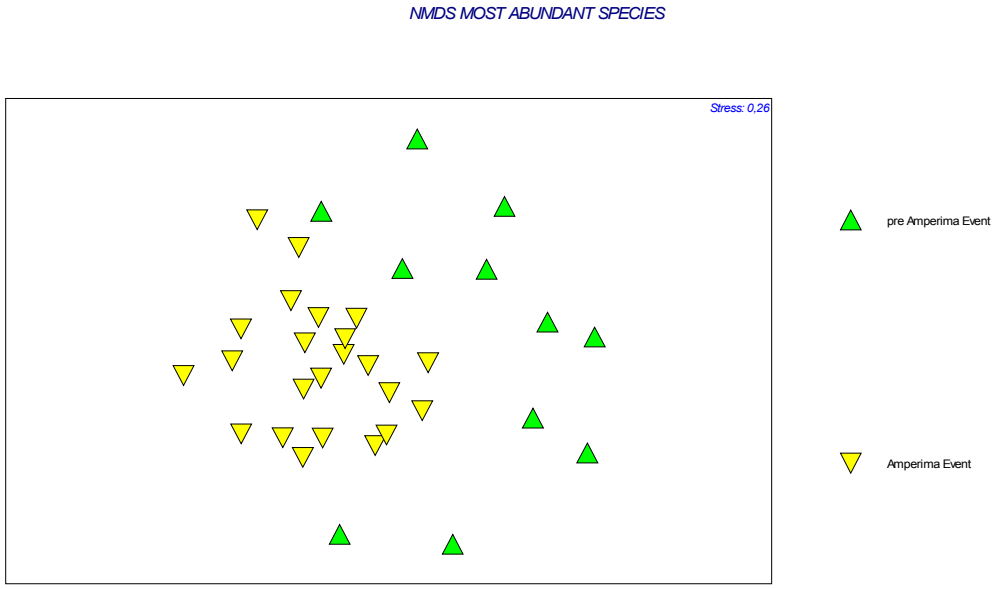


Figure 5.21. Non-metric multidimensional scaling in all polychaete species (a) cruises (b) 'pre-*Amperima*' and '*Amperima* Event' periods.

5.2. Discussion

5.2.1. Long-term changes at species level

Temporal changes were not evident in all deposit-feeder and predator species. Not all the most dominant polychaete species clearly responded to seasonal and interannual organic pulses to the seabed, increasing in abundance, where the deep water column and surficial sediment were enriched. However, some species did not respond through time.

5.2.1.1. Cirratulidae

5.2.1.1.1. Dominant species

Changes in abundance of family Cirratulidae with time were also apparent in the four most abundant cirratulid species; *Aphelochaeta* sp. 13A, *Chaetozone* sp. 1, *Chaetozone* sp. 55A and *Aphelochaeta* sp. 647D. These species accounted for 78.2% of the cirratulid fauna. An apparent response was detected between cruises and periods for *Aphelochaeta* sp. 647D. A similar response was also recorded in *Chaetozone* sp. 1 and *Chaetozone* sp. 55A, but just between cruises. No significant response was detected in *Aphelochaeta* sp. 13A with time.

Aphelochaeta sp. 13A was the most abundant polychaete in the current study (8.3% of all polychaete fauna). Mean abundance of *Aphelochaeta* sp. 13A showed a slight increase with time from 5 individuals in August 1989 to a maximum of 9.4±3.8 in July 1997. However, the differences were not significant ($P>0.1$). Temporal changes for this species do not appear to be responding to the factors which triggered the '*Amperima* Event' as the temporal variation in this species between 'pre-*Amperima*' and '*Amperima* Event' periods also was not significant. Temporal changes in *Aphelochaeta* sp.13A could be associated to seasonal or interannual natural variability.

Chaetozone sp. 1 was the second most abundant polychaete in the current study (7.1% of all polychaete fauna). Although there were significant differences in mean abundance between sampling periods ($P<0.002$), with post-hoc suggesting that the differences were due to high abundance of July 1997 compared to low abundances of May 1991 and September 1996 cruises, the mean abundance recorded for July 1997 was not significantly different from any of the other sample period. However, t-test of 'pre-*Amperima*' and '*Amperima* Event' samples was not significant so there were not higher abundances in these periods when samples are taken together ($P>0.05$). Yet

while there does not appear to be statistically significant changes in abundance and dominance of *Chaetozone* sp. 1 which can be linked to conditions relating to the '*Amperima*' effect, it is worth noting that mean abundance was more than twice as high during the '*Amperima* Event' compared to pre-'*Amperima* Event' period; while the percentage of individuals of this species in relation to total was higher in '*Amperima* Event' period (Fig. 5.22.)

Aphelochaeta sp. 13A and *Chaetozone* sp. 1 together accounted for more than 53% of the total number of individuals recorded for cirratulid polychaetes. Their high abundance, occurrence and dominance indicated that they were permanent residents of study zone. Both species had different temporal patterns, and therefore were major contributors to the temporal variability observed in the polychaete fauna. The temporal changes in these two species were not likely to have been determined by disturbance associated with the '*Amperima* Event'. Oceanographic conditions such as seasonal or interannual variations in food supply, apparently driving the '*Amperima* Event', and biological process such as recruitment and growth may play a more important role in determining changes in abundance and composition observed in these two dominant members of the polychaete assemblage.

Chaetozone sp. 55A accounted for 13.7% of the total number of individuals of Cirratulidae. The mean abundance of *Chaetozone* sp. 55A was highly variable during the pre-'*Amperima* Event' period. A relatively stable pattern with a slight decreasing trend was observed during the '*Amperima* Event' period. Post-hoc test would suggest that significant differences recorded for cruises are due to low abundance in April 1994. The remaining samples are not significantly different from any of the other so differences cannot be attributed to the '*Amperima* Event' conditions. Therefore, it is likely that differences observed are the result of interannual variation.

By contrast, temporal variability shown by *Aphelochaeta* sp. 647D followed a clear increasing trend, where the mean number of individuals per cruise and the proportion of individuals contributing to the total number of polychaetes were significantly greater during the '*Amperima* Event' period ($P<0.005$) (Fig. 5.22.). The response of *Aphelochaeta* sp. 647D was greatest towards the end of the sampling period, so it would be appear that this species was responding to faunal interactions such as bioperturbation, habitat competition and predation that were caused by the '*Amperima* Event' rather than environmental causes of the 'Event' in 1996. Another explanation is that the species was responding to alterations in the nutrient availability. The faecal

pellets of the *Amperima* or the reworking of the organic matter by holothurians produced greater food supply which this species can acquire.

5.2.1.1.2. The cirratulid assemblage

The temporal variability in the cirratulids fauna was mainly defined by variations in number of individuals. However, changes in species composition were also evident during '*Amperima* Event' period. From September 1996, 10% of the increase in abundance can be attributed other species appearing in the samples (Fig. 5.22.). In addition to dominant species many other species increased their abundance and frequency of occurrence. The abundance of the remaining species returned more or less to 'normal values' from July 1997. Nevertheless, the similarity and dissimilarity when comparing both 'pre-*Amperima*' and '*Amperima* Event' periods were highly determined by the abundance of the dominant species. Temporal variability in the mean abundance for the rest of cirratulid species (considered as group) showed a 'bell-shaped' trend. Maximum values were recorded between September 1996 and July 1997, while the minimum values were recorded before and after of this period (Fig. 3, Appendix 1). The increase in abundance for this 'non-dominant' group of species could be explained by '*Amperima* Event' as significant differences were detected between 'pre-*Amperima*' and '*Amperima* Event' periods (P>0.02).

There are many possible reasons for this pattern, for example synchronous recruitment of benthic biota (Vanreusel *et al.*, 2001) and the effect of patchiness of benthic fauna (Gage, 1996; Cosson *et al.,* 1997) generated by biological and/or physical interactions on the seabed. In addition, many of biogeochemical parameters related to food supply input, measured in sediments and near-bed waters at PAP during cruises considered as '*Amperima* Event' period (from September 1996 to September 1998), had their peaks in these dates. Sediment trap data recorded a significant phytodetrital pulse in June-July 1997 (Lampitt *et al*., 2001). Bacterial carbon production (Eardly *et al.,* 2001), phytopigments (Witbaard *et al.,* 2001), lipid compounds (Galéron *et al.,* 2001) and biogenic silica components (Ragueneau *et al*., 2001) had the greatest values for sediments in September 1996. Some of these parameters could have a direct effect on the temporal dynamics of some species of Cirratulidae. Unfortunately, at species level it is not possible to be more specific because the correlative data are missing. However, from tracer experiments carried out with ^{13}C-labelled diatoms, several individuals from a single species of Cirratulidae have recorded the highest degrees of enrichment in

comparison to other macrofauna taxa (Aberle & Witte, 2003). However, in the current study, the main reasons should be considered carefully because several species that belong to same family show different patterns and trends with time. A better understanding of the variations in particulate organic matter that influence ecological and biological processes of polychaete assemblages is needed. In particular, studies and experiments on target species (dominant species) that include these factors are needed to find the real causes generating the observed temporal changes.

5.2.1.1.3. Comparison with other studies

High abundance in cirratulids species have been recorded from a number of studies. For example, *Aphelochaeta* sp. 55, from the EUMELI Project oligotrophic site (4600 m) and mesotrophic site (3100 m), in tropical northeast Atlantic, was the dominant polychaete accounting for 8.9% and 11.2% of the total polychaete community respectively (Cosson-Sarradin *et al*. 1998). *Aphelochaeta bullata* and a new species of *Aphelochaeta* from continental slope off northern California have also been found to be dominant (Doner & Blake, *unpublished*). Other species of Cirratulidae are also the most important components at other deep-sea localities, with a similar contribution to the total polychaete fauna. *Tharyx kirkegaardi* Blake, 1991 in the Gulf of Farallones, northeast Pacific Ocean, at depths between 550 and 3100 m, accounted for nearly 10% of all polychaetes (Hilbig & Blake, 2006), while *Tharyx antarcticus* Hartman, 1978 in the Weddell Sea Basin, Antarctica, at depths between 1000 and 4000 m, contributed ~8.6% of all polychaetes (Blake & Narayanaswamy, 2004).

Blake & Grassle (1994) reported that C*aulleriella* sp. 3 was the top-ranked species representing 14% of the total macrofauna from Station 15, at 2000 m off South Carolina, northwest Atlantic. Cosson-Sarradin *et al*., (1998) recorded *Tharyx* sp. 424 as the second most abundant polychaete in EUMELI Project oligotrophic site (4600 m) from tropical northeast Atlantic with 8.6%. Hilbig *et al*., (2006) recorded a similar dominance for *Monticellina* sp. 2 (8%) in a group of deep-sea stations at depths of 1000 to 2500 m depth, from Weddell Sea, Antarctica.

Species of *Chaetozone* have been found to be dominant in other deep-sea environments. Glover *et al.*, (2001) recorded *Chaetozone* sp. as the dominant species on the Madeira Abyssal Plain (4900 m), tropical northeast Atlantic, while Cosson-Sarradin *et al.*, (1998) indicated that *Chaetozone* sp. 755 (the same species as

recorded in PAP) was one of dominant species at 3100 m and 4600 m depth in EUMELI Project sites, in the tropical northeast Atlantic. Other authors have also detected high abundances of *Chaetozone* species at different deep-sea depths in both northeast Pacific (Hilbig & Blake, 2006; Blake, 2006) and Weddell Sea, Antarctica (Hilbig *et al*., 2006; Blake & Narayanaswamy, 2004). The cirratulid fauna of Porcupine Abyssal Plain is therefore similar to other deep-sea regions in the relative abundance and so the nutrient regime has not led an appreciable different fauna in PAP.

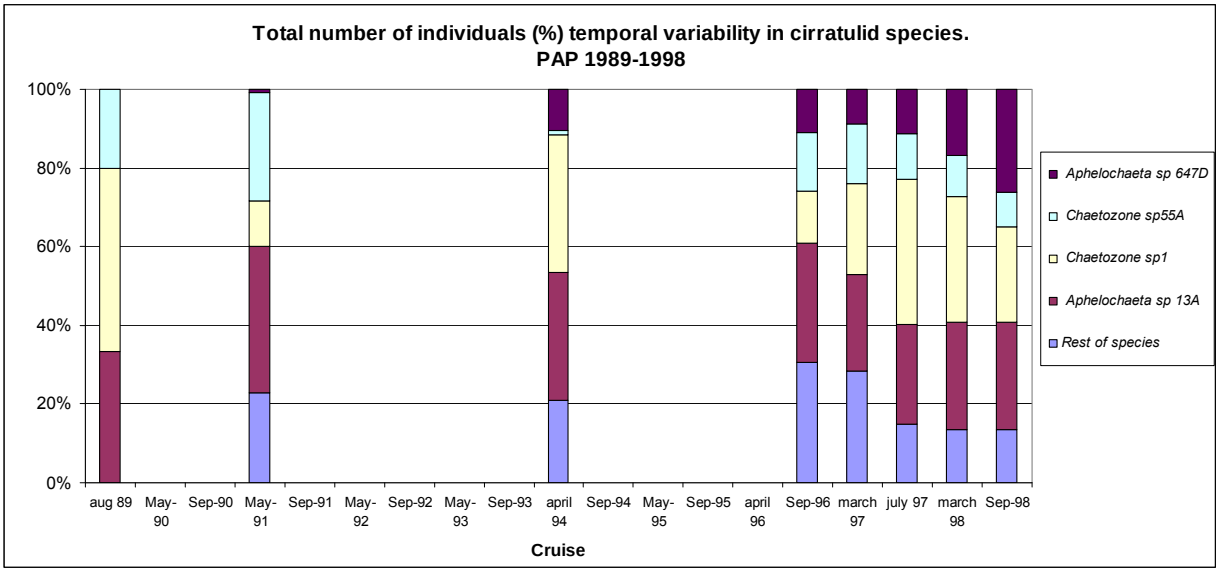


Figure 5.22. Total number of individuals (%) in four most abundant cirratulid species and the rest of cirratulid species between 1989 and 1998.

5.2.1.2. Spionidae

5.2.1.2.1. Dominant species

Analyses of similarity (ANOSIM) showed that the spionid species which mainly contributed to temporal variability were *Minuspio* sp. 4, *Aurospio dibranchiata*, *Prionospio* sp. 81, *Minuspio* sp. 2 and *Prionospio* sp. 613. These five species accounted for 82.2% of spionid fauna and the three most abundant species *Minuspio* sp. 4, *Aurospio dibranchiata*, and *Prionospio* sp. 81 accounted for 59.2%. The main patterns of similarity/dissimilarity between 'pre-*Amperima*' and '*Amperima* Event' samples are due to changes in the abundance of these species. All spionid species showed highly variability in patterns of abundance through time.

Minuspio sp. 4 and *Aurospio dibranchiata* were the two most abundant spionid species with 159 individuals (21%) and 152 individuals (20.1%), respectively accounting for

4.9% and 4.8% of the total polychaete fauna, being the third and fourth most abundant taxa, respectively in the current study.

No species of *Minuspio* have been reported to dominate in deep-sea benthic polychaete assemblages. *Prionospio* species have a similar biology to *Minuspio* (Blake, 1996b) so they are considered to be good species for comparisons. *Prionospio* complex species have been found dominate in some deep-sea macrofaunal communities (Blake & Grassle, 1994; Hilbig & Blake, 2000). *Prionospio fauchaldi* and *Prionospio* sp. 2 have been found to be dominant at 3000 m and 3500 m depths on the U.S. South Atlantic slope off the Carolinas. *Prionospio fauchaldi* between 5.4% and 8.3% of the total macrofauna, while *Prionospio* sp. 2 with contribution between 2.4% and 6.3% (Blake & Grassle, 1994). *Prionospio* sp. was dominant at Madeira Abyssal Plain, northeast Atlantic 4900 m depth (Glover *et al*., 2001). Cosson-Sarradin *et al.* (1998) found that *Prionospio* sp. 13 (the same species as found in PAP) represented 5.3% and 2.3% of the polychaete community, at the EUMELI sites in the tropical Atlantic (3100 m and 4600 m depth, respectively) while *Prionospio* sp. 752 represented 4.3% and 6.3%. *Prionospio delta* represented 5% of the total polychaete abundance. It was the dominant polychaete at depths between 2400-3100 m accounting for 16% in the northeast Pacific, off the Gulf of Farallones, California (Hilbig & Blake, 2006).

Aurospio dibranchiata is an extremely widespread species, occurring over most of the Atlantic Ocean from as far north as the Rockall Trough to as far south as the Argentina Basin (Maciolek, 1981a). The species has also been reported from the Pacific Ocean (Maciolek, 1981b; Hilbig & Blake, 2006; Smith *et al.,* 2008). It was the second most common species, accounting for 5.1% of the fauna at 1760 m off Woods Hole, northwest Atlantic (Grassle, 1977). *A. dibranchiata* has also been found in high densities in the US Mid-Atlantic region off New Jersey, and was the most abundant species at 2000-2100 m depth (Maciolek *et al*., 1987; Blake & Grassle, 1994). This species has also been recorded from several northeast Atlantic abyssal plain stations (Paterson *et al*., 1994; Glover, 2000). A new species of *Aurospio* from Antarctica was found in high densities (>2500 individuals m^2) at depths between 550 m and 4817 m. This species accounted for nearly 97% of the Spionidae at FOODBANCS Project site and ~70% of the polychaete community at some locations (Mincks *et al*., *submitted*). It did not appear to show seasonal cycles in abundance or recruitment in contrast to *A. dibranchiata*.

The relative proportion of individuals were similar in both *Minuspio* sp. 4 and *A. dibranchiata*, nevertheless differences in abundance with time and between periods were recorded for these species. An increasing temporal trend in the mean abundance of *Minuspio* sp. 4 was supported by statistical analyses that showed significant differences between cruises and between 'pre-*Amperima*' and '*Amperima* Event' periods (P<0.05). By contrast *A. dibranchiata* showed no significant differences between cruises and between 'pre-*Amperima*' and '*Amperima* Event' periods (P>0.1).

As PAP is an area with a considerable seasonal phytoplankton bloom (Lampitt *et al*., 2001, 2008), the most dominant spionid species seem to have responded to these changes in food supply. Although it is not possible to establish directly a link between higher levels of organic input and periodic increases in abundance of some spionid species, certain opportunistic behaviour could explain the observed variability in some species such as *A. dibranchiata*. Spionids are regarded as opportunists and characteristic of disturbed habitats (Grassle & Grassle, 1974; Smith & Hessler, 1987) in the deep sea and were observed to be pioneer colonisers in recolonisation tray experiments e.g. *Prionospio* sp. (Desbruyères *et al.,* 1985), occurring in organically enriched sediments (Grassle & Morse-Porteous, 1987) and undergoing rapid mass development when a large food fall becomes available (Hilbig, 2001).

Minuspio sp. 4 was characterized by greatest abundances in March and July 1997 at the time of '*Amperima* Event'. In addition, the proportion of this species that contributed to the total number of polychaetes was greatest (32.8%) during March 1997. Some biogeochemical parameters measured in water column and sediments such as silicic acid (Ragueneau *et al*., 2001), biogenic silica (Lampitt *et al*., 2001) sterols (Galéron *et al*., 2001), particulate organic carbon (Vangriesheim *et al*., 2001), suspended particulate material (e.g. Al, Fe and Mn) (Varnavas *et al*., 2001) DNA and phaephorbides (Witbaard *et al*., 2001) recorded maximum concentrations during that period coinciding with the peaks of abundance observed in *Minuspio* sp. 4. *Minuspio* sp. 4 showed significant differences between cruises and between 'pre-*Amperima*' and '*Amperima* Event' periods (P<0.05). Also the mean number of individuals per sampling was always higher during '*Amperima* Event' cruises. Therefore, the changes in abundance recorded for this species could be attributed to '*Amperima*' effect.

For *Aurospio dibranchiata* the observed temporal variability are difficult to explain. This species showed peaks in mean abundance during '*Amperima* Event' cruises, but the

lowest mean abundance was also recorded during this period. The overall proportion of individuals in relation to all spionids was generally higher for pre-'*Amperima* Event' cruises (Fig. 3.2.) and no significant differences were detected between cruises and periods (P>0.1). There was no apparent '*Amperima*' effect associated with changes in mean abundance of *A. dibranchiata*.

Population densities of spionids from shallow waters are known to vary seasonally and to exhibit patterns of spring/summer abundance in temperate environments (Holland, 1985). A typical season starts with overwintering adults responding to increasing spring temperatures and increased food supply by initiating gametogenesis and producing eggs (Blake, 1996b). *Aurospio dibranchiata* is thought to reproduce seasonally (Mincks *et al*., submitted). Populations of this species off Cape Hatteras, northwest Atlantic, exhibited seasonality in their life history. As a surface deposit feeder this species is more likely to take advantage of seasonal organic pulses than subsurface feeders (Blake, 1993). *Aurospio dibranchiata* populations from PAP did not show evidence of seasonality in their temporal pattern. In addition, a high proportion of juveniles were always found in all samples during the study, which would suggest a lack of distinct reproductive periodicity and seasonality in recruitment (Mincks & Smith, 2007). A similar pattern was reported for *Aurospio* sp. nov from Antarctica (Mincks *et al*., *submitted*). The pattern of decreasing mean abundance observed for the five first cruises would indicate a negative response to '*Amperima* Event' and to some biogeochemical parameters that increased their concentrations during that period. However, the later increases in abundance suggests a late response to food inputs, as reported by Galéron *et al*., (2001) for macrofaunal polychaetes generally, or some kind of 'recuperation' of the population. Even a change in feeding behaviour could be considered. Most spionids have shown to have the ability to switch between suspension feeding and surface deposit feeding (Dauer *et al*., 1981). However, for the PAP case, food input variations could determine some biological processes such as recruitment in *A. dibranchiata* or growth in spionids species. *A. dibranchiata* populations had a high proportion of juveniles and the greatest abundance was recorded in July 1997 and March 1998. Phytodetritus fluxes of lower quality and amount may have been consumed by this population to reach greater densities.

Prionospio sp. 81, *Minuspio* sp. 2 and *Prionospio* sp. 613 were the third, fourth and fifth most abundant spionids in the current study. They accounted for more than 40% of total spionid fauna. Significant differences were detected between cruises for these three

species. The greatest abundance was recorded during 'A*mperima* Event' cruises, with significant differences recorded only for *Prionospio* sp. 81 and *Minuspio* sp. 2 between 'pre-*Amperima*' and '*Amperima* Event' periods. The temporal change in *Prionospio* sp. 81 populations suggests this species was favoured by environmental conditions generated at the time of '*Amperima* Event' (Fig. 5.8.). The observed response was not immediate, abundance increased gradually with time, reaching a peak in March 1998. In the water column, organic and inorganic carbon fluxes (Lampitt *et al*., 2001), phytopigments fluxes, such as Phaeo-a (Fabiano *et al*., 2001) and microbial assemblages (Vanucci *et al*., 2001) showed greater values during that year. In sediments, the total carbohydrate content (Fabiano *et al*., 2001), leucine incorporation (Eardly *et al*., 2001) and total megabenthos tracking (Bett *et al*., 2001) were greatest in 1998. These factors may have influenced the increase in abundance of *Prionospio* sp. 81 in March 1998.

In *Minuspio* sp. 2 the increase in abundance from September 1996 with a maximum in July 1997 and the significant differences recorded between 'pre-*Amperima*' and '*Amperima* Event' periods would indicate an apparent response to environmental conditions triggered during the start of the '*Amperima* Event'. The increase of seasonal fluctuations in the supply of phytodetritus to the seafloor mirrored in September 1996 in greater proportions and the increases in concentrations of several biogeochemical parameters related to higher food availability could explain the variations recorded of this species. Analyses of lipids (Galéron *et al*., 2001) and phytopigments (Witbaard *et al*., 2000) in the surficial sediments confirmed that recently deposited phytodetritus was present in significant quantities in September 1996. Mean contents of sediment lipids, mainly fatty acids, alkanes and alcohols, over the upper 5 cm showed that the highest concentrations occurred in September 1996 (Galéron *et al*., 2001). The distribution and concentrations of specific lipids are considered to be good indicators of the level of benthic activity in the deep sea (Smallwood *et al*., 1999).

Prionospio sp. 613 suddenly increased in mean abundance during July 1997 (Fig. 5.9.). However, this increase was not sustained and returned quickly to values similar to pre-'*Amperima* Event'. The proportion of individuals of this species in relation with all spionid fauna also was greater during pre-'*Amperima* Event' period (12.1% against 10.9%). Possibly, individuals of this species took advantage of favourable environmental conditions in terms of food availability only in late 1996. Several biogeochemical parameters such as sterols, silicic acid, biogenic silica, sterols, particulate organic

carbon, and suspended particulate material were recorded from PAP in higher concentrations between September 1996 and March 1997 and might explain the increase in abundance seen by this species. Later, in the following cruises, this opportunistic behaviour was not successful than July 1997 as a decrease was recorded. The highest densities recorded for *Prionospio* sp. 81 and *Prionospio* sp. 613 from July 1997 would suggest a time-lagged response to the summertime pulse in food input in 1996 in agreement with Galéron *et al*., (2001) for macrofaunal polychaetes from PAP. Drazen *et al*., (1998) recorded increases in density in some macrofaunal taxa in the abyssal Pacific, which occurred about eight months after a peak in the deposition of particulate organic carbon. Long-term dynamics studied from shallow-waters in *Prionospio peruana* have also showed fluctuations and high temporal variability (Carrasco & Moreno, 2006) as well as rapid increases in abundance with organic enrichment (Cañete *et al*., 2000).

5.2.1.2.2. The spionid assemblage

Temporal variability in the family Spionidae was largely defined by the changes in the abundance of the dominant species. The five most abundant species, discussed above, accounted more than 82% of spionid fauna. The species composition showed a similar structure to that of the Cirratulidae. Two to three species dominated in terms of abundance, but a greater number of genera were represented in the Spionidae. Among the less-common species of Spionidae, four species of *Laonice* and two species of *Spiophanes* were recorded throughout sampling periods.

Overall differences were detected between 'pre-*Amperima*' and '*Amperima* Event' periods, where the mean abundance increased twofold (13.6±5.9 against 26.4±10.9) in the second period. Although significant differences were observed between cruises and periods at the family level for Spionidae, these differences were not always apparent in the dominant species. These would indicate that the '*Amperima* Event' did not affect all species in the same way. Some species appeared to respond to short-term environmental reproductive factors and others to longer-term changes.

In relation to the rest of species, it is possible to identify three groups of species. The first group of species appeared from April 1994 or September 1996 with low abundance followed by a slight increase and in the latter samples this abundance is maintained. A second group can be defined by species that only appeared in May 1991 with low abundance but which then disappeared. Finally, a third group with species present

throughout all cruises but with temporal fluctuations in abundance. This analysis shows that there are changes in species composition and that temporal patterns observed in non-dominant species cannot easily be attributed to changes in the nutrient regime. It has not been possible to relate temporal changes of these species to specific factors.

The proportion of individuals belonging to the rest of species in relation with total of spionids was slightly greater during pre-'*Amperima* Event' cruises (Fig. 5.23.). This could indicate that the role of these species was more important during pre- '*Amperima* Event' period and that their prominence diminished with time due to the greater increase of the dominant species. However, it is not possible to establish interactions between non-dominants and dominants species. Significant differences were observed for the non-dominant species group when their abundance is compared between 'pre-*Amperima*' and '*Amperima* Event' periods ($P<0.02$). This would demonstrate that the temporal variability of the non-dominant species, considered as a group, would be mainly determined by the increases in abundance detected during the '*Amperima* Event' cruises. Temporal variability in the mean number of individuals observed in the non-dominant species group coincides with the trend observed by Spionidae (whole family) and the majority of dominant species, where the maximum abundance was recorded from samples taken by cruises after the start of '*Amperima* Event' (e.g. July 1997 and March 1998). Although all dominant species do not show the same pattern and so the response to the environmental forcing is not consistent, a time-lagged response to the deposition of phytodetritus to the seabed which had its peak in 1996 could be hypothesized in the Spionidae at both family and species levels.

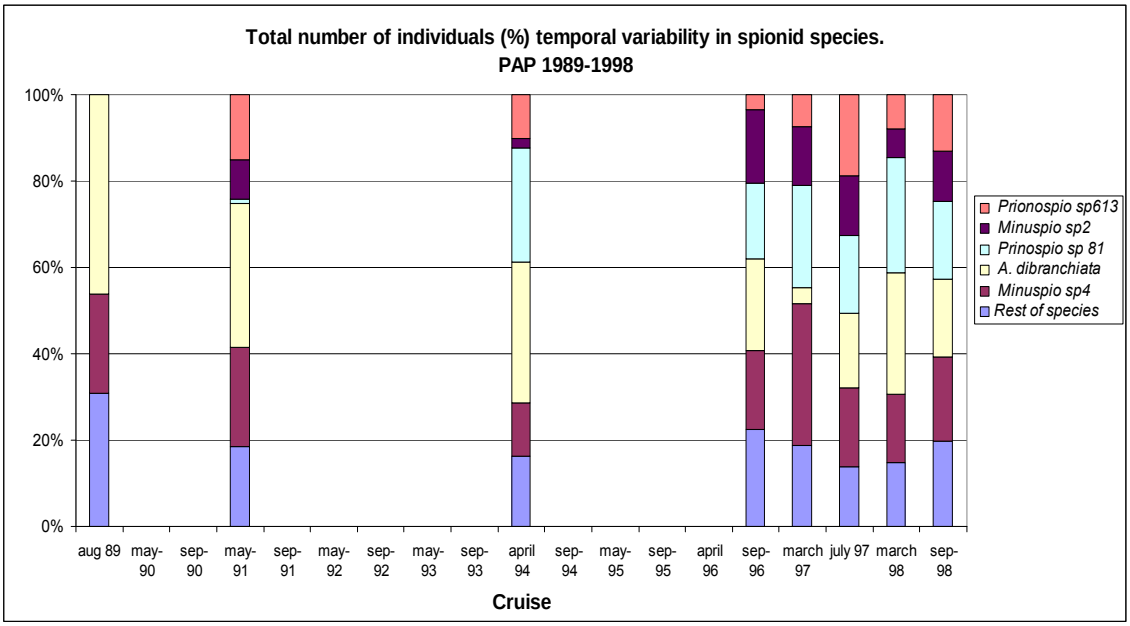


Figure 5.23. Total number of individuals (%) in five most abundant spionid species and the rest of spionid species between 1989 and 1998.

5.2.1.3. Paraonidae

5.2.1.3.1. Dominant species and rest of species group

Temporal variability in the family Paraonidae was characterized by the dominance of *Aricidea* species in terms of number of individuals and species richness. The three most abundant species, *Aricidea* sp. 676, *Aricidea* sp. 36 and *Aricidea* sp. 678E accounted for 45.4% of paraonid fauna, while seven most abundant species, that included two species of *Levinsenia*, accounted for 72.7% of paraonid fauna. The temporal variability of the most abundant paraonids species showed a slight decreasing trend in mean abundance with time. In *Aricidea* sp. 676 the greatest mean abundances were recorded in May 1991 and April 1994 (pre-'*Amperima* Event'). The proportion of individuals in relation with total of paraonids, was higher during pre-'*Amperima* Event' cruises. Variations in abundance between periods showed significant differences (P<0.03).

In *Aricidea* sp. 36 the greatest abundance was recorded in August 1989 but statistical analyses showing no significant differences between cruises and periods (P>0.1). In *Aricidea* sp. 768E despite the higher abundances were observed during '*Amperima* Event', significant differences were not detected between cruises and periods (P>0.1). Analyses of temporal patterns in *Aricidea* sp. 28, *Aricidea* sp. 5, *Levinsenia* sp. 3 and *Levinsenia* sp. 1 also showed little in the way of trends, although there was a potentially

slight decrease (negative response) which coincided with environmental conditions triggered during the '*Amperima* Event'. Any temporal changes that were apparent and abundances in both 'pre-*Amperima*' and '*Amperima* Event' cruises were slight.

Temporal trends observed in dominant species, were also mirrored by the remaining non-dominant species when they were considered together as a group. A decreasing trend also was recorded in this group, with the greatest abundance occurring during the pre-'*Amperima* Event' cruises, but in all cases the number of specimens was very low. No significant differences were observed in mean abundance between cruises (P>0.05), however these differences were significant between 'pre-*Amperima*' and '*Amperima* Event' periods (P<0.03). In addition, the proportion of individuals of this group in relation with all paraonids also was higher during pre-'*Amperima* Event' cruises (Fig. 5.24.). Therefore, the response of the paraonids species to the '*Amperima* Event' could be considered as a slight decrease in mean number of individuals with time.

5.2.1.3.2. The paraonid assemblage

The number of species recorded in Paraonidae (n=24) was greater than in Cirratulidae (n=19) or in Spionidae (n=16), even though that the total number of individuals was four and three time less respectively. This high species richness was also reported by Hilbig & Blake (2006), for the northeast Pacific at depths between 550 and 3100 m, where 41 species of Paraonidae were recorded. In a survey of the continental slope conducted off San Francisco, paraonids were the most diverse polychaete family with 33 species (SAIC, 1992), while on the Carolina continental slope, northwest Atlantic 35 species of paraonids were recorded with 15 species of *Aricidea* (Hilbig, 1994). In contrast, the ANDEEP programme conducted during 2002 and 2005 in the Scotia and Weddell seas, Antarctica found only fourteen species of paraonids (Blake *et al*., *unpublished*).

Variation of species diversity may be related to productivity in the northeast Atlantic because greater richness was recorded in the EUMELI Project at an eutrophic site (n=9), while at the mesotrophic and oligotrophic sites 6 and 1 species of Paraonidae were recorded, respectively (Cosson-Sarradin *et al*., 1998). Similar results were obtained by Glover (2000) who found more species of paraonids at an Atlantic site (n=20) than at EqPac and NODULE sites in the Pacific (n=10 and 8, respectively). However, the relationship between productivity and species diversity is not very clear (Paterson *et al*., 1998; Glover *et al*., 2002; Paterson *et al*., 2006). So care must be taken when trying to relate diversity to productivity.

In overall terms, total and mean numbers of individuals in Paraonidae species were one order of magnitude lower than in Cirratulidae and Spionidae. In some species abundance decreased with time although the total numbers collected were very small. These decreasing patterns were apparent during the '*Amperima* Event' period as significant differences were not detected between cruises and periods (P>0.1). *Aricidea* sp. 676 was the only species that recorded significant differences in its abundance between 'pre-*Amperima*' and '*Amperima* Event' periods. However this difference was due to significantly higher abundances recorded between August 1989 and April 1994 in contrast to the '*Amperima*' period.

The response of the paraonids to '*Amperima* Event' was very different to that of the cirratulids and spionids. Multivariate analyses would indicate that changes in species composition were more important than changes in number of individuals through time. Several species were recorded only in pre-'*Amperima* Event' cruises, while others species were recorded only during '*Amperima* Event' cruises. The high average dissimilarity (76.8%) observed between groups would support these conclusions. Environmental factors related to behaviour, feeding strategy and/or competition with other deposit-feeder populations, such as cirratulids or spionids, or even some megafaunal components, could explain the temporal variability observed in paraonid species.

Species of Paraonidae were not the dominant component of the polychaete community. The Paraonidae accounted for 7.3% of all polychaetes. The most abundant paraonid, *Aricidea* sp. 676 only accounted for 1.4% of total polychaete fauna recorded in whole study period.

However, paraonids have been found to be dominant in some deep-sea polychaete assemblages. *Aricidea simplex* was ranked second in terms of abundance (8% of all polychaetes) in the northeast Pacific, California with peak abundances at 2400-2500 m (Hilbig & Blake, 2006). The species *Aricidea ramosa, Paraonella monilaris, Levinsenia* sp. 5 and *Levinsenia* nr. *flava* were common also at other depths. Several paraonids have been recorded as dominant species, such as *Cirrophorus brevicirratus* from Antarctic Peninsula (Hilbig *et al.* 2006), *Aricidea* sp. from Madeira Abyssal Plain, northeast Atlantic (Glover *et al*., 2001), *Aricidea* sp. 752 from EUMELI Project oligotrophic site, 4600 m (Cosson-Sarradin *et al*., 1998), *Aricidea tetrabranchia* from the NW Atlantic abyss (Paterson *et al*., 1994), *Aricidea* sp. 1 and *Aricidea* sp. 2 from

Antarctica (Blake & Narayanaswamy, 2004), *Levinsenia gracilis* and *Paraonella* sp. 1 from northwest Gulf of Mexico (Pérez-Mendoza *et al*., 2003).

5.2.1.3.3. Causes explaining the paraonids response

Low abundance and overall decrease in paraonids could be related to lower food supply availability and competition with other polychaete populations. Although the scheme for trophic groups described in Fauchald and Jumars (1979) remains untested for deep-sea species and, therefore represent only a hypothesis of trophic preferences (Paterson *et al*., 1998), paraonids would be considered as surface deposit feeding, motile and with other feeding structures or non-jawed (SMX) (Fauchald & Jumars, 1979; Paterson *et al*., 1998; Glover, 2000). However, Blake (1996c) considered them to be subsurface deposit feeders. Paraonids appear to live in vertical burrows and some species, such as *Levinsenia gracilis*, twist their bodies into a tight corkscrew and this may facilitate water movement through the burrow. In this study paraonids are considered to be surface deposit feeders.

Cirratulids and spionids were highly dominant in the current study. They are surface deposit feeders like paraonids, however cirratulids are motile and tentaculates, while spionids are also tentaculates, discretely motile and considered to be opportunistic (Grassle & Morse-Porteous, 1987; Hilbig, 2001). Spionids also may switch between deposit and suspension feeding strategies (Blake, 1996b). Therefore, cirratulids and spionids were perhaps better able to take advantage of the increased nutrients arriving at the sediment surface because of their morphological and behaviour traits. As a result they increased in abundance during the '*Amperima* Event' conditions. One of the consequences to this increase could be the decreasing of paraonid species due to competition for food. Studies showing the most rapid uptake of ^{13}C-labelled diatoms signatures by Cirratulidae and Spionidae indicate that nutrients were readily assimilated. This investigation assumes that strong competition for food in the abyssal benthic food-web was present, and therefore the development of different feeding strategies took place. Highly specialized surface deposit-feeding organisms seemed to out-compete or perhaps were better able to assimilate incoming nutrients than other types of deposit feeders, e.g. subsurface deposit-feeders (Aberle & Witte, 2003). Experiments made in the Carolina margin, northwest Atlantic, showed that specimens of *Aricidea* sp. consumed rapidly phytodetritus (Aberle & Witte, 2003). However, current results from

PAP indicate that species of cirratulids and spionids were more successful in this sense, because they significantly increased in abundance while paranoid species not.

Competition for food also could be linked to megafaunal organisms. The increase in the abundance of the deposit feeding holothurians such as *Amperima rosea* was particularly striking (Bett *et al*., 2001). They were so abundant that they were consuming the influx of phytodetritus as quickly as it arrived (Iken *et al*., 2001). Many polychaetes feed directly on phytodetritus, and so are likely to respond quickly and directly to its accumulation on the seabed (Vanreusel *et al*., 2001). However species which rely on the accumulation and migration of nutrients into the sediment are likely to be at a disadvantage in these kinds of situations, so species belonging to the Paraonidae had less food and therefore they were less abundant.

Another explanation for the temporal response observed in Paraonidae could be linked with the possible development of a subsurface deposit feeding behaviour. Species of paraonids showed a decreasing pattern with time. However, the mean number of individuals in the 1-3 cm sediment layer increased by a factor of two between September 1996 and July 1997. While the proportion of individuals in the 0-1 cm top layer decreased from September 1996, the proportion of individuals in the 1-3 cm sediment layer increased from the same date, becoming greater than 0-1 cm sediment layer in March 1998. In March 1998 ~50% of paraonids were concentrated in 1-3 cm sediment layer, while ~45% were concentrated in 0-1 cm sediment layer. It seems likely that paraonids species responded to high competition for food in the surface sediment layers. Therefore, paraonids were distributed throughout the sediment column and they had moved deeper into the sediment because there was more food available in the subsurface layers for them. Jumars *et al.* (1990), claimed that when food is scarce it is advantageous to store food, out of the reach of competitors, and therefore most organisms in these highly food-limited abyssal regions are found beneath the sediment surface. In the face of food scarcity and strong competition changes in the vertical distribution were observed in paraonids developing a feeding strategy typical of subsurface deposit feeder polychaetes. In July 1997 the surficial layer of sediment, became impoverished in labile lipids (Galéron *et al.*, 2001) and phytopigments (Witbaard *et al*., 2000), probably as a result of benthic megafaunal and microbial utilisation during this period. In July 1997, higher quantities of phytopigments occurred in the 1-2 cm layer than in the 0-1 cm layer of sediment (Witbaard *et al*., 2000). Small infaunal species may have responded to the chemical properties of the sediment by

changing their vertical distributions (Lambshead *et al*., 1995, Soetaert *et al*., 1997). In contrast, Paterson *et al*., (1998) concluded for an oligotrophic site that low abundance of nutrients were unlikely to be bioturbated into deeper layers of the sediment, this would mean that subsurface species were unlikely to be able to survive in deeper layers. It is likely that surface groups such as the paraonids may be able to migrate within the sediment following the availability of food. A similar situation could be happening in PAP.

Finally, a higher bioturbation of the top layer of sediment, as a result of the increase of large megafaunal deposit feeders (e.g, holothurians) and deposit feeders polychaetes, may also have contributed to a downward movement of paraonids and/or their decrease in abundance, as suggested by Lambshead *et al*., (1995) for infaunal organisms seeking to avoid physical disturbances. This hypothesis already has been postulated by Glover *et al*., (2001) for PAP site in terms of high megafaunal activity and bioturbation enhance the depth profiles of polychaetes. These authors would suggest when there is more food available with depth more species are able to survive. This would account for the ability of paraonids to survive in subsurface layers. This is supported by the observation that there was an increase in paraonid abundance in the 1-3 cm sediment layer in July 1997, while a decrease in abundance was recorded in the top 0-1 cm sediment layer. In addition, the proportion of paraonids in the 1-3 cm sediment layer in March 1998 was higher than in the 0-1 cm sediment layer.

In the first case, downward mixing of phytopigments into the subsurface sediments would be being made by holothurians. Holothurians by means of their feeding and locomotory activities contributed to some of the churning up of the phytodetritus with the sediment (Bett *et al*., 2001). Significant phytodetrital material pulses occurred in June-July 1997 (Lampitt *et al*., 2001) and may also have been subducted into subsurface layers of sediment by burrowers such as echiurans (Bett & Rice, 1993) and sipunculids, which were found in the 1-3 cm layer of sediment. Macrofaunal deposit feeder polychaetes may have contributed also to biomixing of the organic matter (Galéron *et al.,* 2001). In addition, infauna may play a major role in reworking the arriving organic material by incorporation, redistribution and vertical mixing within the sediment column (Aberle & Witte, 2003).

In the second situation, the bioturbation of the surface layer resulting from the feeding and locomotion activities of megafauna and due to the increase in abundance and activity of several macrofaunal organisms, polychaetes included, may have contributed

to exodus of paraonids species, and therefore, the decrease of paraonids population in that site. This hypothetical change would suggest avoiding physical disturbances of their habitat and the search of better conditions to live.

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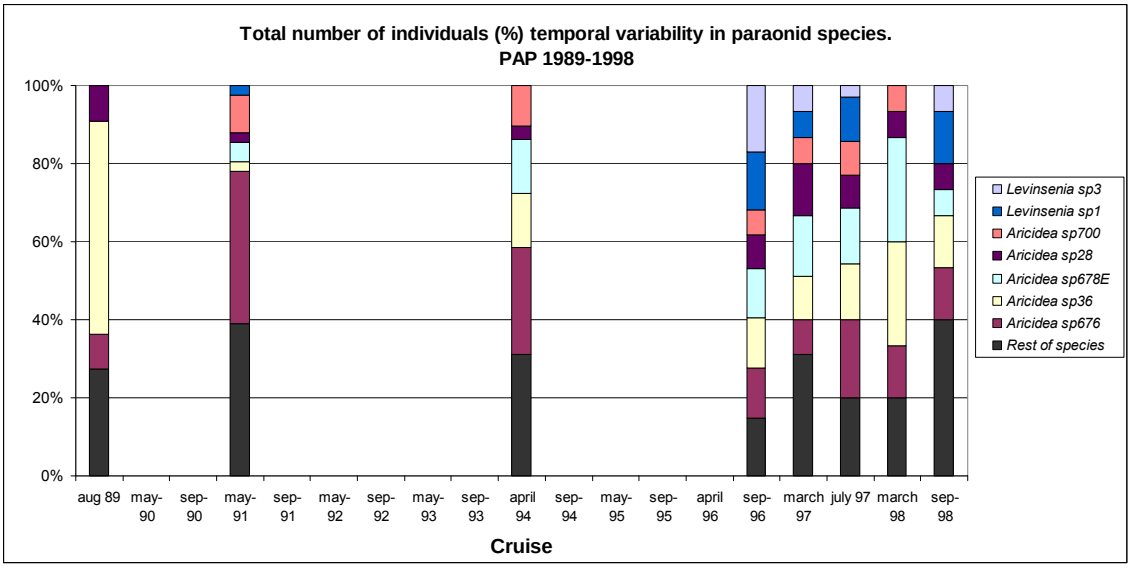

Figure 5.24. Total number of individuals (%) in the seven most abundant paraonid species and the rest of paraonid species between 1989 and 1998.

5.2.1.4. Pilargidae

5.2.1.4.1. *Sigambra magnuncus* and the pilargid assemblage

The Pilargidae was not a common family in terms of abundance. In addition to Cirratulidae, Spionidae and Paraonidae, several other polychaete families, such as Opheliidae, Sabellidae, Capitellidae and Ampharetidae were more abundant than the Pilargidae. The total fauna of the Pilargidae contributed with only 3.2% of all polychaetes. In trophic terms, the pilargids were the most abundant predator group (family) in the PAP sediments followed by syllid polychaetes.

Temporal changes in the Pilargidae were defined by the high dominance of *Sigambra magnuncus* in terms of abundance and frequency of occurrence. *Sigambra magnuncus* was as abundant as several species of Cirratulidae and Spionidae and greater than any species of Paraonidae.

Sigambra tentaculata from Sigsbee Basin, northwestern Gulf of Mexico has been reported among the most abundant species (Pérez-Mendoza *et al*., 2003). Studies made in different north east abyssal Atlantic sites such as Cap Verde abyssal plain (CVAP), Madeira (MAP), Tagus (TAP) and Porcupine (PAP) Abyssal Plains have found

high abundances of *Sigambra magnuncus* (Paterson *et al*., 1994; Glover *et al*., 2001 called S*igambra* sp., Paterson & Glover, 2000). This species is larger at sites with phytodetrital input (Paterson *et al*., 2006). These authors, together with Blake (1997), suggested that *Sigambra* species such as *S. magnuncus* are predators or omnivores. The increase of other polychaete populations together with macrofaunal and meiofaunal organisms (Galéron *et al.*, 2001) during the '*Amperima* Event' would provide a wider food supply (prey species) for *S. magnuncus* such as nematodes, foraminiferans, etc. Although there is no direct evidence pilargids would eat deposit feeder polychaetes because there is little observational evidence on their feeding habits (Fauchald & Jumars, 1979), several authors conclude that pilargids are carnivores (Day, 1967; Blake, 1997; Salazar-Vallejo, 1990). They have eversible proboscis should be capable of capturing preys despite the lack of armature (Blake, 1997). Therefore, it is possible that there was some kind of predation of pilargids on deposit feeder polychaetes at PAP site; however this hypothetical predation would not be exclusive of pilargids. Predation on deep-sea polychaetes would be also attributed to other predator polychaetes and some megafaunal organisms.

A second possible explanation to increase in abundance of *S. magnuncus* in '*Amperima* Event' cruises could be related to development of opportunistic behaviour in the deep sea. Several authors have reported large numbers of a few species of dorvilleid and hesionid polychaetes, which are predators like pilargids, colonising organically-enriched sediment trays (Desbruyères *et al*., 1980; Grassle & Morse-Porteous, 1987; Snelgrove *et al*., 1994, 1996). These species seem to be opportunistic, able to respond quickly to relatively high levels of organic enrichment (Vanreusel *et al*., 2001) and also feeding on a number of different food sources. Pilargids are free-living, surface sediment dwellers (Glasby *et al*., 2000). Paterson & Glover (2000) however found this species within the sediment rather than on the surface at Atlantic deep-sea sites. Perhaps a similar behaviour could be expected in deep-sea pilargids in response to higher levels of organic input. The presence of chambers in each segment of *Sigambra* species would improve the digestion of detrital material contributing probably to develop a deposit feeding behaviour (S. Salazar-Vallejo, *Pers. comm.*). However, investigations carried out on *Nepthys* and *Nereis* suggests that digestion in polychaetes generally would happen up near the junction of the pharynx and foregut (G. Paterson, *Pers. comm*.)

The rest of pilargids species were characterized by very low abundance and presence in all cruises. Increases in abundance at the time of the '*Amperima* Event' were evident

in the total of pilargid species. The sudden increase in abundance in September 1996 would appear to support this hypothesis. Significant differences were detected in both total Pilargidae and *Sigambra magnuncus* between periods (P<0.02). In terms of species richness, an increase was observed from September 1996, though this variation could be associated with sample number. PAP pilargids were not very diverse coinciding with the results reported by Glover (2000) for PAP and Pacific sites, and with the results reported by Hilbig & Blake (2006) in the northeast Pacific. Multivariate and Similarity analyses suggest that temporal changes in species of this family could be related to '*Amperima*' effect. In addition, all species of pilargids were recorded during '*Amperima* Event' cruises. Also the increase in *S. magnuncus* mean abundance was observed from September 1996 cruise. Significant differences between 'pre-*Amperima*' and '*Amperima* Event periods (P<0.02) were observed in the rest of species group (*Sigambra magnuncus* not considered). The pilargids population increased almost three times the mean number of individuals per cruise. Therefore, the community structure in terms of species composition and the number of individuals were highly affected at the time of '*Amperima* Event'.

5.2.1.5. Glyceridae

5.2.1.5.1. *Glycera* sp. 726 and the glycerid assemblage

The Glyceridae are not common in the deep sea. Glycerids are less diverse than in typical shallow-water assemblages (Hilbig, 1994). Deep-sea species belonging to this family have been found in Antarctic sediments (Hilbig, 2004; Blake & Narayanaswamy, 2004; Hilbig *et al*., 2006; Schüller, 2007), north Atlantic (Glover, 2000), Pacific U.S. sites (Glover, 2000; Hilbig & Blake, 2006; Smith *et al.,* 2008) and Gulf of Mexico (Pérez-Mendoza *et al*., 2003), but they always have been recorded in low abundance. Exceptions have been reported by Paterson (1993) from the Rockal Trough, NE Atlantic, where *Glycera tesselata* is one of the most common species and Blake & Grassle (1994), from U.S. South Atlantic slope off the Carolinas, where two glycerids such as *Glycera capitata* and *Glycinde profunda* were dominant. Hilbig *et al*., (2006) found high abundance of *Glycera kerguelensis* from Weddell Sea and Antarctic Peninsula. The identification and description of PAP glycerid specimens will need more work, so they could contribute to the record of new deep-sea species in the northeast Atlantic site.

Temporal variability in Glyceridae was characterized by the appearance of the majority of species from September 1996, albeit with low mean abundance. *Glycera* sp. 726 was the only one species that appeared in cruises pre-'*Amperima* Event' (e.g. April 1994). This species was recorded in all subsequent cruises but its mean abundance was always low. Temporal patterns in mean number of individuals were similar in both Glyceridae and *Glycera* sp. 726. Despite species and mean abundances that were recorded during the '*Amperima* Event' cruises, there was little variation in the mean number of individuals between cruises which did not suggest that any of these changes were due to '*Amperima* effect'. In fact, no significant differences were detected between cruises in Glyceridae and *Glycera* sp. 726 (P>0.3). However, these differences were significant in Glyceridae between 'pre-*Amperima*' and '*Amperima* Event' periods (P<0.003). Although multivariate analyses did not show clearly differences, major changes occurred between September 1996 and July 1997, where the mean abundance and species richness were greater. The higher phytodetritus input from the surface and organic enrichment of the sediments had place during these periods (Lampitt *et al*., 2001; Witbaard *et al.*, 2001; Rabouille *et al*., 2001), which generated an overall increase in meiofauna, macrofauna and megafaunal organisms (Galéron *et al.*, 2001; Billett *et al*., 2001; Bett *et al.*, 2001). Therefore, a greater supply of prey was available for predators. Glyceridae are considered to be carnivores, discretely motile and jawed (CDJ) (Fauchald & Jumars, 1979), so increases in abundance of glycerids would respond to development of this trophic condition. Glycerids eat polychaetes (Fauchald & Jumars, 1979) and amphipods (Retière, 1967; Michel, 1970), while *Glycera alba* is a carnivore, preying upon a range of motile infaunal or epifaunal invertebrates (Rouse & Pleijel, 2001). All these organisms were abundant during '*Amperima* Event' cruises (Galéron *et al.*, 2001). Therefore, glycerids probably were favoured by the general increase in abundance of macrofauna. In contrast, several authors have reported detritivore habits for glycerids (MacGinitie & MacGinitie, 1968; Hartmann-Schröder, 1971; Wolff, 1973; Qafaiti & Stephens, 1988). Fauchald & Jumars (1979) postulated that bathyal and abyssal glycerids may able to use both modes of feeding and that glycerids living in nutrient-rich environments may supplement either feeding mode by direct uptake of dissolved organic matter. This omnivore/predatory feeding strategy might explain the higher abundance observed from September 1996, where greater and better nutrient conditions and a greater amount of prey were characteristic conditions in the PAP seabed. An explanation why this increase was not large and

persistent in time, as in some cirratulid and spionid species, could be related to competition with other predators such as species of Syllidae or Pilargidae.

5.2.1.6. Dominant species

Multivariate analyses would indicate that changes were evident between 'pre-*Amperima*' and '*Amperima* Event' periods. The most dominant species of Cirratulidae and Spionidae such as *Aphelochaeta* sp. 13A, *Chaetozone* sp. 1, *Minuspio* sp. 4, *Aurospio dibranchiata* and *Prionospio* sp. 81 played a major role into the polychaetes assemblage. The higher abundance and frequency of occurrence recorded in these species defined and characterized the temporal variability observed in the PAP sediments. These species should be considered as permanent residents of the PAP seabed. Changes in some of these species were evident, with significant differences being detected between cruises and 'pre-*Amperima*' and *Amperima* Event' periods. However, no response was observed in some dominant species. A different response was observed in paraonid species, where significant changes in mean abundance were not as evident during '*Amperima* Event' cruises, although there was a slight decreasing temporal pattern with time. Analyses also would demonstrate that changes in species composition were present in the overall temporal evolution. Studies of dominant species offer some explanation of the observed variability within polychaete families, however, not all species showed the same response to the same phenomena and environmental conditions. The high diversity of species recorded in Cirratulidae and Spionidae, whether a great number of behaviour and life histories take place could be related to the different responses observed. Some paraonid species possibly developed a subsurface deposit feeding strategy and, therefore, they showed a different temporal pattern and response with time. A small burrowing opheliid polychaete species appeared to demonstrate episodic recruitment as it was present only as small juveniles individuals (<400 μm) at one period in the time series (September-October 1996) (Vanreusel *et al.*, 2001). Observations on capitellids also could suggest a similar situation.

Predator species such as pilargids and glycerids did not show the same pattern as the surface deposit feeders. Abundance and species richness in the first group was remarkably lower than in surface deposit feeders and its presence in pre-'*Amperima* Event' was scarce. Finally, all surface deposit-feeder species did not show the same observed temporal variability as at family level. This last observation suggests that

carrying on with the time series at species level in other less abundant families such as Syllidae, Opheliidae, Sabellidae and Ampharetidae would provide more data with which to test some of the observations discussed. Analyses of body size may prove useful in relating polychaete ecology to the effect to levels of food input.

This study indicated that the '*Amperima* Event' had an important effect in some polychaete species in terms of changes in abundance and frequency of occurrence with time. However, the influence of the '*Amperima* Event' on some polychaete species may be indirect. The '*Amperima* Event' generated a change in the physical and ecological conditions of the seabed environment. The sudden increases in abundance of two holothurian species, *Amperima rosea* and *Ellipinion molle*, by three orders of magnitude, had important implications for organic material cycling at the sediment surface (Billett *et al*., 2001). The effect of these holothurians could have increased the diversity of polychaete species through repackaging organic matter. The increase in megafaunal activity (holothurians and ophiuroids) was also having a significant impact on sediment geochemistry and hence on the rest of the benthic communities (Ginger *et al*., 2001) as in polychaete assemblages. The increase of bioperturbation and the physical disturbances could explain the different responses shown by some dominant species. However, competition should be carefully considered as disturbance more often resets any competitive situation because it removes competitors or creates new space which is then colonised by a new group of species and it takes time for competition to start.

So in summary, the increase in the seasonal deposition of phytodetrital had as its main consequence the organic enrichment of the deeper water column and of the sediments and the increase in the concentration of several associated biogeochemical components. The benthic response to these food inputs was evident among many deposit feeder polychaete species, as a rapid increase in abundance at the time when this natural phenomenon was detected. The organic matter supply input to the seabed through the deposition of phytodetritus was mainly the processes responsible for the observed changes in polychaete abundance and species dominance. Some dominant species clearly were favoured by this greater food supply, although not all responded in the same way.

CHAPTER 6

6. GENERAL DISCUSSION

Long-term variability was detected in the polychaete assemblages on the Porcupine Abyssal Plain. The greatest temporal changes in abundance and diversity at the family level occurred during the '*Amperima* Event'. Several differences were statistically significant. These were changes in mean abundance of polychaete assemblage through time, in the 0-1 and 1-3 cm sediment layers, the families Cirratulidae, Spionidae and Opheliidae, and certain trophic groups (surface deposit feeders, predators and burrowers). Significant differences were also found in mean abundance by sediment layers, some families, trophic groups and species when samples were grouped into pre-'*Amperima* Event' and '*Amperima* Event' periods.

At the species level *Aphelochaeta* sp. 647D, *Prionospio* sp. 81 and *Minuspio* sp. 4 showed a clear response. The temporal variability of these species showed significant differences in mean abundance between cruises and between pre-'*Amperima* Event' and '*Amperima* Event' periods. *Aphelochaeta* sp. 647D and *Prionospio* sp. 81 showed a trend of an increase in abundance with time. *Minuspio* sp. 4 recorded the greatest abundances during the '*Amperima* Event' cruises. So such changes are likely to be a response to the environmental factors associated with the '*Amperima* Event'. Considering only the statistical analyses results, these species showed a similar response to that observed at family level. However the underlying patterns of temporal variability were not necessarily the same.

While significant differences were observed for some elements of the fauna, this was not always mirrored by all polychaete families, species or their abundance in the different sediment layers. No significant differences in mean abundance were detected for 3-5 cm sediment layer (between cruises) or in the family Paraonidae (between cruises and pre-'*Amperima* Event' and '*Amperima* Event' periods).

At the family level, mainly in Cirratulidae and Spionidae, there was an obvious and significant response. However, many of the species within these families did not show a clear response. Differences detected by the ANOVAs did not always result from changes associated with the '*Amperima* Event'. This situation was observed in the temporal variability of *Chaetozone* sp. 1, *Chaetozone* sp. 55A and *Prionospio* sp. 613. The response of these species was complex and was characterized by low or high

abundance in particular cruises. It was this variation which generated significant differences detected by ANOVA analyses of cruises. There was no '*Amperima*' effect on temporal variability of these species, although greater abundances have been recorded in some cases during the '*Amperima* Event' cruises. The causes, which might explain these responses, are diverse and difficult to isolate. Whatever signal these species were responding to it was not associated with this Event.

Aphelochaeta sp. 13A and *Aurospio dibranchiata* did not show an apparent response at all through time. Despite that the highest abundance was recorded during the '*Amperima* Event' cruises no significant differences were detected. In these two species temporal changes could not be attributed to the '*Amperima* Event' conditions *per se*. It is likely that they may be related to variations in the organic matter flux but more data are needed to verify this.

The answer to the question: Why do many of the species not show a response when there is an obvious and significant response at family level? is complex and remains without a clear answer. The assessment of changes and what drives it should be undertaken carefully. To explain temporal changes in deep-sea polychaete species is not easy, particularly as the biology of these species is unknown. Only in *Aurospio dibranchiata* have investigations of recruitment and seasonal reproduction been studied (Blake & Watling, 1994). The current results have demonstrated a range of responses through time even among species belonging to the same genus and family. Therefore, there is a clear conclusion that the most abundant species did not always mirror the temporal variability observed at family level.

This is not surprising as species within the same family may have very different responses to environmental stressors. For example, certain *Prionospio* species may inhabit an area where the temperature range is quite high (~5 to 6º C), whilst other spionids, e.g. *Spiophanes kroyeri,* can inhabit regions where the temperature range is quite low (<1ºC). If the results from the different species are aggregated into one family, differences between areas or time are not as noticeable as those between species. Narayanaswamy *et al*., (2003) concluded that in the deep sea, species-level identification of polychaetes is preferable to that of family level-identification.

A high diversity of species within a family would allow the development of a greater number of strategies and behaviours. Different species may develop different patterns and responses with time. In foraminiferans, Murray (1967) has predicted that the majority of species seem to have population densities which are relatively stable, or at

least change in a random, non-seasonal manner which may reflect spatial patchiness rather than temporal change (niche partitioning theory). This theory could be considered for deep-sea surface deposit-feeder species such as cirratulids and spionids. In fact, Narayanaswamy *et al*., (2003) argued that increased numbers of species leads to potentially greater variability of responses between the species and, therefore, when environmental factors are particularly variable this might account for the different patterns observed. Therefore, biogeochemical parameters of the sediment and depth water column will have a significant effect on polychaete composition and abundance. Species-level analyses also would indicate that other environmental variables, not measured or unknown, might account for a higher proportion of the variability at species level.

However, in the most abundant paraonid species the temporal response was very similar to the family level. A different response was only observed in *Aricidea* sp. 676. This species showed significant differences between pre-'*Amperima* Event' and post-'*Amperima* Event' periods, while at family level these differences were not detected. Different responses between paraonid and cirratulid/spionid species could be related to the development of subsurface deposit feeding behaviour in paraonids. Paraonids decreased in abundance with time and they changed their vertical distribution within the sediment, increasing in abundance in the 1-3 cm sediment layer from September 1996. The temporal pattern in cirratulids and spionids was totally different.

Therefore, the hypothesis, which is related to the decrease in abundance of surface deposit feeder polychaetes due to the seasonal variations of organic matter and the large increase in some holothurian population in the study site, should be accepted in consideration to paraonid polychaetes. By contrast, this hypothesis should be rejected because cirratulid and spionid populations increased in abundance at the time of the '*Amperima* Event'.

The general response of the PAP polychaete assemblage could be related to seasonal and interannual variations of organic matter input to the seafloor. A similar response has been documented by Drazen *et al*., (1998) in the Station 'M', Pacific Ocean. Protozoans and five dominant metazoan macrofaunal taxa (nematodes, polychaetes, harpacticoid, tanaids and isopods) exhibited seasonal increases in density during winter months after detrital aggregates had disappeared from the seafloor. Density and biomass of macrofaunal protozoans, mainly agglutinated foraminifera, increased significantly over a 4 week period following the deposition of phytodetritus. In the

same study site, small individuals of the holothurian *Peniagone* sp. increased substantially from October 1994 to June 1995 following a major phytodetrital pulse during the summer and autumn of 1994, suggesting a possible reproductive response (Lauerman & Kaufmann, 1998).

Rates of oxygen uptake also reflect the overall response of benthic communities to fluxes within a small area of seafloor (Gooday, 2002). Witbaard *et al*., (2000) measured the Sediment Community Oxygen Consumption (SCOC) at PAP among September 1996 and September 1998, obtaining non significant differences. The lack of response in some deposit feeders species could reflect differences in the quality of the organic matter reaching the seafloor (Turley & Lochte, 1990).

In the PAP, populations of meiofaunal species, a foraminiferan and an opheliid polychaete, responded to a pulse of organic input in summer 1996 with a rapid increase in abundance. The macrofaunal polychaetes showed a lagged response to the same event by slowly increasing in density. Tanaidaceans, bivalves and isopods moved down the sediment column in response to 1) the impoverishment and bioturbation of the surface layer and 2) the downward mixing of organic matter in the sediment (Galéron *et al*., 2001). Undoubtedly the clearest response to the organic matter supply, seen in benthic organisms was observed in the megafauna. Actiniarians, annelids, pycnogonids, tunicates, ophiuroids and particularly some holothurians increased significantly in abundance (Billett *et al*., 2001).

Although the megafauna showed a massive response this was not reflected in the polychaetes. The response in the most dominant polychaete species was much less pronounced. Only three species: *Aphelochaeta* sp. 647D, *Prionospio* sp. 81 and *Minuspio* sp. 4 showed a similar response than the families. However, *Chaetozone* sp. 1, *Chaetozone* sp. 55A, *Prionospio* sp. 613, *Aphelochaeta* sp. 13A and *Aurospio dibranchiata* showed differences with the family level when comparisons between cruises and periods were made.

The response at family level is the result of a wide variety of responses from different species. Each species will respond in a particular way to environmental factors in relation with their biology, behaviour and feeding strategies. The different temporal and spatial distribution of the species in the seafloor and therefore the different exposing to organic matter fluxes, levels of competition, physical disturbances and other factors also will determine different levels of response in the species that make up a family. Therefore, the ecology of a family is not necessarily the expression of the ecology of the

most dominant species. The current study would demonstrate that in deep-sea polychaete families with a high diversity of species, the overall response would be determined for the role of all members of that family, whether species with different abundance and occurrence are participating.

In this sense, it will be possible to observe different and similar responses among the most dominant species and their respective family as well as for the non-dominant species as well. Therefore, the assessment of the temporal changes and its meaning at family level should be considered carefully as many times the responses at species level are so different that they may respond to another causes.

Temporal variability at family level should be determined by a series of factors and variables, while temporal changes at species level should be explained by factors solely related to that species.

This study shows the importance of looking at all levels as the underlying patterns are complex and will tell us something about how the polychaete assemblages are likely to respond to change.

CHAPTER 7

7. CONCLUSIONS

7.1. Taxonomy

15 species of bitentaculate cirratulids were described. The majority of these species belonged to *Chaetozone* (8) and *Aphelochaeta* (6) genera. One *Tharyx* also was described.

Specimens were often characterised by being in poor condition and frequently showed an absence of the main characters. Nevertheless it was possible to separate different species based on a range of consistent morphological characters. The main taxonomic characters used in descriptions were the prostomium shape, the thoracic body shape, the position of the palps, the buccal region length, the presence or absence of 'bottle-brush' chaetae and its starting position, the chaetae length and the presence of acicular spines. A great deal of morphological variability was observed in these characters.

13 species of spionids were described most of them belonged to *Prionospio* complex such as *Minuspio* (3), *Prionospio* (2) and *Aquilaspio* (1). Two species of *Laonice* and two *Spiophanes* also were described. Difficulties in describing the morphotypes of this taxon mainly were in the absence and bad condition of the branchiae and missing posterior end. Characters such as prostomium shape, kind and number of branchia, occipital antenna, nuchal organ, dorsal crests, genital pouches, sabre chaetae, and presence and starting position of hooks were relevant in descriptions.

PAP deep-sea polychaetes are very small, which made descriptions difficult. This tendency would be related to a greater presence of broken and incomplete bodies on samples rather than the species are evolutionarily simplified. Therefore, new characters were found in order to establish more consistent diagnosis.

The current investigation constitutes a very important approach to taxonomy of deep-sea polychaetes from abyssal plains. The high diversity of observed forms and a more detailed description of the found species will allow the record of new deep-sea polychaetes species.

7.2. Temporal variability at family level

Temporal variability in the abundance, composition and family richness of polychaete assemblages was evident on the Porcupine Abyssal Plain between August 1989 and September 1998, occurring at the same time of the '*Amperima* Event'. Significant differences in abundance through time among families, trophic groups and in different layers within sediment were observed.

Changes in mean abundance were observed with time, the 0-1 and 1-3 cm sediment layers, the families Cirratulidae, Spionidae and Opheliidae, certain trophic groups (surface deposit feeders, predators and burrowers) and among pre-'*Amperima* Event' and post '*Amperima* Event' periods. No significant differences were detected for 3-5 cm sediment layer and the family Paraonidae.

These changes may be the response to changing ecological and oceanographic factors, the main one being an increase in food supply generated by seasonal nutrient inputs and particulate flux to the seabed from water column through the deposition of phytodetritus. While it is not possible to rule out a response to the sediment alteration and disturbance caused by large numbers of holothurians, this is perhaps less likely as the dominant groupings in terms of family and trophic group did not change. The reduced response of the polychaetes and other infaunal elements do suggest that the holothurians have been more successful in utilizing the nutrient influx.

The response of the infaunal polychaetes within the same time frame as both the megafauna and other infaunal components, such as the meiofauna, point to a widespread phenomena operating on short ecological timescales. This rapid response indicates that there is a much closer linkage between the processes operating in the upper ocean and the abyss. Climatic forcing which has been implicated in upper water column ecology may have a much more direct role in the abyssal sediment systems than was first thought.

7.3. Temporal variability at species level

At the species level a wide range of responses were observed with time. The most abundant cirratulid and spionid species not always appear to respond in the same way as the family. In some cases significant differences were detected between cruises and periods, while in another species none apparent response was detected with time. In the Paraonidae, where no apparent response was detected, the species level response in the most abundant species showed a similar pattern.

The diversity of responses would be determined by the high number of species, whether the biology of each species is different and its ecology highly variable in time.

Temporal changes in some polychaete species could be attributed to '*Amperima* Event' conditions. However, for polychaete species that did not response in a clear way to the '*Amperima* Event', their temporal variability observed appear to be related to interannual and seasonal variations in organic matter input to the seabed throughout the deposition of phytodetritus.

Food supply variations would be the main processes responsible for the observed changes in abundance and species dominance. The temporal variability showed in the polychaete fauna was more significant in abundance rather than species composition.

The most dominant species clearly were favoured by a greater organic matter flux because they are surface deposit feeders. Therefore, cirratulid and spionid species mainly defined and characterized the polychaete assemblage in PAP sediments. The increase in the seasonal deposition of phytodetrital pulses had as main consequence the organic enrichment of the deeper water column and of the sediments, as well as the increase in the concentration of several associated biogeochemical components. The benthic response to these food inputs was evident in some surface deposit feeder polychaete species such cirratulids and spionids, which increased quickly in abundance at the time when this natural phenomenon was evident. Species of paraonids that showed a possible subsurface deposit feeding behaviour responded in opposite way or they did not show an evident response to environmental conditions, while some predator species recorded a lower response than surface deposit feeder species. Changes in the nutrient flux did not have a generalised impact on polychaete species and macrofauna.

The '*Amperima* Event' caused a positive effect in some species of polychaetes. In these species this 'Event' defined temporal trends of increasing abundance. However, some

dominant polychaete species did not response or decreased in abundance. In greater or lesser degree, the '*Amperima* Event' would have defined the response of only some polychaete species.

7.4. Hypothesis review

This study set out to test the following hypothesis: Considering the seasonal variations of organic matter input such as the deposition of phytodetritus, and the large increase in some holothurian populations on the Porcupine Abyssal Plain during the periods 1996 to 1998, hypothesize polychaete community structure, in terms of ecological parameters such as abundance and family richness, increased at the time of '*Amperima* Event'.

Hypothesize that abundance of polychaetes, particularly surface deposit feeders may be depressed as a result.

The hypothesis that the polychaete community structure, in terms of ecological parameters such as abundance and family richness, increased at the time of '*Amperima* Event' should be partially accepted. The PAP polychaete assemblage showed an overall increase at the time of '*Amperima* Event'. However, some important member of the polychaete community such as paraonids did not increase during that period. Nor was the response uniform within the sediment column with only polychaetes living within the top 0-3 cm showing a response.

The second part of the hypothesis should be rejected. The abundance of surface deposit feeders was not depressed as a result of the activities of the holothurians. The majority of surface deposit feeder polychaetes such as cirratulids and spionids increased significantly in abundance during the periods 1996 to 1998. However, it should also be noted that many species showed no obvious response during the '*Amperima* Event'. In contrast some paraonids showed a slight decreasing trend in abundance with time; however the response was not statistically significant.

7.5. Future work and directions

The current investigation has demonstrated the temporal variability of a section of the polychaetes assemblage living at PAP in response to specific phenomena which determined the physical, biogeochemical and biological conditions of the studied environment. However, it would be interesting to improve the assemblage assessment by increasing the temporal coverage to study the response of the different polychaete populations to conditions 'post' phenomena ('*Amperima* Event'). This study should focus on the ecological parameters of the polychaete assemblages, such as abundance, composition and richness, in relation to biogeochemical parameters of the sediment and the deep water column. Thus, it would be possible determine the temporal 'evolution' of polychaetes in period whether the natural conditions do not be altered.

Longer time-series data would also resolve whether polychaetes have a specific response-time to an influx of new food; whether they exhibit a reproductive pulse as consequence of this food flux or show different life-history strategies in response to different food supply situations.

Food supply is one of the main factors driving the development of benthic communities in the deep sea. The current investigation showed species belonging to same trophic group responded in a different way to nutrients flux. Studies of the diet and of the gut and stomach contents in polychaetes would indicate their true feeding strategy. It also will help to find out the causes that determined the observed temporal variability in polychaetes.

Feeding strategies and behaviour remain untested for the deep-sea polychaetes (Paterson *et al*., 1998). Future studies should focus on physiological aspects with the aim of revealing the mechanisms and feeding strategies of the most dominant species when different sorts of food is available.

Megafaunal activity have demonstrated having a significant impact on sediment geochemistry and hence on the rest of the benthic community (Ginger *et al*., 2001). The phytosterols removal from the surficial sediments (Ginger *et al*., 2001) and the organic matter repackaging by holothurian species (D. Billett, *Pers. comm.)* would evidence certain link of this activity and the abundance of some deep-sea taxa. The availability of these components may be an important factor controlling the abundance of deep-sea polychaetes. Therefore, the comprehensive study of the food web

structure of the benthic fauna, focused on macrofauna such as Bivalvia, Tanaidacea, Isopoda and Polychaeta together with their temporal changes, would allow a better understanding of the energy flow from the sediment surface, particularly the potential impact of megafaunal activity. Also such a study would shed light on the possible ecological relationships among macrofaunal communities. Body-size studies in deep-sea polychaetes would improve our knowledge of each population in terms of growth, recruitment events, presence of larvae, juveniles and adult stages and reproductive cycles. Temporal and spatial body-size changes could be related to levels of nutrient flux variations. This would allow a greater test of the hypotheses suggested by Paterson *et al.,* (2006) that polychaetes in areas with higher nutrient fluxes reproduce earlier and are therefore smaller in body size (the allometric plasticity hypothesis). Therefore, the effect of seasonal or periodic food supply on polychaete body size should be investigated.

The regional influences on local species diversity require knowledge of the phylogenetic history of species (Glover, 2000). A comprehensive taxonomic study of the species belonging to this site would improve considerably its ecological knowledge. Future morphological and particularly molecular progress in deep-sea taxonomy would help further the historical understanding of the diversity and community structure.

What this and other studies on the PAP have demonstrated is that there is a much closer relationship between benthic processes and events in the upper ocean, and presumably the atmosphere. However much research is needed to determine how such links actually operate. The next steps should focus on establishing the role of climatic forcing in the abyssal sediment systems. Time-series studies that combine contemporaneous upper water column and sediment biogeochemistry with functional ecology of the deep-sea benthic communities. The studies have begun with programmes such as those at PAP and Station M in the Pacific. But further work over longer time periods is needed to provide the information needed.

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APPENDICES

APPENDIX 1

Raw data: Temporal variability at family and species level

Family level

Overall number of individuals

	August 89	May 91	April 94	September 96	March 97	July 97	March 98	September 98
total	53	354	203	682	641	703	288	324
mean	53	59	50.8	97.4	106.8	140.6	144	108
sd		13.6	12.8	11.3	14.3	32.8	121.6	29.8
se		5.6	6.4	4.3	5.8	14.7	86	17.2
ci		10.9	12.6	8.4	11.5	28.7	168.6	33.7
sn	1	6	4	7	6	5	2	3

Table 1. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se), confidence interval of 95% (ci) and samples number (sn).

Sediment layers

0-1 cm	Aug 89	May 91	April 94	Sept 96	Mar 97	July 97	Mar 98
total	27	162	119	382	379	327	162
mean	27	27	29.8	54.6	63.2	65.4	81
sd		8.8	13.3	21.2	12.1	31.9	106.1
se		3.6	6.6	8.0	4.9	14.3	75
ci		7.0	13.0	15.7	9.6	28.0	147
1-3 cm							
total	19	124	62	178	201	260	86
mean	19	20.7	15.5	25.4	33.5	52	43
sd		6.1	4.1	7.5	12.4	7.9	11.3
se		2.5	2.1	2.8	5.1	3.5	8
ci		4.9	4.0	5.6	10.0	6.9	15.7
3-5 cm							
total	7	68	22	122	61	116	40
mean	7	11.3	5.5	17.4	10.2	23.2	20
sd		9.5	0.6	7.7	5.7	14.7	4.2
se		3.9	0.3	2.9	2.3	6.5	3
ci		7.6	0.6	5.7	4.6	12.9	5.9

Table 2. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in 0-1 cm, 1-3 cm and 3-5 cm sediment layer between August 1989 and March 1998. There was no layers information in September 1998 cruise.

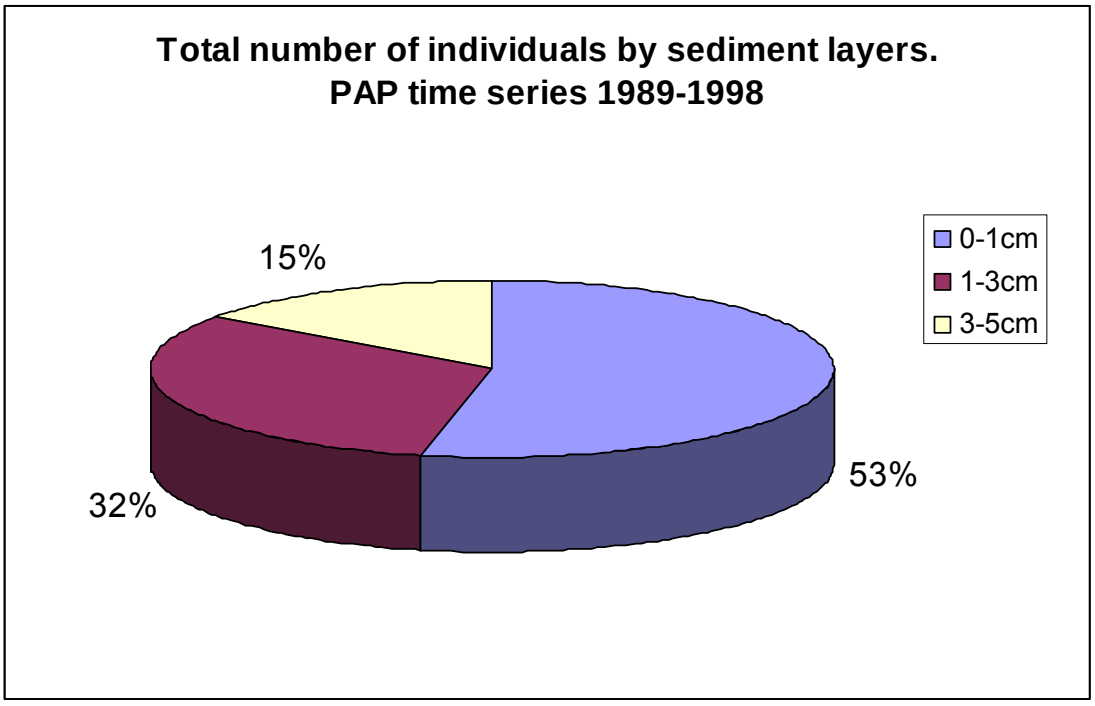

Figure 1. Total number of individuals (%) by sediment layers.

Family richness

	Aug 89	May 91	April 94	Sept 96	Mar 97	July 97	Mar 98	Sept 98
Richness	10	17	17	37	31	29	26	24

Table 3. Number of families in each sampling period between August 1989 and September 1998.

Main families

Cirratulidae	**Aug 89**	**May 91**	**April 94**	**Sept 96**	**Mar 97**	**July 97**	**Mar 98**	**Sept 98**
total	15	123	86	163	191	188	66	103
mean	15	20.5	21.5	23.3	31.8	37.6	33.0	34.3
sd		5.3	5.9	5.6	7.1	8.7	21.2	4.5
se		2.2	2.9	2.1	2.8	3.9	15.0	2.6
ci		4.3	5.8	4.1	5.6	7.6	29.4	5.1
Spionidae								
total	13	87	49	142	134	196	75	61
mean	13	14.5	12.2	20.3	22.3	39.2	37.5	20.3
sd		10.7	5.1	4.4	4.1	7.3	36.1	7.7
se		4.3	2.5	1.6	1.7	3.2	25.5	4.4
ci		8.6	5.0	3.2	3.3	6.4	49.9	8.8
Opheliidae								
total	3	0	1	16	42	61	33	30
mean	3	0	0.3	2.3	7	12.2	16.5	10
sd		0	0.5	2.0	5.7	8.5	19.1	4.6
se		0	0.3	0.7	2.3	3.8	13.5	2.6
ci		0	0.5	1.5	4.5	7.5	26.5	5.2

Paraonidae								
total	11	41	29	47	45	35	15	15
mean	11	6.8	7.2	6.7	7.5	7.0	7.5	5.0
sd		2.6	3.9	2.3	2.3	1.6	3.5	2.6
se		1.0	1.9	0.8	0.9	0.7	2.5	1.5
ci		2.0	3.8	1.7	1.8	1.4	4.9	2.9

Table 4. Total number of individuals, mean number of individuals (mean; Individuals/ 0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in Cirratulidae, Spionidae, Opheliidae and Paraonidae families, between August 1989 and September 1998.

Trophic groups

Surface deposit-feeding	Aug 89	May 91	April 94	Sept 96	Mar 97	July 97	Mar 98	Sept 98
total	45	277	180	486	477	524	188	203
mean	45	46.2	45	69.4	79.5	104.8	94	67.6
sd		14.7	14.3	15.5	11.1	24	79.2	11.1
se		6	7.1	5.8	4.5	10.7	56	6.4
ci		11.8	14	11.5	8.9	21	109.8	12.5
Predators								
total	5	44	18	102	88	84	45	42
mean	5	7.3	4.5	15	15	17	23	14
sd		2.4	2.1	5.3	4.1	4.7	17.7	5.3
se		0.9	1.0	2	1.7	2.1	12.5	3.1
ci		1.9	2.0	3.9	3.3	4.1	24.5	6.0
Burrowing								
total	3	33	5	94	74	95	55	79
mean	3	5.5	1.3	13	12	19	28	26.3
sd		6.7	1.0	9.3	6.7	10	24.8	19.0
se		2.7	0.5	3.5	2.7	4.7	17.5	11.0
ci		5.4	0.9	6.9	5.3	9.2	34.3	21.5

Table 5. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in Predator, Surface deposit feeding and Burrowing trophic groups, between August 1989 and September 1998.

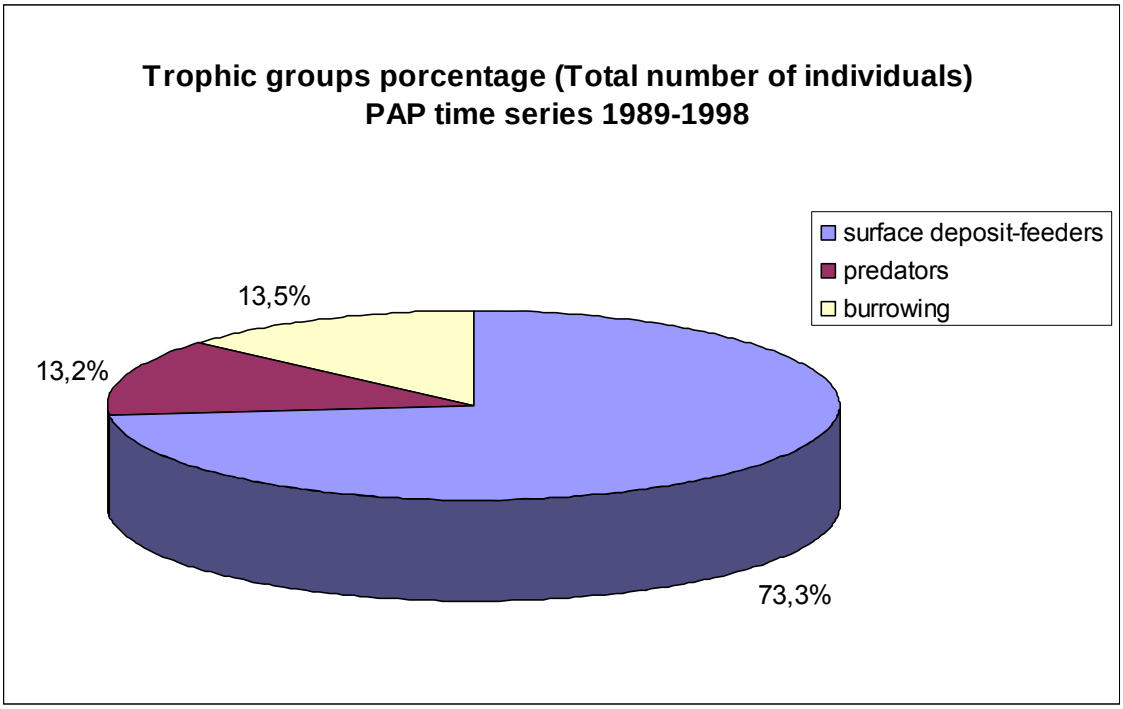

Figure 2. Total number of individuals' distribution (%) by trophic groups.

Species level

Cirratulidae

***Aphelochaeta* sp A**	**Aug 89**	**May 91**	**April 94**	**Sep 96**	**Mar 97**	**July 97**	**Mar 98**	**Sep 98**
total	5	46	28	49	47	47	18	28
mean	5	7.7	7.0	7.0	7.8	9.4	9.0	9.3
sd		1.6	2.5	5.9	1.5	3.8	7.1	3.8
se		0.7	1.3	2.2	0.6	1.7	5.0	2.2
ci		1.3	2.5	4.3	1.2	3.3	9.8	4.3
***Chaetozone* sp1**								
total	7	14	30	22	44	68	21	25
mean	7	2.3	7.5	3.1	7.3	13.6	10.5	8.3
sd		2.9	1.7	2.7	2.7	5.5	10.6	1.5
se		1.2	0.9	1.0	1.1	2.5	7.5	0.9
ci		2.3	1.7	2.0	2.2	4.8	14.7	1.7
***Chaetozone* sp 55**								
total	3	34	1	24	29	21	7	9
mean	3	5.7	0.3	3.4	4.8	4.2	3.5	3.0
sd		4.9	0.5	1.4	3.3	1.9	2.1	4.4
se		2.0	0.3	0.5	1.4	0.9	1.5	2.5
ci		3.9	0.5	1.0	2.6	1.7	2.9	4.9
***Aphelochaeta* sp 647D**								
total	0	1	9	18	17	21	11	27
mean	0	0.2	2.3	2.6	2.8	4.2	5.5	9.0
sd		0.4	1.9	3.7	1.9	1.9	0.7	4.6

se		0.2	0.9	1.4	0.8	0.9	0.5	2.6
ci		0.3	1.9	2.8	1.5	1.7	1.0	5.2
Rest of species								
total	0	28	18	50	54	31	9	14
mean	0	4.7	4.5	7.1	9.0	6.2	4.5	4.7
sd		2.3	1.1	3.5	3.3	2.1	1.6	1.1
se		0.9	0.6	1.3	1.3	0.9	1.1	0.6
ci		1.8	1.1	2.6	2.7	1.8	2.2	1.2

Table 6. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in Cirratulidae species and rest of species group between August 1989 and September 1998.

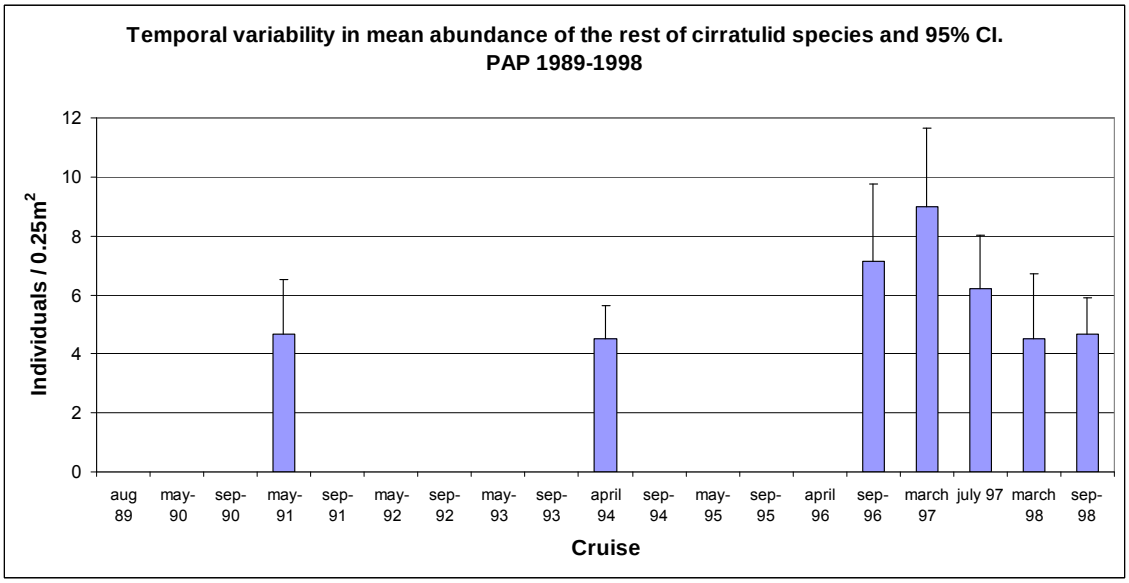

Figure 3. Mean number of individuals for rest of cirratulid species between 1989 and 1998. Mean and 95% confidence limit.

Spionidae

***Minuspio* sp 4**	**Aug 89**	**May 91**	**April 94**	**Sep 96**	**Mar 97**	**July 97**	**Mar 98**	**Sep 98**
total	3	20	6	26	44	36	12	12
mean	3	3.3	1.5	3.7	7.3	7.2	6.0	4.0
sd		2.4	0.6	3.5	3.5	2.3	7.1	2.6
se		0.9	0.3	1.3	1.4	1.0	5.0	1.5
ci		1.9	0.5	2.6	2.8	2.0	9.8	2.9
A. dibranchiata								
total	6	29	16	30	5	34	21	11
mean	6	4.8	4.0	4.3	0.8	6.8	10.5	3.6
sd		6.5	3.7	3.9	0.7	5.9	12.0	1.5
se		2.6	1.8	1.5	0.3	2.6	8.5	0.9
ci		5.2	3.6	2.9	0.6	5.2	16.6	1.7

***Prionospio* sp 81**								
total	0	1	13	25	32	35	20	11
mean	0	0.2	3.2	3.6	5.3	7.0	10.0	3.7
sd		0.4	1.7	2.6	1.9	2.4	11.3	0.6
se		0.2	0.8	0.9	0.8	1.1	8.0	0.3
ci		0.3	1.6	1.9	1.6	2.1	15.7	0.6
***Prionospio* sp 613**								
total	0	13	5	5	10	37	6	8
mean	0	2.1	1.2	0.7	1.6	7.4	3	2.7
sd		2.3	1.5	0.9	1.0	2.1	0	3.1
se		0.9	0.7	0.3	0.4	0.9	0	1.8
ci		1.8	1.5	0.7	0.8	1.8	0	3.5
Rest of species								
total	4	16	8	32	25	27	11	12
mean	4	2.7	2.0	4.6	4.2	5.4	5.5	4.0
sd		8.4	4.8	10.6	12.6	15.3	7.0	4.6
se		3.4	2.4	4.0	5.1	6.8	4.9	2.6
ci		6.7	4.7	7.8	10.1	13.4	9.7	5.2

Table 7. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in Spionidae species and rest of species group between August 1989 and September 1998.

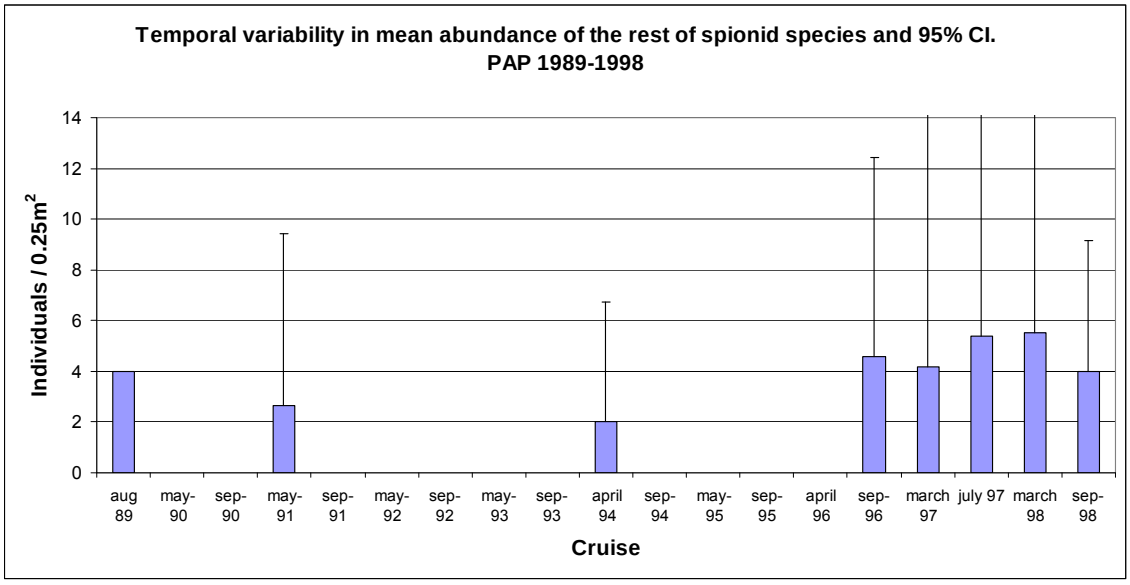

Figure 4. Mean number of individuals for rest of spionid species between 1989 and 1998. Mean and 95% confidence limit.

Paraonidae

Aricidea sp 678E	Aug 89	May 91	April 94	Sep 96	Mar 97	July 97	Mar 98	Sep 98
total	0	2	4	6	7	5	4	1
mean	0	0.3	1.0	0.8	1.2	1.0	2.0	0.3
sd		0.5	1.1	1.2	0.4	1.2	1.4	0.6
se		0.2	0.6	0.4	0.1	0.5	1.0	0.3
ci		0.4	1.1	0.9	0.3	1.1	1.9	0.6
***Aricidea* sp 676**								
total	1	16	8	6	4	7	2	2
mean	1	2.7	2.0	0.9	0.7	1.4	1	0.6
sd		1.7	2.3	1.1	0.5	1.1	0	0.6
se		0.7	1.2	0.4	0.2	0.5	0	0.3
ci		1.4	2.3	0.8	0.4	1.0	0	0.6
***Aricidea* sp 36**								
total	6	1	4	6	5	5	4	2
mean	6	0.2	1.0	0.8	0.8	1.0	2	0.7
sd		0.4	1.1	1.9	0.9	1.2	0	0.6
se		0.2	0.6	0.7	0.4	0.5	0	0.3
ci		0.3	1.1	1.4	0.8	1.1	0	0.6
Rest of species								
total	3	16	9	7	14	7	3	6
mean	3	2.7	2.3	1.0	2.3	1.4	1.5	2.0
sd		1.4	1.3	0.8	1.0	0.9	0.7	0.0
se		0.5	0.6	0.3	0.4	0.4	0.5	0.0
ci		1.1	1.2	0.6	0.8	0.8	0.9	0.0

Table 8. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in Paraonidae species and rest of species group between August 1989 and September 1998.

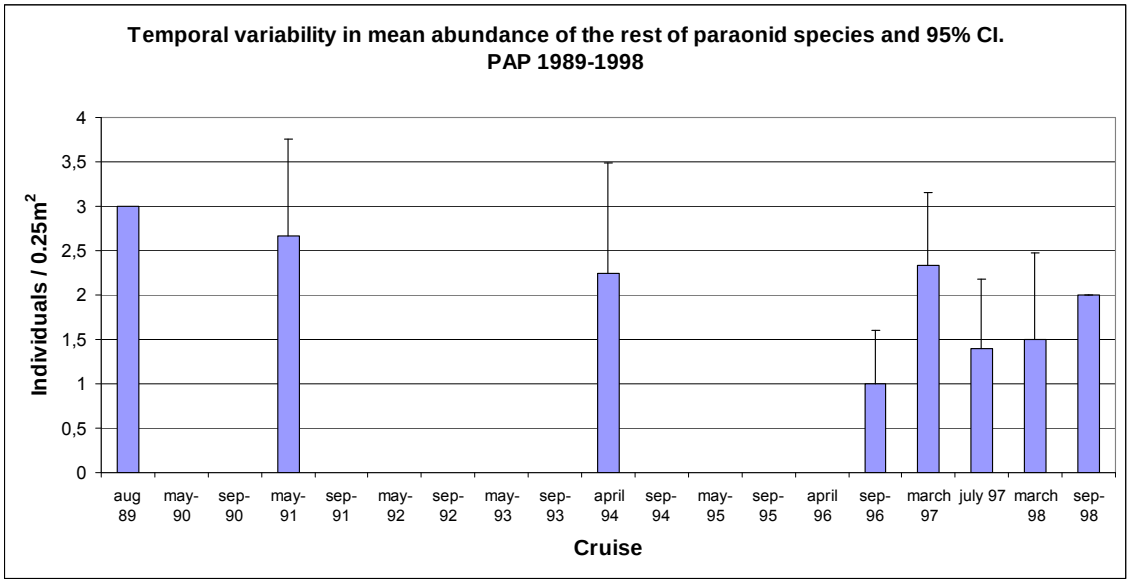

Figure 5. Mean number of individuals for rest of paraonid species between 1989 and 1998. Mean and 95% confidence limit.

Pilargidae

Pilargidae	Aug 89	May 91	April 94	Sep 96	Mar 97	July 97	Mar 98	Sep 98
total	1	11	7	27	25	12	8	13
mean	1	1.8	1.7	3.8	4.2	2.4	4	4.3
sd		1.2	1.7	1.1	2.3	1.3	0	1.5
se		0.5	0.8	0.4	0.9	0.6	0	0.9
ci		0.9	1.7	0.8	1.8	1.2	0	1.7
S. magnuncus								
total	1	11	7	22	24	11	8	10
mean	1	1.8	1.7	3.1	4.0	2.2	4	3.3
sd		1.2	1.7	1.3	2.4	1.1	0	1.5
se		0.5	0.8	0.5	1.0	0.5	0	0.9
ci		0.9	1.7	1.0	1.9	0.9	0	1.7

Table 9. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in Pilargidae species between August 1989 and September 1998.

Glyceridae

Glyceridae	Aug 89	May 91	April 94	Sep 96	Mar 97	July 97	Mar 98	Sep 98
total	0	0	1	7	4	4	0	2
mean	0	0	0.2	1	0.7	0.8	0	0.7
sd			0.5	1.4	0.8	0.8	0	0.6
se			0.2	0.5	0.3	0.4	0	0.3
ci			0.1	1.0	0.6	0.7	0	0.6
***Glycera* sp726**								
total	0	0	1	3	2	2	0	1
mean	0	0	0.2	0.4	0.3	0.4	0	0.3
sd			0.5	0.8	0.5	0.5	0	0.6
se			0.2	0.3	0.2	0.2	0	0.3
ci			0.5	0.6	0.4	0.5	0	0.6

Table 10. Total number of individuals (total), mean number of individuals (mean; Individuals /0.25 m^2), standard deviation (sd), standard error (se) and confidence interval (ci) in Glyceridae species between August 1989 and September 1998.

APPENDIX 2

Statistical analyses: Temporal variability at family and species level

Family level

Mean abundance

ANOVA: single factor.						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
Between cruises	0.70	5	0.14	1822	**0.001**	2.60
Within cruises	0.19	25	0.007			
KRUSKAL-WALLIS test						
Source	F	DF1	DF2	P		
Mean abundance	15.96	5	24	**0.003**		

Table 1. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test.						
Source	**Mean**	**Variance**	**Observations**	**df**	**p**	**t (statistical)**
Mean abundance Pre-*Amperima*	1.73	0.01	10	16	**0.001**	-7.7
Amperima	2.03	0.008	21			
Mann-Whitney U test:						
Source	**U**	**z**	**p**			
Mean abundance	1	4.96	**0.001**			

Table 2. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

Sediment layers

ANOVA: single factor.						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
0-1cm Between groups	0.67	4	0.16	3.42	**0.02**	2.79
Within groups	1.13	23	0.04			
1-3cm Between groups	0.79	4	0.19	11.03	**0.001**	2.79
Within groups	0.41	23	0.01			
3-5cm Between groups	0.91	4	0.22	2.47	0.07	2.79
Within groups	2.11	23	0.09			
KRUSKAL-WALLIS test						
Source	***F***	***DF1***	***DF2***	***P***		
0-1cm	4.69	4	22	**0.008**		
1-3cm	10.34	4	22	**0.002**		
3-5cm	3.85	4	22	**0.018**		

Table 3. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test.						
Source	**Mean**	**Variance**	**Observations**	**df**	**p**	**t (statistical)**
0-1cm Pre-*Amperima*	1.42	0.02	10	24	**0.0001**	-4.17
Amperima	1.73	0.05	18			
1-3cm Pre-*Amperima*	1.25	0.01	10	24	**0.0001**	-4.29
Amperima	1.51	0.03	18			
3-5cm Pre-*Amperima*	0.87	0.14	10	14	**0.02**	-2.20
Amperima	1.17	0.06	18			
Mann-Whitney U test:						
Source	**U**	**z**	**p**			
0-1cm	19	3.60	**0.006**			
1-3cm	23.5	3.33	**0.005**			
3.5cm	43	2.27	**0.02**			

Table 4. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

Family richness

ANOVA: single factor.						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
Richness Between groups	0.58	5	0.11	23.52	**0.001**	2.60
Within groups	0.12	25	0.005			
KRUSKAL-WALLIS test						
Source	**F**	**DF1**	**DF2**	**P**		
Richness	10.51	5	24	**0.003**		

Table 5. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test.						
Source	**Mean**	**Variance**	**Observations**	**df**	**p**	**t (statistical)**
Richness Pre-*Amperima*	0.97	0.006	10	14	**0.001**	-10.13
Amperima	1.26	0.003	21			
Mann-Whitney U test:						
Source	**U**	**z**	**p**			
Richness	0.5	5.03	**0.001**			

Table 6. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

ANOSIM (Analysis of similarities)

Global Test
Sample statistic (Global R): 0.822
Significance level of sample statistic: 0.0%
Number of permutations: 5000 (Random sample from 286097760)
Number of permuted statistics greater than or equal to Global R: 0

SIMPER (Similarity percentages - species contributions)

Group 1 Average similarity: 65.75					
Family	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Cirratulidae	20.36	30.14	4.64	45.85	45.85
Spionidae	13.55	16.22	2.06	24.67	70.52
Paraonidae	7.36	10.13	2.47	15.41	85.93
Sabellidae	3.36	3.43	1.41	5.22	91.15
Group 2 Average similarity: 65.38					
Family	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Cirratulidae	30.91	22.60	4.53	34.57	34.57
Spionidae	26.43	17.47	4.62	26.73	61.30
Paraonidae	6.83	4.94	3.35	7.56	68.86
Opheliidae	7.91	3.13	1.23	4.79	73.66
Pilargidae	3.70	2.60	2.07	3.97	77.63
Sabellidae	5.17	2.13	1.05	3.26	80.90
Ampharetidae	4.30	2.07	1.24	3.16	84.06
Syllidae	3.52	2.01	1.68	3.08	87.13
Flabelligeridae	3.17	1.41	0.99	2.15	89.29
Acrocirridae	3.00	1.40	1.24	2.14	91.43
Groups 1 & 2 Average dissimilarity = 44.64					
	Group 1	Group 2			
Family	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Spionidae	13.55	26.43	8.23	1.49	18.44	18.44
Cirratulidae	20.36	30.91	6.94	1.52	15.54	33.98
Opheliidae	0.36	7.91	4.01	1.26	8.99	42.96
Capitellidae	2.73	3.91	3.02	0.87	6.76	49.72
Sabellidae	3.36	5.17	2.36	1.30	5.29	55.01
Ampharetidae	0.55	4.30	2.31	1.06	5.17	60.18
Paraonidae	7.36	6.83	1.89	1.35	4.23	64.42
Acrocirridae	0.00	3.00	1.79	1.06	4.01	68.42
Flabelligeridae	0.27	3.17	1.76	1.07	3.95	72.37
Syllidae	1.36	3.52	1.50	1.40	3.36	75.73
Pilargidae	1.73	3.70	1.41	1.33	3.15	78.88
Fauveliopsidae	0.18	1.87	1.15	0.85	2.58	81.45
Lumbrineridae	0.45	1.65	0.89	1.31	2.00	83.45
Phyllodocidae	0.82	1.43	0.83	0.93	1.85	85.30
Owenidae	0.00	1.43	0.75	0.63	1.67	86.97
Chrysopetalidae	1.18	0.87	0.70	1.14	1.56	88.53
Orbiniidae	0.09	1.04	0.61	0.68	1.38	89.91
Cossuridae	0.09	1.04	0.61	0.75	1.36	91.27

Table 7. Similarity percentages for pre and '*Amperima* Event' groups. Family contributions

Main families

ANOVA: single factor.						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
Cirratulidae Between groups	0.41	5	0.08	7.12	**0.001**	2.60
Within groups	0.29	25	0.01			
Spionidae Between groups	1.18	5	0.23	3.62	**0.013**	2.60
Within groups	1.63	25	0.06			
Opheliidae Between groups	5.07	5	1.01	15.80	**0.001**	2.60
Within groups	1.60	25	0.06			
Paraonidae Between groups	0.05	5	0.01	0.54	0.73	2.6
Within groups	0.53	25	0.02			

KRUSKAL-WALLIS test						
Source	***F***	***DF1***	***DF2***	***P***		
Cirratulidae	10.69	5	24	**0.003**		
Spionidae	7.43	5	24	**0.006**		
Opheliidae	14.8	5	24	**0.003**		
Paraonidae	0.43	5	24	0.82		

Table 8. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test.						
Source	**Mean**	**Variance**	**Observations**	**df**	**p**	**t (statistical)**
Cirratulidae Pre-*Amperima*	1.29	0.017	10	16	**0.001**	-3.94
Amperima	1.48	0.014	21			
Spionidae Pre-*Amperima*	1.01	0.16	10	10	**0.01**	-2.71
Amperima	1.37	0.02	21			
Opheliidae Pre-*Amperima*	0.03	0.009	10	25	**0.001**	-8.31
Amperima	0.76	0.14	21			
Paraonidae Pre-*Amperima*	0.875	0.02	10	15	0.48	0.04
Amperima	0.872	0.01	21			

Mann-Whitney U test:						
Source	**U**	**z**	**p**			
Cirratulidae	24.5	3.60	**0.002**			
Spionidae	26.5	3.49	**0.01**			
Opheliidae	11.5	4.45	**0.001**			
Paraonidae	101	0.15	0.87			

Table 9. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

Trophic groups

ANOVA: single factor.						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
Surface deposit feeding Between groups	0.53	5	0.11	9.1	**0.001**	2.60
Within groups	0.29	25	0.01			
Predators Between groups	1.27	5	0.25	10.73	**0.001**	2.60
Within groups	0.59	25	0.02			
Burrowing Between groups	3.49	5	0.69	7.04	**0.001**	2.60
Within groups	2.47	25	0.09			

KRUSKAL-WALLIS test						
Source	***F***	***DF1***	***DF2***	***P***		
Surface deposit feeding	7.98	5	24	**0.006**		
Predators	8.85	5	24	**0.003**		
Burrowing	5.39	5	24	**0.003**		

Table 10 . Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered.

'*Amperima* Event' comparison

T-test.						
Source	**Mean**	**Variance**	**Observations**	**df**	**p**	**t (statistical)**
Surface deposit feeding Pre-*Amperima*	1.64	0.02	10	16	**0.001**	-5.25
Amperima	1.89	0.01	21			
Predators Pre-*Amperima*	0.75	0.04	10	12	**0.001**	-5.60
Amperima	1.15	0.01	21			
Burrowing Pre-*Amperima*	0.48	0.16	10	13	**0.001**	-4.75
Amperima	1.16	0.06	21			

Mann-Whitney U test:						
Source	**U**	**z**	**p**			
Surface deposit feeding	15	4.11	**0.002**			
Predators	5	4.72	**0.001**			
Burrowing	18.5	3.92	**0.001**			

Table 11. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

Species level

Cirratulidae

ANOVA: single factor						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
***Aphelochaeta* sp 13A** Between groups	0.11	5	0.023	0.83	0.53	2.6
Within groups	0.71	25	0.028			
***Chaetozone* sp 1** Between groups	2.15	5	0.43	7.60	**0.001**	2.6
Within groups	1.41	25	0.05			
***Chaetozone* sp 55A** Between groups	1.29	5	0.25	2.81	**0.03**	2.6
Within groups	2.29	25	0.09			
***Aphelochaeta* sp 647D** Between groups	2.09	5	0.42	4.53	**0.004**	2.6
Within groups	2.31	25	0.09			
Rest of species Between groups	0.27	5	0.05	1.49	0.22	2.6
Within groups	0.92	25	0.03			

Kruskal-Wallis test:				
Source	**F**	**df1**	**df2**	**p**
***Aphelochaeta* sp 13A**	0.74	5	24	0.58
***Chaetozone* sp 1**	7.69	5	24	**0.006**
***Chaetozone* sp 55A**	2.14	5	24	0.096
***Aphelochaeta* sp 647D**	4.36	5	24	**0.007**
Rest of species	1.61	5	24	0.19

Table 12. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test. Unequal variance assumed

Source	**Mean**	**Variance**	**Observations**	**df**	**p**	**t (statistical)**
***Aphelochaeta* sp 13A** Pre-*Amperima*	0.91	0.01	10	29	0.44	-0.14
Amperima	0.92	0.03	21			
***Chaetozone* sp 1** Pre-*Amperima*	0.62	0.12	10	16	0.06	-1.66
Amperima	0.84	0.10	21			
***Chaetozone* sp 55A**	0.44	0.20	10	12	0.13	-1.17

Pre-*Amperima*						
Amperima	0.62	0.07	21			
***Aphelochaeta* sp 647D** Pre-*Amperima*	0.21	0.07	10	25	**0.005**	-2.79
Amperima	0.55	0.15	21			
Rest of species Pre-*Amperima*	0.73	0.01	10	27	**0.02**	-2.03
Amperima	0.86	0.04	21			

Mann-Whitney U test:

Source	U	z	p
***Aphelochaeta* sp 13A**	99.5	0.21	0.82
***Chaetozone* sp 1**	71.5	1.39	0.16
***Chaetozone* sp 55A**	79	1.08	0.27
Aphelochaeta sp 647D	53	2.25	**0.02**
Rest of species	68	1.55	0.12

Table 13. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

ANOSIM (Analysis of similarities)

Global Test
Sample statistic (Global R): 0.286
Significance level of sample statistic: 0.1%
Number of permutations: 5000 (Random sample from 286097760)
Number of permuted statistics greater than or equal to Global R: 5

SIMPER (Similarity percentages - species contributions)

Group 1 Average similarity: 52.14					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Aphelochaeta sp 13A	7.18	30.27	4.73	58.06	58.06
Chaetozone sp 1	4.64	12.64	1.03	24.24	82.30
Chaetozone sp 55A	3.45	5.27	0.60	10.12	92.42

Group 2 Average similarity: 54.63					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Aphelochaeta sp 13A	8.22	19.03	2.90	34.84	34.84
Chaetozone sp 1	7.83	14.85	1.69	27.18	62.02
Chaetozone sp 55A	3.91	8.32	1.48	15.23	77.25
Aphelochaeta sp 647D	4.09	6.34	0.86	11.61	88.86
Aphelochaeta sp 643C	1.00	1.22	0.52	2.24	91.10

Groups 1 & 2 Average dissimilarity = 49.56						
	Group 1	Group 2				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Chaetozone sp1	4.64	7.83	10.16	1.43	20.50	20.50
Chaetozone sp55A	3.45	3.91	7.67	1.39	15.47	35.97
Aphelochaeta sp 647D	0.91	4.09	7.36	1.12	14.85	50.82
Aphelochaeta sp 13A	7.18	8.22	6.80	1.14	13.71	64.53

Aphelochaeta sp 643C	0.82	1.00	2.51	0.95	5.07	69.60
Chaetozone sp 605B	0.64	0.87	1.97	0.94	3.97	73.57
Aphelochaeta sp9	0.00	0.91	1.88	0.46	3.79	77.35
Chaetozone sp 685	0.45	0.65	1.62	0.89	3.27	80.62
Chaetozone sp10	0.18	0.74	1.48	0.90	2.98	83.60
Aphelochaeta sp11	0.27	0.52	1.38	0.75	2.77	86.38
Chaetozone sp 657E	0.27	0.57	1.34	0.74	2.71	89.09
Tharyx sp1	0.09	0.52	1.15	0.57	2.32	91.41

Table 14. Analysis of similarity (ANOSIM) and similarities percentages (SIMPER) in Cirratulidae

Spionidae

ANOVA: single factor						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
***Minuspio* sp 4** Between groups	1.01	5	0.20	2.98	**0.03**	2.6
Within groups	1.70	25	0.06			
A. dibranchiata Between groups	0.94	5	0.18	1.42	0.24	2.6
Within groups	3.31	25	0.13			
***Prionospio* sp 81** Between groups	2.41	5	0.48	14.76	**0.001**	2.6
Within groups	0.81	25	0.03			
***Prionospio* sp 613** Between groups	1.72	5	0.34	4.63	**0.004**	2.6
Within groups	1.86	25	0.07			
Rest of species Between groups	0.47	5	0.09	1.43	0.24	2.6
Within groups	1.66	25	0.06			

Kruskal-Wallis test:				
Source	**F**	**df1**	**df2**	**p**
***Minuspio* sp 4**	3.27	5	24	**0.02**
A. dibranchiata	1.53	5	24	0.22
***Prionospio* sp 81**	8.84	5	24	**0.003**
***Prionospio* sp 613**	4.33	5	24	**0.005**
Rest of species	1.73	5	24	0.16

Table 15. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test. Unequal variance assumed

Source	Mean	Variance	Observations	df	p	t (statistical)
***Minuspio* sp 4** Pre-*Amperima*	0.49	0.06	10	20	**0.01**	-2.46
Amperima	0.74	0.08	21			
A. dibranchiata Pre-*Amperima*	0.54	0.20	10	14	0.49	-0.008
Amperima	0.55	0.12	21			
***Prionospio* sp 81** Pre-*Amperima*	0.26	0.10	10	13	**0.001**	-4.14
Amperima	0.72	0.04	21			
***Prionospio* sp 613** Pre-*Amperima*	0.34	0.10	10	20	0.20	-0.84
Amperima	0.45	0.13	21			
Rest of species Pre-*Amperima*	0.46	0.08	10	15	**0.016**	-2.36
Amperima	0.70	0.05	21			

Mann-Whitney U test:

Source	U	z	p
***Minuspio* sp 4**	51	2.32	**0.018**
A. dibranchiata	102.5	0.08	0.92
***Prionospio* sp 81**	27	3.49	**0.005**
***Prionospio* sp 613**	90.5	0.6	0.54
Rest of species	45.5	2.58	**0.009**

Table 16. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

ANOSIM (Analysis of similarities)

Global Test
Sample statistic (Global R): 0.542
Significance level of sample statistic: 0.0%
Number of permutations: 5000 (Random sample from 286097760)
Number of permuted statistics greater than or equal to Global R: 0

SIMPER (Similarity percentages - species contributions)

Group 1 Average similarity: 32.36					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
A. dibranchiata	4.64	11.85	0.84	36.62	36.62
Minuspio sp 4	2.64	11.17	1.43	34.53	71.15
Prionospio sp 613	1.64	3.76	0.52	11.63	82.78
Prionospio sp 81	1.64	3.76	0.52	11.63	82.78

Group 2 Average similarity: 51.40					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Prionospio sp 81	5.35	13.32	1.92	25.91	25.91
Minuspio sp 4	5.65	13.27	1.36	25.82	51.73
Minuspio sp 2	3.52	8.08	1.55	15.72	67.45
A. dibranchiata	4.39	6.82	1.05	13.27	80.72
Prionospio sp 613	2.87	4.36	0.87	8.48	89.20
Spiophanes sp 619	0.96	1.65	0.60	3.21	92.40

Groups 1 & 2 Average dissimilarity = 64.37						
	Group 1	Group 2				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
A. dibranchiata	4.64	4.39	11.84	1.31	18.39	18.39
Prionospio sp 81	1.27	5.35	11.05	1.54	17.17	35.56
Minuspio sp 4	2.64	5.65	10.75	1.22	16.71	52.27
Minuspio sp 2	0.82	3.52	8.65	1.46	13.45	65.71
Prionospio sp 613	1.64	2.87	6.49	1.23	10.08	75.79
Spiophanes sp 619	0.73	0.96	3.31	0.91	5.15	80.94
Laonice sp 640	0.36	0.78	2.27	0.89	3.53	84.47
Spionidae indet (6A)	0.73	0.30	2.02	0.86	3.13	87.61
Spiophanes sp 1	0.09	0.57	1.73	0.63	2.69	90.30

Table 17. Analysis of similarity (ANOSIM) and similarities percentages (SIMPER) in Spionidae

Paraonidae

ANOVA: single factor						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
***Aricidea* sp 676** Between groups	0.48	5	0.09	1.69	0.17	2.6
Within groups	1.43	25	0.05			
***Aricidea* sp 36** Between groups	0.14	5	0.02	0.50	0.77	2.6
Within groups	1.43	25	0.05			
***Aricidea* sp 678E** Between groups	0.20	5	0.04	0.93	0.47	2.6
Within groups	1.09	25	0.04			
Rest of species Between groups	0.35	5	0.07	2.48	0.06	2.6
Within groups	0.70	25	0.02			

Kruskal-Wallis test:

Source	**F**	**df1**	**df2**	**p**
***Aricidea* sp 676**	1.74	5	24	0.16
***Aricidea* sp 36**	0.63	5	24	0.68
***Aricidea* sp 678E**	0.99	5	24	0.45
Rest of species	2.42	5	24	0.06

Table 18. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test. Unequal variance assumed

Source	Mean	Variance	Observations	df	p	t (statistical)
***Aricidea* sp 676** Pre-*Amperima*	0.45	0.08	10	14	**0.02**	2.22
Amperima	0.23	0.04	21			
***Aricidea* sp 36** Pre-*Amperima*	0.12	0.04	10	20	0.20	0.85
Amperima	0.19	0.05	21			
***Aricidea* sp 678E** Pre-*Amperima*	0.15	0.04	10	18	0.17	0.94
Amperima	0.23	0.04	21			
Rest of species Pre-*Amperima*	0.52	0.02	10	22	**0.02**	2.11
Amperima	0.38	0.03	21			

Mann-Whitney U test:

Source	U	z	p
***Aricidea* sp 676**	52.5	2.31	**0.02**
***Aricidea* sp 36**	88.5	0.75	0.46
***Aricidea* sp 678E**	85	0.88	0.38
Rest of species	64.5	1.81	0.06

Table 19. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

ANOSIM (Analysis of similarities)

Global Test
Sample statistic (Global R): 0.241
Significance level of sample statistic: 0.1%
Number of permutations: 5000 (Random sample from 286097760)
Number of permuted statistics greater than or equal to Global R: 5

SIMPER (Similarity percentages - species contributions)

Group 1 Average similarity: 25.27					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Aricidea sp 676	2.27	15.04	1.10	59.52	59.52
Aricidea sp 700	0.64	2.56	0.44	10.13	69.65
Aricidea sp 601	0.55	1.92	0.34	7.58	77.23
Aricidea sp 36	1.00	1.89	0.32	7.48	84.71
Aricidea sp 678E	0.55	1.27	0.33	5.02	89.73
Aricidea sp 7	0.36	0.73	0.24	2.89	92.63

Group 2 Average similarity: 31.08					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Aricidea sp 676	0.91	7.10	0.76	22.86	22.86
Aricidea sp 678E	1.00	6.05	0.78	19.46	42.33
Levinsenia sp 1	0.70	5.00	0.63	16.10	58.43

Aricidea sp 36	0.96	4.36	0.53	14.04	72.47
Aricidea sp 28	0.65	1.96	0.38	6.32	78.80
Levinsenia sp 3	0.57	1.67	0.34	5.38	84.17
Aricidea sp 700	0.43	1.29	0.34	4.16	88.33
Aricidea sp 721	0.26	1.16	0.24	3.73	92.07

Groups 1 & 2
Average dissimilarity = 76.82

	Group 1	Group 2				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Aricidea sp 676	2.27	0.91	12.68	1.20	16.51	16.51
Aricidea sp 36	1.00	0.96	9.64	0.90	12.55	29.05
Aricidea sp 678E	0.55	1.00	6.95	1.09	9.05	38.10
Aricidea sp 700	0.64	0.43	5.29	0.87	6.89	44.99
Levinsenia sp 1	0.09	0.70	5.25	0.93	6.83	51.82
Aricidea sp 28	0.27	0.65	4.95	0.72	6.45	58.27
Aricidea sp 601	0.55	0.04	4.10	0.75	5.34	63.61
Levinsenia sp 3	0.00	0.57	3.90	0.60	5.07	68.6
Aricidea sp 721	0.18	0.26	3.25	0.63	4.24	72.92
Aricidea sp 7	0.36	0.13	3.07	0.67	3.99	76.91
Paradoneis sp 1	0.18	0.30	2.70	0.67	3.52	80.43
Paraonidae indet1	0.09	0.30	2.49	0.62	3.24	83.67
Levinsenia sp A	0.18	0.00	1.75	0.46	2.28	85.95
Aricidea sp 8	0.09	0.13	1.66	0.47	2.17	88.11
A. cf *neosuecica*	0.27	0.00	1.63	0.60	2.13	90.24

Table 20. Analysis of similarity (ANOSIM) and similarities percentages (SIMPER) in Paraonidae

Pilargidae

ANOVA: single factor						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
Pilargidae Between groups	0.52	5	0.10	3.32	**0.019**	2.6
Within groups	0.78	25	0.03			
Sigambra magnuncus Between groups	0.33	5	0.06	1.86	0.13	2.6
Within groups	0.89	25	0.03			

Kruskal-Wallis test:				
Source	**F**	**df1**	**df2**	**p**
Pilargidae	3.03	5	24	**0.03**
Sigambra magnuncus	1.52	5	24	0.23

Table 21. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test. Unequal variance assumed

Source	Mean	Variance	Observations	df	p	t (statistical)
Pilargidae Pre-*Amperima*	0.40	0.04	10	14	**0.003**	-3.16
Amperima	0.64	0.02	21			
Sigambra magnuncus Pre-*Amperima*	0.40	0.04	10	15	**0.013**	-2.44
Amperima	0.58	0.02	21			

Mann-Whitney U test:

Source	U	z	p
Pilargidae	40	2.86	**0.005**
Sigambra magnuncus	53	2.25	**0.02**

Table 22. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

ANOSIM (Analysis of similarities)

Global Test
Sample statistic (Global R): 0.125
Significance level of sample statistic: 7.6%
Number of permutations: 5000 (Random sample from 286097760)
Number of permuted statistics greater than or equal to Global R: 381

SIMPER (Similarity percentages - species contributions)

Group 1 Average similarity: 58.18					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Sigambra magnuncus	1.73	58.18	1.70	100.00	100.00
Group 2 Average similarity: 65.03					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Sigambra magnuncus	3.26	64.11	3.05	98.59	98.59

Groups 1 & 2 Average dissimilarity = 45.78						
	Group 1	Group 2				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Sigambra magnuncus	1.73	3.26	37.97	1.41	82.94	82.94
Sigambra sp 2	0.00	0.30	5.38	0.42	11.75	94.69

Table 23. Analysis of similarity (ANOSIM) and similarities percentages (SIMPER) in Pilargidae

Glyceridae

ANOVA: single factor						
Source	**SS**	**df**	**MS**	***F***	**p**	**F (critique)**
Glyceridae Between groups	0.22	5	0.04	1.09	0.38	2.6
Within groups	1.01	25	0.04			
***Glycera* sp 726** Between groups	0.05	5	0.01	0.48	0.78	2.6
Within groups	0.58	25	0.02			

Kruskal-Wallis test:				
Source	**F**	**df1**	**df2**	**p**
Glyceridae	1.18	5	24	0.34
***Glycera* sp 726**	0.50	5	24	0.79

Table 24. Analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test. Cruises with 3 or more samples considered

'*Amperima* Event' comparison

T-test. Unequal variance assumed

Source	Mean	Variance	Observations	df	p	t (statistical)
Glyceridae Pre-*Amperima*	0.03	0.009	10	29	**0.002**	-3.07
Amperima	0.20	0.047	21			
***Glycera* sp 726** Pre-*Amperima*	0.03	0.009	10	27	0.051	-1.69
Amperima	0.10	0.026	21			

Mann-Whitney U test:

Source	U	z	p
Glyceridae	58.5	2.27	**0.03**
***Glycera* sp 726**	80	1.35	0.20

Table 25. T-test and non-parametric Mann-Whitney U test. Unequal variances assumed

ANOSIM (Analysis of similarities)

Global Test
Sample statistic (Global R): -0.279
Significance level of sample statistic: 100%
Number of permutations: 12 (All possible permutations)
Number of permuted statistics greater than or equal to Global R: 12

SIMPER (Similarity percentages - species contributions)

Group 1 Less than 2 samples in group						
Group 2 Average similarity: 32.91						
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**	
Glycera sp 726	0.73	26.61	0.73	80.85	80.85	
Glyceridae sp 4	0.27	2.85	0.23	8.66	89.50	
Glyceridae sp 5	0.27	2.85	0.23	8.66	98.16	
Groups 1 & 2 Average dissimilarity = 46.97						
	Group 1	Group 2				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Glycera sp 726	1.00	0.73	18.18	0.80	38.71	38.71
Glyceridae sp 4	0.00	0.27	9.85	0.55	20.97	59.68
Glyceridae sp 5	0.00	0.27	9.85	0.55	20.97	80.65
Glyceridae sp 2	0.00	0.09	4.55	0.30	9.68	90.32

Table 26. Analysis of similarity (ANOSIM) and similarities percentages (SIMPER) in Glyceridae

All species

ANOSIM

Global Test
Sample statistic (Global R): 0.59
Significance level of sample statistic: 0.0%
Number of permutations: 5000 (Random sample from 286097760)
Number of permuted statistics greater than or equal to Global R: 0

SIMPER (Similarity percentages - species contributions)

Group 1 pre 'Amperima Event' Average similarity: 42.28					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Aphelochaeta sp 13A	7.18	14.26	4.91	33.74	33.74
Chaetozone sp 1	4.64	5.88	1.04	13.90	47.64
A. dibranchiata	4.64	3.89	0.83	9.21	56.85
Minuspio sp 4	2.64	3.49	1.47	8.27	65.11
Aricidea sp 676	2.27	2.70	1.06	6.37	71.49
Sigambra magnuncus	1.73	2.60	1.24	6.15	77.64
Chaetozone sp 55A	3.45	2.52	0.58	5.97	83.61
Prionospio sp 613	1.64	1.26	0.55	2.98	86.59
Prionospio sp 81	1.27	0.70	0.39	1.65	88.24
Chaetozone sp 605B	0.64	0.51	0.45	1.20	89.43
Spionidae indet (6A)	0.73	0.45	0.45	1.06	90.50
Group 2 'Amperima Event' Average similarity: 51.22					
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Aphelochaeta sp 13A	8.22	8.59	2.76	16.78	16.78
Chaetozone sp 1	7.83	6.69	1.67	13.05	29.83

Minuspio sp 4	5.65	5.03	1.40	9.82	39.65
Prionospio sp 81	5.35	4.98	1.93	9.73	49.38
Chaetozone sp 55A	3.91	3.71	1.45	7.24	56.62
Sigambra magnuncus	3.26	3.57	2.07	6.97	63.58
Minuspio sp 2	3.52	3.07	1.53	5.99	69.58
Aphelochaeta sp 647D	4.09	2.88	0.84	5.61	75.19
A. dibranchiata	4.39	2.63	1.01	5.13	80.32
Prionospio sp 613	2.87	1.74	0.85	3.40	83.72
Aricidea sp 676	0.91	0.71	0.76	1.38	85.10
Aricidea sp 678E	1.00	0.68	0.76	1.33	86.42
Spiophanes sp 619	0.96	0.61	0.64	1.18	87.60
Aphelochaeta sp 643C	1.00	0.56	0.52	1.08	88.69
Levinsenia sp 1	0.70	0.51	0.64	0.99	89.67
Chaetozone sp 605B	0.87	0.45	0.53	0.89	90.56

Groups 1 pre 'Amperima Event' & 2 'Amperima Event'
Average dissimilarity = 58.14

	Group 1	Group 2				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Chaetozone sp 1	4.64	7.83	4.64	1.42	7.99	7.99
A. dibranchiata	4.64	4.39	4.28	1.19	7.35	15.34
Prionospio sp 81	1.27	5.35	3.85	1.50	6.63	21.97
Minuspio sp 4	2.64	5.65	3.60	1.37	6.19	28.16
Chaetozone sp 55A	3.45	3.91	3.57	1.34	6.13	34.29
Aphelochaeta sp 647D	0.91	4.09	3.43	1.08	5.90	40.19
Aphelochaeta sp 13A	7.18	8.22	3.12	1.12	5.36	45.55
Minuspio sp 2	0.82	3.52	3.00	1.50	5.16	50.72
Prionospio sp 613	1.64	2.87	2.32	1.17	3.99	54.71
Sigambra magnuncus	1.73	3.26	1.85	1.23	3.18	57.89
Aricidea sp 676	2.27	0.91	1.64	1.19	2.81	60.71
Aricidea sp 36	1.00	0.96	1.30	0.82	2.23	62.94
Aphelochaeta sp 643C	0.82	1.00	1.16	0.95	2.00	64.94
Spiophanes sp 619	0.73	0.96	1.09	1.02	1.87	66.81
Chaetozone sp 605B	0.64	0.87	0.90	0.94	1.55	68.36
Aricidea sp 678E	0.55	1.00	0.89	1.11	1.53	69.89
Aphelochaeta sp 9	0.00	0.91	0.88	0.46	1.51	71.41
Laonice sp 640	0.36	0.78	0.75	0.96	1.30	72.7
Chaetozone sp 685	0.45	0.65	0.74	0.88	1.28	73.98
Spionidae indet 6A	0.73	0.30	0.71	0.86	1.23	75.21
Chaetozone sp10	0.18	0.74	0.70	0.89	1.20	76.40
Aricidea sp 28	0.27	0.65	0.67	0.70	1.15	77.55
Aricidea sp 700	0.64	0.43	0.65	0.94	1.12	78.68
Levinsenia sp 1	0.09	0.70	0.65	0.97	1.12	79.80
Aphelochaeta sp 11	0.27	0.52	0.63	0.76	1.08	80.87
Chaetozone sp 657E	0.27	0.57	0.61	0.74	1.05	81.93
Aricidea sp 601	0.55	0.04	0.56	0.68	0.97	82.89
Spiophanes sp 1	0.09	0.57	0.56	0.67	0.96	83.85
Laonice sp 1	0.09	0.61	0.54	0.68	0.93	84.79
Levinsenia sp 3	0.00	0.57	0.54	0.55	0.93	85.72
Tharyx sp 1	0.09	0.52	0.54	0.59	0.92	86.64
Chaetozone sp 2	0.27	0.48	0.53	0.63	0.91	87.55
Aquilaspio sp 1	0.09	0.57	0.52	0.79	0.89	88.45
Spionidae (sp10)	0.09	0.48	0.45	0.76	0.77	89.22
Aricidea sp 7	0.36	0.13	0.43	0.64	0.73	89.95
Chaetozone sp 12	0.27	0.22	0.39	0.61	0.67	90.62

Table 27. Analysis of similarity (ANOSIM) and similarities percentages (SIMPER) in all species

APPENDIX 3

List of characters: Taxonomy

Bitentaculate Cirratulidae (adapted from Glover, 2000 and APIP. For details of specific morphology see Glover, 2000)

Anterior end

Prostomium shape
0) Rounded
1) Pointed, conical rounded tip
2) Pointed, conical blunt tip
3) Pointed, conical, tapering from peristomium
4) Pointed, snout-like
5) Curved with rounded tip
6) Indented prostomium - dummy-shaped
7) Duck-bill shape in lateral view

Tip shape
0) Rounded
1) Sharply pointed
2) Blunt tip

Pharynx
0) Everted
1) Not everted. (Not observed)

Peristomium. The buccal region in this sense is the peristomial region, including the fused segment

Buccal region shape
0) Elongate
1) Compact
2) Semi-elongate

Buccal region length
0) Long about broad

Peristomial surface
0) Smooth
1) Grooved

Eyes
0) Absent
1) Present

Peristomial annulations
0) Absent
1) Present (How many?)

Position of the palps
0) Less than 2 branchial widths to chaetiger 1
1) More than 2 branchial widths to chaetiger 1

Thoracic region

Branchiae
0) First branchiae in same chaetiger as tentacular filaments
1) First branchiae arising from segment posterior to tentacular filaments

Nature of branchiae
0) Short
1) Long

Thoracic body shape
0) Uniform width throughout
1) Swollen anterior end (just below peristomium)
2) Swollen mid region
3) Swollen posterior region
4) 'Hour-glass' shaped

Thoracic region surface
0) Smooth
1) Grooved

Thoracic Region Length
0) Number of chaetigers

Very long ('bottle-brush') chaetae
0) Absent
1) Present

'Bottle-brush' chaetae length
0) Number of chaetigers

Thoracic 'bottle-brush' chaetae appearance
0) Absent
1) From chaetiger 1
2) From chaetiger n.

Thoracic neurochaetae
0) All simple capillaries
1) Acicular spines present

Thoracic neurochaetae length
0) Number of chaetigers

Number of thoracic neurochaetae per fascicle
0) Number

Thoracic notochaetae
0) All simple capillaries
1) Acicular spines present

Thoracic notochaetae length
0) Number of chaetigers

Number of thoracic notochaetae per fascicle
0) Number

Thoracic acicular spines
0) Absent
1) Begin on chaetiger 1
2) Begin on chaetiger n

Intermediary body region

Intermediary body region between thorax and abdomen
0) Present
1) Absent

Intermediary body region length
0) Number of chaetigers

Intermediary body region chaetae
0) All simple capillaries
1) Acicular spines present
2) 'Bottle-brush' chaetae

Eggs
0) Absent
1) Present

Abdominal region

Abdominal region
0) Absent (missing)
1) Present

Abdominal region shape
0) Conical, tapering to pygidium
1) Uniform width
2) Necklace-shaped (moniliform)
3) Flared, not rounded
4) Not observed

Abdominal region length
0) Number of chaetigers

Abdominal acicular spines
0) Absent
1) Present, Notopodia
2) Present, Neuropodia
3) Present, Both

Nature of posterior spines
0) Broad
1) Curved
2) Blunt-tip
3) Bidentate

Abdominal cinctures
0) Absent (partial)
1) Present (complete)

Abdominal ‘bottle-brush’ chaetae
0) Absent
1) Present, Notopodia
2) Present, Neuropodia
3) Present, Both

Abdominal knob-tipped spines
0) Absent
1) Present

Abdominal ‘banana’ shaped spines
0) Absent
1) Present

Posterior end

Pygidium
0) Absent
1) Present

Pygidium shape
0) Simple lobe (rounded)
1) Short
2) Long
3) Terminal anus
4) Pointed

Spionidae

Spiophanes Grube, 1860

Main taxonomic features (taken from Blake, 1996b)

- Branchiae absent
- Chaetiger 1 with 1-2 large curved neuropodial hooks in addition to normal capillaries

Diagnosis (List of the main characters)

- Prostomium broad anteriorly rounded or bell-shaped with frontal horns developed top varying degrees.
- Eyes present or absent
- Occipital antenna present or absent
- Branchiae absent
- Chaetigers 1-4 shifted dorsally
- Form, shape and develop of dorsal and ventral lamellae
- Chaetigers 5-16 usually with interramal threads glands. Bacillary chaetae.
- Parapodia of Chaetiger 5 and subsequent segments poorly developed. Neuro and notopodia reduced, laterally placed.
- Anterior notochaetae capillaries
- Nuchal organ shape
- Lateral pouches present or absent
- Hooks or crotchets only in neuropodia from about Chaetiger 15; bi-tri- or quadridentate, with or without hood.
- 1-2 large curved spines in neuropodia in middle and posterior neuropodia.
- Ventral sabre chaetae present in middle and posterior chaetigers
- Pygidium with 2 or more anal cirri, with or without processes or papillae.

Laonice Malmgren, 1867

Main taxonomic features (taken from Blake, 1996b)

- Anterior notopodial postchaetal lamellae large, triangular leaf like, often surrounding setal fascicles; interparapodial genital pouches present; nuchal organ usually long extending posteriorly for numerous segments; occipital antenna always present

Diagnosis (List of the main characters)

- Prostomium anteriorly rounded or medially incised.
- Frontal horns present or absent
- Occipital antenna (tentacle) usually present
- Nuchal organ (caruncle) extending posteriorly for variable number of chaetigers
- Peristomium reduced, usually lacking lateral wings
- Eyes present or absent

- Branchiae from chaetiger 2, on variable number of chaetigers
- Branchiae separate from or partially fused with dorsal lamellae
- Branchiae apinnate or with digitiform pinnules
- Notopodia with capillaries
- Hooded hooks present or absent
- Neuropodia with capillaries, bi-tri- or multidentate hooded hooks
- Sabre chaetae neuropodial
- Interparapodial genital pouches present
- Pygidium with anal cirri.

Aurospio Maciolek, 1981

Main taxonomic features (taken from Blake, 1996b and Maciolek, 1981a)

- Branchiae from chaetiger 3, limited to 2 very short, apinnate pairs

Diagnosis (List of the main characters)

- Prostomium broadly, rounded anteriorly prolonged posteriorly as a keel
- Eyes present or absent, 0-2 pairs
- Occipital antenna absent
- Peristomium partially fused to ch1, not well developed into wings or hood
- Branchiae 2 pairs in chaetiger 3-4
- Branchiae cirriform
- Branchiae partially fused to notopodial lamellae
- Anterior chaetae capillaries
- Noto and neuropodial multidentate hooded hooks posteriorly, lacking secondary hood
- One ventral sabre chaetae posteriorly
- Pygidium with 1 long medial and 2 short lateral cirri

Prionospio and *Aurospio* comparison

Genus	**Gills**	**Secondary hood**
Prionospio	Stouter, rounder; separated from lamellae	Present (inconspicuous)
Aurospio	Thin and flat; partially fused to the notopodial lamellae	Lacking

***Prionospio* Complex** (general taxonomic characters)

1. Slender, cylindrical bodies
2. Branchiae of various form (simple or with pinnules or flattened plates). First present from chaetiger 1-3 and limited to the anterior part of the body.
3. Prostomium relatively simple, without frontal horns, and occipital antenna. Usually red eyes
4. Bi- to multidentate hooded hooks in both noto and neuropodia

5. Well developed anterior parapodial lamellae
6. Hard- membraned eggs

Genus	Branchiae from	Type of branchiae
Prionospio (sensu stricto) Malmgren, 1867	Chaetiger 2, 2-15 pairs	Cirriform and digitiform pinnules
Apoprionospio Foster, 1969	Chaetiger 2, 4 pairs	First 3 pairs cirriform; 4 pair pinnate (platelike)
Paraprionospio Caullery, 1914	Chaetiger 1, 3 pairs	Pinnate (platelike pinnules)
Aquilaspio Foster, 1971	Chaetiger 2, 2-4 pairs	Pinnate (digitiform pinnules)
Minuspio Foster, 1971	Chaetiger 2, 4-40 pairs	All apinnate (smooth, wrinkled or cirriform)

Taken from Blake (1996b) and Maciolek (1985).

Prionospio Malmgren, 1867

Main taxonomic features (taken from Blake, 1996b)

- Branchiae both pinnate and apinnate

Diagnosis (List of the main characters)

- Prostomium anteriorly rounded or truncate, sometimes weakly incised, without frontal horns.
- Prostomium subtriangular, rectangular or oval
- Caruncle extending at least to chaetiger 1
- Eyes present or absent
- Occipital antenna present
- Peristomium partially fused to chaetiger 1; often surrounding prostomium with free, flattened lateral wings
- Parapodia of chaetiger 1 reduced
- Noto and neuropodial lamellae largest in branchial region
- Notopodial lamellae often connected by low to high dorsal ridges or crests
- Branchiae from chaetiger 2, limited to anterior chaetigers 2-15 pairs
- Branchiae apinnate, pinnate or combination
- Branchiae pinnate with pinnules digitiform, not platelike. Each branchiae entirely free from dorsal lamellae
- Interparapodial (lateral) pouches present or absent
- Anterior chaetae limbate capillaries
- Posterior noto and neuropodial hooded hooks present; bi-tri or multidentate with secondary hood
- Neuropodial sabre chaetae present
- Pygidium with 1 long dorsomedial cirrus and 2 shorter ventrolateral lobes, all 3 sometimes fused

Apoprionospio Foster, 1969

Main taxonomic features (taken from Blake, 1996b)

- Branchiae with first 3 pairs apinnate and fourth pair with platelike pinnules

Diagnosis (List of the main characters)

- Prostomium subtriangular, broad anteriorly, often with medial peak
- Caruncle extends posteriorly to end of chaetiger 1
- Occipital antenna absent
- Peristomium reduced, fused with chaetiger 1 surrounding prostomium posteriorly as a yoke
- Lateral wings absent
- Notopodial postchaetal lamellae of anterior chaetigers lateral rather than dorsomedial
- Neuropodial postchaetal lamellae enlarged on chaetiger 2
- Branchiae from chaetiger 2, 4 pairs. First 3 pairs apinnate, fourth pair larger, with flattened platelike pinnules
- Anterior chaetae all capillaries
- Multidentate hooded hooks present in posterior noto and neuropodia
- Neuropodial sabre chaetae present
- Pygidium with 1 long dorsomedial cirrus and 2 shorter ventrolateral lobes

Paraprionospio Caullery, 1914

Main taxonomic features (taken from Blake, 1996b)

- Branchiae from chaetiger 1, with flattened bifoliate pinnules, with transverse ridge or membrane between branchial bases of chaetiger 1

Diagnosis (List of the main characters)

- Prostomium elongate to spindle shaped
- Posterior caruncle absent
- Eyes present or absent
- Peristomium fused with achaetous first segment
- Large lateral wings enclosing prostomium
- Chaetiger 1 well developed, distinct from preceding segments
- Notopodial postchaetal lamellae largest on first 5 chaetigers
- Three pairs of branchiae present from chaetiger 1, with flattened flabellate or bifoliate platelike pinnules
- Distinct transverse ridge or membrane between branchial bases on chaetiger 1
- Anterior chaetae all capillaries
- Multidentate hooded hooks with conspicuous striated secondary hood
- Ventral sabre chaetae in middle and posterior neuropodia
- Pygidium with one long medial cirrus and two shorter ventrolateral lobes

Aquilaspio Foster, 1971

Main taxonomic features (taken from Blake, 1996b)

- Branchiae pinnate from chaetiger 2. 2-4 pairs; digitiform pinnules

Diagnosis (List of the main characters)

- Hooded hooks from chaetiger 16
- Three secondary hood

Minuspio Foster, 1971

Main taxonomic features (taken from Blake, 1996b)

- Branchiae apinnate, from chaetiger 2 smooth or wrinkled

Diagnosis (List of the main characters)

- Prostomium triangular, bluntly or broadly rounded
- Apical peak absent or present
- Caruncle narrow or ending bluntly at posterior edge
- Pair of eyes present
- Peristomium dorsally fused with chaetiger 1
- Lateral wings present or absent
- Branchiae apinnate cylindrical from chaetiger 2
- Branchiae wrinkled or sculptured
- Chaetiger 1 well developed
- Notopodial postchaetal lamellae present
- Noto and neuropodial postchaetal lamellae variable shape (triangular, foliose, rounded)
- Membranous crests present or absent
- Interparapodial pouches lacking
- Anterior chaetae capillary moderately granulated, with distinct sheath
- Neuropodial hooded hooks from chaetiger 12-13
- Pairs of small teeth variable
- Ventral sabre chaetae from chaetiger 10-12
- Pygidium with 1 long dorsomedial and 2 shorter ventrolateral cirri

Taken from *M. ligthi* (Maciolek, 1985)

APPENDIX 4

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Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean.

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Abstract

Temporal variability in deep-sea polychaete assemblages was assessed at the Porcupine Abyssal Plain Sustained Observatory, NE Atlantic, over a 9-year period (8 cruises between August 1989 and September 1998). The polychaete communities were characterized by high number of individuals (abundance) and high family richness. Highest abundances occurred in the upper 1 cm sediment layer (53.2% of total abundance). The most abundant families were the Cirratulidae, Spionidae, Opheliidae and Paraonidae. Surface deposit feeders were the dominant trophic group (67.4% of total abundance). Significant temporal variability was evident in polychaete abundance with significant differences in polychaete abundance between sampling periods (cruises) ($p<0.01$). Stepwise increases in abundance in September 1996 and March 1997 coincided with similar increases in abundance in large invertebrates (megafauna) in the same area (known as the '*Amperima* Event' after a species of holothurian that increased in abundance by over three orders

of magnitude). Similar patterns were observed for abundances across different layers of the sediment, main families and trophic groups showing significant differences between cruises ($p<0.05$). A comparison of samples taken 1) before the '*Amperima* Event' (1989-1994) and 2) during the '*Amperima* Event' (1996-1998) showed significant differences in the polychaete abundance in the upper 3 cm of the sediment. There were significant differences in some trophic groups (predators, deposit feeders and burrowers) and the dominant families (Cirratulidae, Spionidae and Opheliidae). Not all elements of the polychaete community showed a response (e.g. the Paraonidae). Changes in surface deposit feeders were particularly evident. The temporal variability is likely to be related to seasonal and interannual variability in organic matter input. Greater food supply in some years may allow the growth and development of deposit-feeding polychaetes.

Introduction

Studies of abyssal assemblages have shown tentative relationships between the flux of organic material to the ocean floor and the abundance and biomass of benthic assemblages in some areas (Sibuet *et al.* 1993; Glover *et al.* 2002; Smith *et al.* 2006; Smith & Rabouille, 2002). However, these studies were unable to reveal how intimately climate and upper ocean events might be linked to benthic processes. Links between climate, surface production and deep-sea processes are becoming clearer as a result of long time-series in the NE Pacific and NE Atlantic Oceans. In the NE Pacific there have been two long time series, one centred on 'Station M' (Smith & Druffel, 1998) and the other at the Hawaiian Ocean Time Series (HOT) station (Smith *et al.* 2002; Karl *et al*. 1996). A comprehensive set of benthic samples have been taken at 'Station M'. Changes have been observed in both the abundances of benthic communities (larger macrofauna and megafauna) and community oxygen consumption over a seven-year period. These variations have been tentatively linked to seasonality in food supply (Lauerman *et al.* 1996; Smith & Druffel, 1998; Smith *et al.* 2006; Ruhl, 2007).

In the NE Atlantic a similar long-term study of particle flux and benthic communities has been conducted on the Porcupine Abyssal Plain (PAP). This site has been the focus of several European Union-funded projects, including BENGAL (High-resolution temporal and spatial study of the BENthic biology and Geochemistry of a northeastern Atlantic Locality) in the NE Atlantic since 1989 (Billett & Rice, 2001). Significant temporal changes have been observed in protozoan meiofaunal (Gooday *et al*. 2008), metazoan meiofaunal (Vanreusel *et al.* 2001; Kalageropoulou *et al*. 2008)**,** macrofaunal (Galéron *et al.* 2001) and megafaunal communities

(Bett *et al.* 2001; Billett *et al.* 2001). Changes in the vertical distribution of some components of the infaunal sediment community were evident and were thought to be related to the apparent impoverishment of organic matter at the sediment surface and/or the effects of increased disturbance and bioturbation (Vanreusel *et al.* 2001). Long-term changes were most clearly seen in the abundances of the invertebrate megafauna. Changes occurred in the abundances of actiniarians, annelids, ophiuroids, pycnogonids and tunicates and particularly in holothurians (Billett *et al.* 2001). The sudden increase in abundance of some holothurians in the mid 1990s, such as *Amperima rosea* and *Ellipinion molle*, by three orders of magnitude, had important consequences for organic material cycling at the sediment surface (Bett *et al.* 2001). This event was known as 'The *Amperima* Event' (Billett & Rice, 2001).

Macrofaunal studies at PAP indicated potential long-term changes in this size fraction of the benthic community. An increase in the abundance of opportunistic species was recorded, with various taxa, such as foraminiferans, opheliid polychaetes and other polychaetes responding to the changes on the seabed at different rates (Galéron *et al.* 2001; Vanreusel *et al.* 2001). Polychaetes are the dominant component of the deep-sea macrofauna, constituting between 30 and 70% of the macrofaunal abundance (Blake & Grassle, 1994; Gage & Tyler, 1991; Glover *et al.* 2001; Grassle & Maciolek, 1992; Paterson, *et al.* 1994; Tyler, 2003). Polychaetes generally also dominate the macrofauna in terms of biomass (Brown, 1991). Nevertheless, long-term variability in deep-sea polychaete assemblages is very poorly understood, and to date there have been no studies on this subject. This study addresses the gap in long-term studies polychaete population succession, recruitment and reproductive patterns.

Other studies have shown links between surface productivity and benthic parameters, at both seasonal and interannual time scales (Billett *et al.* 1983; Lampitt, 1985; Rice *et al.* 1994). In the current investigation, long-term variability in deep-sea polychaetes at the PAP time series was studied. In particular we test whether the polychaetes respond to changes in the biogeochemical environment as noted for other elements of the abyssal fauna, and, if so, whether all elements of the assemblage do so equally. We also test whether there are changes in the vertical distribution of polychaetes within the sediment. The high numbers of megafaunal sediment deposit feeders was thought to affect the quantity and quality of nutrient available in the surface layers. We test whether the abundances of polychaetes, particularly surface deposit feeders, were diminished as a result.

Methods

Study site

All samples were collected from a central locality (48º 50'N 16º 30'W) on the Porcupine Abyssal Plain Sustained Observatory (PAPSO) NE Atlantic about 270 km southwest of Ireland 4850 m of depth (Fig. 1). It was chosen because it is a relatively flat area, remote from both the continental slope to the east and the mid-ocean ridge to the west, and so is unlikely to be influenced strongly by downslope or advective processes (Billett & Rice, 2001). This abyssal region is known to be subject to strong seasonal fluctuations in fluxes of organic matter that reflect the seasonal cycle of primary production in the euphotic layer with pronounced maxima in summer (Rice *et al.* 1994; Lampitt *et al.* 2001). The depth of winter mixing of the upper water column is about 500 m (Rice *et al.* 1994). Table 2 gives a summary of the main geochemical characteristic of the study area.

Sampling and processing

Polychaete samples were collected using an USNEL spade boxcorer (total surface area 0.25 m^2) (Hessler & Jumars, 1974). Samples were processed immediately after recovery. The core was subsampled routinely using a subcore with a square cross section (92 x 92 mm) and another with a circular cross section (55 mm diameter). Large xenophyophores and perforated tubes were removed before the core was subdivided into six horizontal layers (0-1, 1-3, 3-5, 5-10, 10-15, 15-20 cm) manually with a trowel. The 0-1 and 1-3 cm layers were immediately placed into 4% borax-buffered formaldehyde until they were sieved in order to avoid the deterioration of organisms. The deeper layers were placed in cold sea-water. Sieving was carried out on a stack of 1000, 500, 300 and 250 µm sieves for the four upper layers, while the two deepest (10-15 and 15-20 cm) layers were washed through two sieves (1 mm and 500 µm). In the laboratory, all preserved samples were sorted into higher taxa (Polychaeta, Peracarida, Mollusca, etc.) and counted to evaluate abundance.

Polychaete family identification was carried out by stereo microscope (Leica, model WILD MZ8) and light microscope (Olympus) with video camera support (Panasonic F10 CCD). Unknown specimens were drawn using a light microscope with camera lucida attached (Olympus). A photographic record was kept of unknown and main species using a digital photograph camera.

All macrobenthic samples and data were taken during eight oceanographic cruises between 1989 and 1998 (Table 1). While further sampling for macrofauna has been undertaken since 1998, it was not possible to include this material in a 3-year PhD study. These later samples will be analysed in a subsequent study.

Statistical analyses

The temporal variation in polychaete abundance was analysed. In addition to total abundance, a hierarchical approach was taken to identify whether all elements of the fauna responded in a similar way. So abundance of polychaetes in different sediment horizons, dominant families and finally different trophic groupings were analysed. The trophic groups classification applied for each family was simplified from the scheme proposed by Fauchald and Jumars (1979) with individuals being assigned to broad feeding categories – predators (carnivores plus omnivores), surface deposit feeders, burrowing subsurface deposit feeders (here after termed burrowers) and filter feeders. Family richness also was calculated. To get a consistent data set the statistical analyses were made only on a specific subset of samples. This was because 1) the high variability in the number of samples available for each sampling period and 2) the different types of data available for each cruise. Consequently, analyses were carried out only on data from individuals retained in the 300 to 500 μm fractions. We are confident that while this will have reduced the overall abundance it did not affect the overall comparison between cruises or pre and post '*Amperima* Event' analyses significantly. An analysis of samples, where a full set of sieve fractions was retrieved, indicates that the greatest abundance of polychaetes (62.9 %) occurred in the 300 to 500 μm size fraction (Fig. 2).

Analyses of variance (ANOVA) and a non-parametric Kruskal-Wallis test (only cruises with >2 samples) were used to test for significant differences in abundance between sampling periods (cruises), while a *t*-test was used for pre-'*Amperima*' and versus '*Amperima* Event' periods. Data were log-transformed, and 'STATISTICA' statistical software was used (www.statsoft.com). For the comparison between pre-'*Amperima*' and '*Amperima* Event' periods, samples from August 1989, May 1991 and April 1994 were used as pre-'*Amperima*' and from September 1996, March 1997, July 1997, March 1998 and September 1998 for the '*Amperima* Event'. No corrections were made for multiple testing when multiple comparisons were made.

Results

Temporal variability in polychaete abundance

A total of 3338 polychaetes were recorded during eight cruises between August 1989 and September 1998. Mean abundance varied with sampling period (cruise). The greatest abundances were recorded in July 1997 (145 ± 31 specimens per 0.25 m^2, n = 5). The lowest mean abundance was recorded in 1989 (45 specimens per 0.25 m^2, n = 1) which probably

reflects that only a single sample was available for this analysis. A stepwise increase in the abundance of polychaetes occurred between 1994 and 1996, and then again in early 1997. The trend with time after July 1997 was a small but consistent decrease in mean abundance with time (Fig. 3). ANOVA demonstrated significant differences between sampling periods ($F_{5, 25}$=20.3, p<0.05). A non-parametric Kruskal-Wallis test confirmed that observed differences were highly significant between cruises (p<0.001). A *t*-test conducted on the same data demonstrated significant changes between pre-'*Amperima*' samples (1989-1994) and '*Amperima* Event' samples (1996-1998) (p<0.001). Mean abundance in pre-'*Amperima*' samples was 54.4±14 (n=11) specimens per 0.25 m^2, while the mean abundance in the '*Amperima* Event' was 195.7±37 (n=23) specimens per 0.25 m^2. The mean abundance of polychaetes during all periods (1989-1998) was 98.2±44 (n=34) specimens per 0.25 m^2.

Temporal change in abundance in relation to depth in sediment

Only results from the 0-1, 1-3 and 3-5 cm sediment layers were analyzed because they were the only layers processed using a 300µm sieve. A total 1596 specimens (53.2 % of polychaete total numbers) were recorded in the top 1 cm and 958 specimens between 1 and 3 cm (31.9 %). Between 3 and 5 cm 446 specimens were recorded. (14.9 %). A total of 3000 individuals were recorded in the upper (0-1, 103 and 3-5 cm) sediment layers (all sieve sizes). For the 0-1 and 1-3 cm layers, polychaete abundances changed with time (Fig. 4). In contrast, polychaete abundances in the 3-5 cm layer showed no obvious trends (Fig. 4).

Statistical analysis (ANOVA) confirmed significant differences in two first layers between sampling periods (0-1 cm layer, $F_{4, 23}$=4.3, p<0.01 and 1-3 cm layer, $F_{4, 23}$=11.9, p<0.001). No significant changes were recorded in the 3-5 cm layer between sampling periods ($F_{4, 23}$=1.8, p>0.1). A *t*-test of pre-'*Amperima*' and '*Amperima* Event' periods showed significant differences in the two uppermost sediment layers (0-1 cm layer, p<0.005 and 1-3 cm layer, p<0.01), but not in the 3 to 5 cm sediment layer (p>0.05).

Temporal change in family richness

A total of 44 polychaete families were recorded from the eight cruises between August 1989 and September 1998. The lowest richness (10 families) was recorded in August 1989, which probably reflects the fact that only one sample was processed. Family richness was greatest at the time of the '*Amperima* Event', increasing from 16 families in April 1994 to 36 families in September 1996. Subsequently the number of different families declined (Fig 5). The apparent changes in family richness were not sample-size dependent (R^2= -0.1). Pre-'*Amperima*' and

'*Amperima* Event' samples showed highly significant differences in family richness and faunal composition. Some families were present during all sampling periods, such as Ampharetidae, Chrysopetalidae Cirratulidae, Paraonidae, Pilargidae and Spionidae. Others, such as Nepthyidae, Nereididae, Pisionidae and Trochochaetidae were recorded only once or twice with only one individual. The rarity of some families and constancy of others is typical of deep-sea polychaete communities. Some families such as Acrocirridae, Maldanidae and Oweniidae that were not recorded in 1994 were present in 1996. Some families that occurred only in low abundances in 1994, such as Opheliidae Fauveliopsidae, Glyceridae and Lumbrineridae, became abundant in September 1996.

Temporal changes in abundance of the dominant polychaete families

Cirratulidae was the most abundant family sampled at the Porcupine Abyssal Plain (29.8%), followed by Spionidae (20.9%). Paraonidae and Opheliidae accounted for 8.1% and 5.4%, respectively. Changes in abundances of these families over the study period were not uniform. Cirratulidae, Spionidae and Opheliidae increased in abundance, reaching a peak during the '*Amperima* Event', with greatest abundances during July 1997 (Cirratulidae and Spionidae) and March 1998 (Opheliidae) (Fig 6). In contrast, the abundance of Paraonidae did not vary greatly during the study. ANOVAs showed significant differences between sampling periods for Cirratulidae ($F_{5, 25}$=9.16, $p<0.001$), Spionidae ($F_{4, 23}$=3.75, $p<0.05$) and Opheliidae ($F_{5, 26}$=15.83, $p<0.001$). These differences were not observed for Paraonidae ($F_{5, 25}$=1.33, $p>0.1$). Differences in the number of individuals of opheliids were evident from September 1996 cruise owing to a recruitment event of small opheliids during that period (Vanreusel *et al.* 2001). A *t*-test for pre-'*Amperima*' and '*Amperima* Event' periods showed significant differences for Cirratulidae, Spionidae and Opheliidae ($p<0.05$). No significant changes were observed in Paraonidae between these periods ($p>0.05$).

Changes in abundance of trophic groups.

Polychaete families present could be assigned to various feeding guilds including surface deposit-feeders, burrowers (subsurface deposit feeders), filter feeders and predators (carnivores plus omnivores). Surface deposit feeders were the dominant trophic group (67.4%), with Cirratulidae and Spionidae as the main families. Burrowers contributed 16.5% of the individuals, mainly opheliid polychaetes. Predators and filter-feeding polychaetes were represented by 13.7% and 2.4% of total number of individuals, respectively. Despite the clear dominance of surface deposit-feeders, large numbers of predators and burrowers were found

during several cruises (group richness). In burrowers, highly significant differences were recorded with time ($F_{5, 25}$=7.25, p<0.001). Significant changes between sampling periods also were observed for surface deposit feeders ($F_{5, 25}$=9.2, p<0.001), and predators ($F_{6, 26}$=2.8, p<0.05). There were no significant differences in the abundances of filter feeders between cruises ($F_{5, 25}$=0.9, p>0.1). A *t*-test made on pre-'*Amperima*' and the '*Amperima* Event' periods showed significant differences for predators (p<0.01) and highly significant differences in surface deposit feeders and burrowers (p<0.005). In filter feeders the changes observed between periods were not significant (p>0.1).

Discussion

Abundance

Polychaete abundance showed a significant increase during the '*Amperima* Event'. The size of the increase was, however, smaller than observed for the holothurian megafauna species, being just two to three times the abundance of pre-'*Amperima*' samples, compared with two orders of magnitude for the megafauna. Polychaete abundances before the '*Amperima* Event' were comparable to abundances determined for other abyssal localities lying under eutrophic and seasonally productive surface waters. However, polychaete abundances at the PAP during the '*Amperima* Event' were much greater than any other abyssal region measured previously, highlighting that there has been a response to a changing nutrient regime.

Polychaetes were not the only infaunal group to increase during the '*Amperima* Event'. Galéron *et al.* (2001) noted that infaunal bivalves showed an increase during this period. Within the meiofauna, Gooday *et al*. (2008) reported a similar response in protozoan meiofauna, while Kalageropoulou *et al*. (2008) observed increases in abundance with metazoan harpacticoid copepods and nematodes. However these increases in the infaunal elements were again considerably smaller than observed for the megafauna, particularly the holothurians (Billett *et al.* 2001; 2008; Bett *et al*. 2001) by two orders of magnitude. These results suggest that whatever the process which that resulted in the increase in abundance of the megafauna, it was also affecting the infauna. The reduced magnitude of the response of the infauna in comparison with the surface-dwelling megafauna points to some mediation or amelioration of the effects. In other words while there may have been an increase in nutrient flux to the ocean floor a smaller proportion of it appears to have been available to the infauna.

The '*Amperima* Event' may be a tentative response to increases in the flux of organic matter to the seabed. Water column fluxes in total organic carbon and total nitrogen (Kiriakoulakis *et al.* 2001), phytopigments (Fabiano *et al.* 2001) and biogenic silica (Lampitt *et al.* 2001) were

greatest during the July 1997 and September 1998 periods. In sediments, bacterial carbon production (Eardly *et al.* 2001), phytopigments (Witbaard *et al.* 2001), lipid compounds (Galéron *et al.* 2001) and biogenic silica components (Ragueneau *et al.* 2001) were greatest in September 1996. These values coincide with first increase in abundance in the polychaete assemblages. Unfortunately, there were no sediment trap data available just prior to the '*Amperima* Event' (Lampitt *et al.* 2001), but subsequent work has shown that fluxes at this site can change by an order magnitude from year to year (Lampitt *et al.* 2008). It is possible, therefore, that enhanced organic matter inputs to the deep-sea floor have caused changes in the meiofaunal, macrofaunal and megafaunal size fractions of the benthic community (Billett et *al.* 2001; Gooday, 2002). However, the relationship between the '*Amperima* Event' and surface ocean export flux is still tentative (Billet *et al.* 2008).

In considering the response of polychaete assemblages, two potential factors must be considered. Firstly, there was an increase in the nutrient flux to the abyssal ocean floor and, secondly, the massive increase in surface-feeding megafauna, particularly holothurians, may have acted as competitors for this influx. We do not consider holothurians are to be potential consumers of the polychaete infauna as many species appear to be quite restricted in particle size selection (Hudson *et al.* 2003), although ophiuroids may impact small juveniles and settling larvae. The megafauna may, however, repackage the available nutrients in the form of excretory products such as faeces and so increase nutrients, albeit of a reduced and potentially different nature, which may then be available for infaunal groups. Holothurian assimilation efficiencies are estimated to be around 30% when phytodetritus is present but drop and become negative when it is absent (Ginger *et al.* 2001, Sibuet, 1988). Holothurians appear to be selective, able to preferentially feed on newly deposited phytodetritus (Wigham *et al.* 2003). Therefore, nutrients may be still available to sediment-dwelling infauna given the assimilation efficiencies, but it may be of reduced 'quality' in that key sterols have been removed or reduced. Lipid concentrations such as phytoplankton-derived sterols and other labile lipids were dramatically depleted in the surficial sediments in 1997 (Ginger *et al.* 2001). The absence of phytodetritus and chlorophyll concentrations (Witbaard *et al.* 2001) in the surficial sediments also was apparent between 1997 and 1998. As phytosterols are energetically 'expensive' to biosynthesise, Ginger *et al.* (2001) suggest that their availability may be an important factor controlling the abundance of some deep-sea taxa.

Two further aspects of megafaunal feeding need to be considered. Firstly it is still not clear what are the assimilation of ophiuroids as they also are surface deposit feeders but likely to be less selective and so may be reducing available nutrients. Secondly it is unknown how often the

same area of the ocean floor is revisited by mobile deposit-feeding megafauna. So while 30% efficiency would perhaps appear to leave a considerable amount of nutrient available, it may in fact be much less as the sediment may be processed a number of times and the 'quality' of the remaining nutrients much reduced. Separating competition and/or alternative nutrient effects is not possible with the data available, particularly given the lack of sediment trap data. As long as 100% assimilation efficiency of the added nutrient flux by the mobile epifauna was not achieved, increased infaunal abundance would be expected. Repackaging and conversion of chemical form by the mobile epifauna might be expected to favour some infaunal taxa more than others.

Abundance: vertical distribution (sediment layers).

Polychaetes were most abundant in the top 1 cm layer of sediment (Fig. 4) confirming the PAP results of Galéron *et al.* (2001) who used all sieve size fractions in which 62% of the polychaetes occurred in the top 1 cm layer of the sediment. This is similar to results reported from PAP and MAP (Glover *et al.* 2002). By contrast results from the oligotrophic EUMELI site on the Cap Verde Abyssal Plain showed that the 0-1 cm layer contained >80% of the fauna and in the mesotrophic ECHO site in the Pacific with the top 0-1 cm layer accounted for 75% of the fauna (Paterson *et al.* 1998).

Temporal changes in abundance were observed in the 0-1 and 1-3 cm sediment layers, but not in deeper layers within the sediment. Downward and upward movements within the sediment were not evident in total abundance following the '*Amperima* Event'. Overall proportions of polychaete abundance in the upper layers did not change substantially with time so there appeared to be a general up-lift in abundance within the 0-3 cm layers. This suggests that whatever process was operating it affected the surface and upper sediment rather than occurring within the sediment column as a whole. The nature of the response of polychaetes supports the observation of that they were affected by the same process (es) that drove the '*Amperima* Event'.

A similar vertical distribution and dominance was reported for harpacticoid copepods (>63%), bivalves (45-80%), tanaidaceans (~40%) and isopods (>60%) at the PAP (Galéron *et al.* 2001). The abundances recorded in this study declined significantly with depth in the sediment ($p<0.005$). This may be related to lipid concentrations (Galéron *et al.* 2001) and phytopigments (Witbaard *et al.* 2001) in the surficial sediment. Between September 1996 and July 1997, the total organic carbon (TOC) content of the sediment declined from 0.37% at the surface to 0.15% at 15-cm depth, except in September 1996 when the surficial TOC content was 0.45%

(Rabouille *et al*. 2001). The TOC profiles in September 1996 suggest that a large phytodetritus deposition event had occurred in the sediment surface. This is consistent with the presence of phytodetritus on core surfaces collected during this month, and concentrations of chlorophyll a, phaeophorbides and hydrolysable proteins that were higher than during 1997 (Witbaard *et al*. 2000; Fabiano *et al*. 2001).

Faunal composition and family richness

Variability in faunal composition, diversity and family richness are evident in benthic communities on a variety of spatial scales relating to depth (Paterson & Lambshead, 1995) and regional biogeography (Rex *et al*. 1993). Changes in the faunal composition may also be caused by disturbance (Grassle & Morse-Porteous, 1987; Gage, 2003) or physical effects (Grassle & Maciolek, 1992). Seasonal or interannual variability has been recorded for only a few taxa and at a limited number of localities (Billett *et al*. 2001). In the current study, a stepwise increase in the number of polychaete families was recorded from September 1996 onward, coincident with the '*Amperima* Event'. The increase was not directly correlated with sampling effort and so appeared to be the result of a general increase in the overall abundance of polychaetes. At the PAP, 23 families were recorded prior to the '*Amperima* Event' and 43 families during the Event. Dominant families did not change during the study, rather polychaetes increased in abundance generally and represented a corresponding immigration of individuals from a greater range of families.

The families that showed the greatest response were those that most often dominate deep-sea polychaete infaunal assemblages –Cirratulidae, Paraonidae and Spionidae (Hilbig & Blake, 2006). The former families were described by Smith & Hessler (1987) as opportunists (species that wait for optimal conditions and respond quickly to high levels of organic enrichment to accumulate energy). Nowell *et al*. (1984) have showed some Spionids change their feeding type from suspension to deposit feeding in the case of changing food supply. Two of these families (Cirratulidae and Spionidae) showed temporal variation, increasing in abundance at the time of the '*Amperima* Event'. Cirratulidae dominated the polychaete families in seven of eight cruises. Spionidae dominated only in July 1989 (Fig. 6). By contrast the Paraonidae did not show any significant changes in abundance.

One other family that increased notably in abundance was the Opheliidae. Opheliids are burrowers and appear to be non-selective subsurface deposit feeders. Studies made by Hermans (1978) in shallow-waters opheliids and Renaud *et al.* (1999) on opheliids on the shelf off North Carolina also suggest that they are opportunists. Vanreusel *et al*. (2001) found a large influx of

post-larval individuals of an unknown opheliid species at PAP during the '*Amperima* Event' and suggested that this influx was an opportunistic response to an increase in nutrient flux. Jumars (1978) similarly observed patches of opheliids of homogeneous length, suggestive of cohorts. These life history traits may explain the temporal variability noted for the PAP opheliid polychaetes.

The rise in overall abundance and the response of opportunistic polychaetes points to a quantitative rather than a qualitative change in nutrient input. In experiments using a variety of different substrates, early colonisers are usually from different families to those observed here. In particular members of the Dorvilleidae are particularly common (Grassle & Morse-Porteous, 1987; Snelgrove *et al*., 1994) in sediment rich in organic material to approach or reach anoxia. In the PAP samples there was not a major shift in the dominant families, although there was a large increase in the abundance of opheliids; this is thought to be a recruitment event of one species.

Trophic groups

The nature of the polychaete response in the upper sediment layers suggests that trophic groups which exploit the surface were favoured. At PAP, surface deposit-feeders polychaetes were indeed the most important trophic group, representing 67.4% of total abundance. Their temporal variability showed a trend of increasing abundance from September 1996 (Fig. 7) probably owing to surface sediment enrichment by a summer 1996 pulse of organic supply (Lampitt *et al.* 2001; Witbaard *et al.* 2000). Burrowing polychaetes represented 16.6% of total abundance. The observed increase in abundance was due partly to a high number of opheliid polychaetes (juveniles) recorded from March 1997. Predators (13.7%) and filter feeders (2.4%) were minor components of the polychaete community. These trophic groups did not show any significant temporal trends despite the density of predators being higher than deposit feeders in several cruises.

Qualitative changes in the organic flux might regulate essential dietary compounds required by benthic populations (Ginger *et al.* 2001), and changes in the composition of phytodetritus may drive changes in the composition of the benthic communities (Wigham *et al.* 2003). However there were no obvious changes in the trophic composition of the polychaete groups to support this conclusion. Once again it appears there was a general increase in surface deposit and burrowing deposit feeders, with exceptional increase of the opportunistic opheliid deposit feeders.

Deposit feeders are the dominant trophic group in the deep sea (Dauer, 1983; Jumars *et al.* 1990). Studies made by various authors have recorded similar trophic groups' composition and

dominance. Glover *et al.* (2001) found deposit-feeder dominance in PAP, EOS and MAP sites. Only at TAP did they find that burrowers dominated (opheliid polychaetes). Similar results were found by Aberle & Witte (2003) during May and June 2000 from PAP, Paterson & Lambshead (1995) in the Rockall Trough, and at the Climax II, ECHO, PRA and Domes sites in the Pacific Ocean (Hessler & Jumars, 1974; Paterson *et al.* 1998).

Conclusion

Temporal variability in the abundance and family richness of polychaete assemblages was evident on the Porcupine Abyssal Plain between August 1989 and September 1998. Significant differences in abundance through time among families, trophic groups and in different layers within sediment were observed. These changes may be the response to changing ecological and oceanographic factors, the main one being an increase in food supply generated by seasonal nutrient inputs and particulate flux to the seabed from water column through the deposition of phytodetritus. While it is not possible to rule out a response to the sediment alteration and disturbance caused by large numbers of holothurians, it this is perhaps less likely as the dominant families and trophic groups did not change. The reduced responses of the polychaetes and other infaunal elements do suggest that the holothurians have been more successful in utilizing the nutrient influx. Further studies of the polychaetes at the species level will enable us to test this idea further.

The response of the infaunal polychaetes within the same time frame as both the megafauna and other infaunal components, such as the meiofauna, point to a widespread phenomenon operating on short ecological time scales. This rapid response indicates that there is a close linkage between the processes operating in the upper ocean and the abyss. Climatic forcing, which has been implicated in upper water column ecology, may have a much more direct role in abyssal sediment systems than was first thought.

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Figures

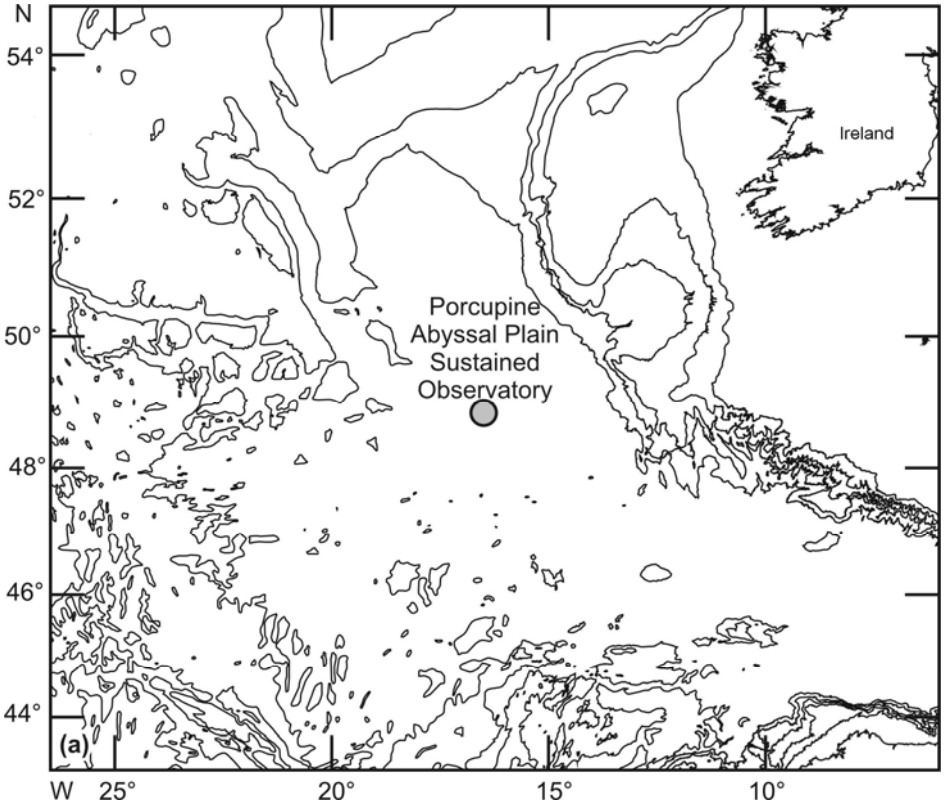

Fig. 1. Study site at Porcupine Abyssal Plain (PAP). NE Atlantic Ocean

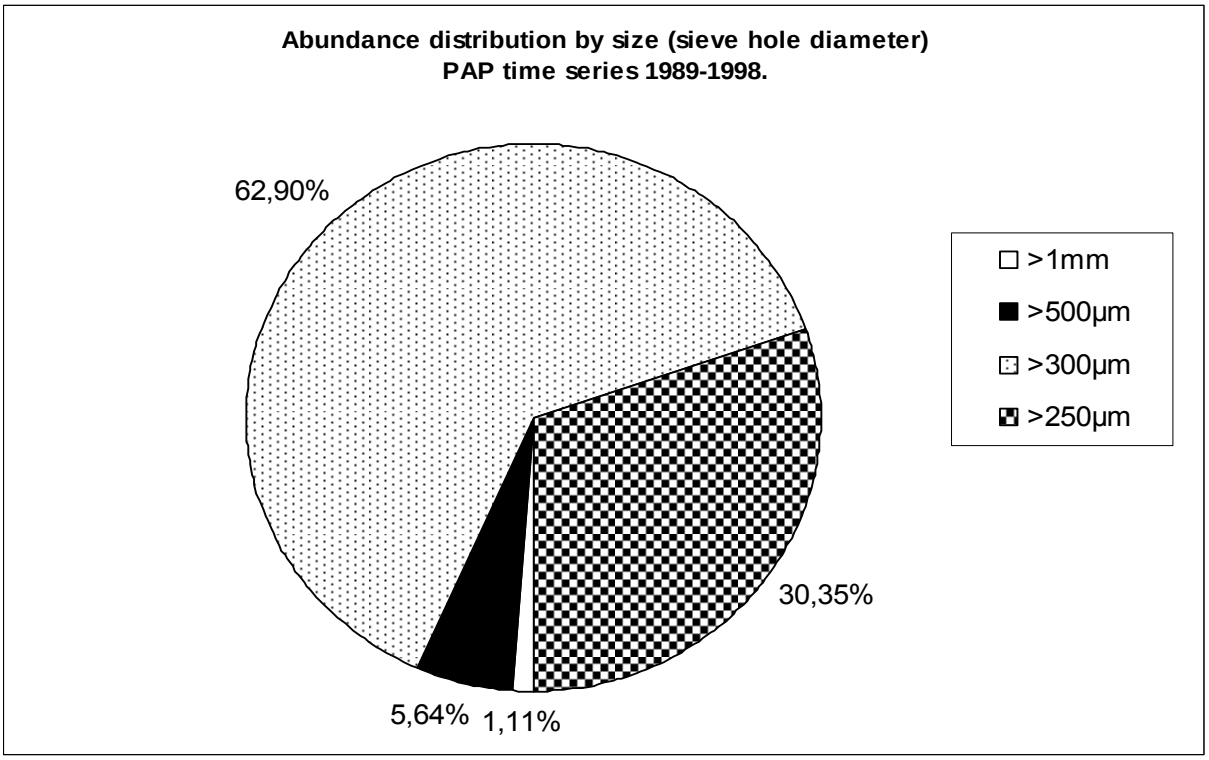

Fig. 2. Total number of individuals by size (mesh diameter). All sieve fractions considered

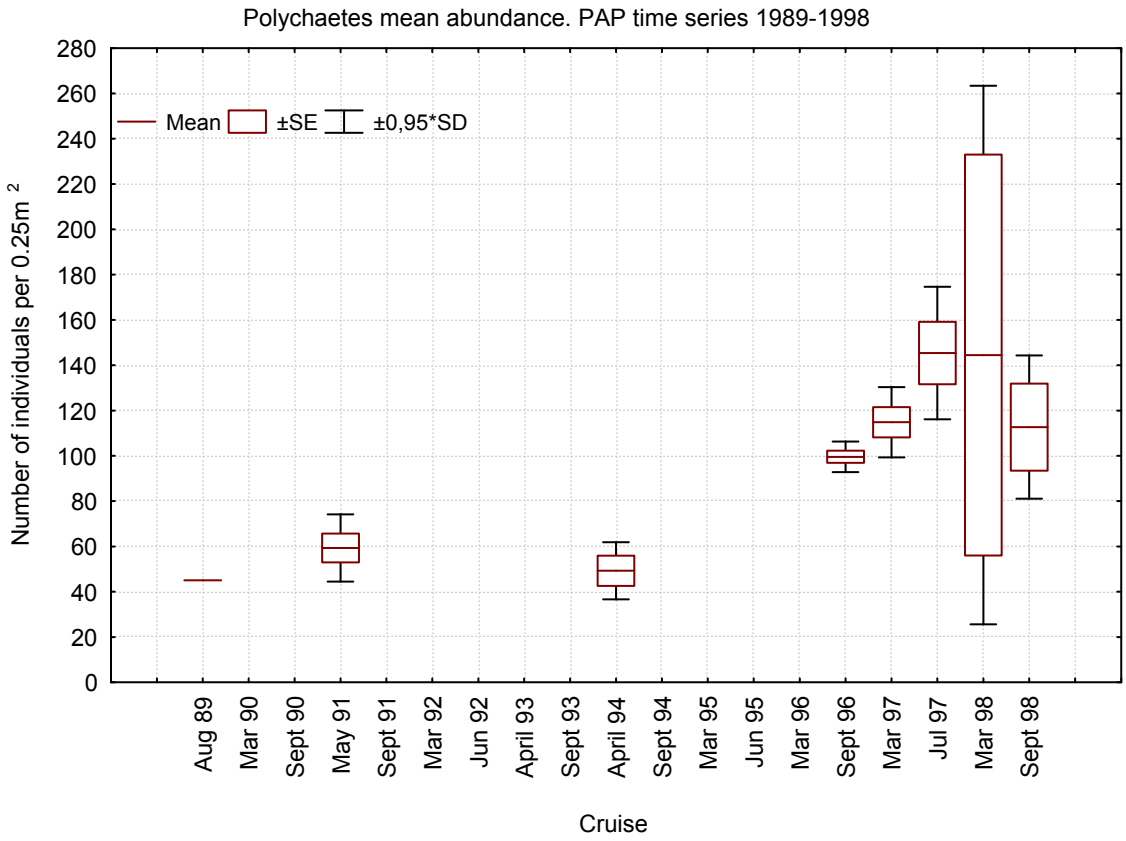

Fig 3. Temporal variability in mean abundance of polychaetes. PAP 1989-1998. Mean abundance, standard error and standard deviation (95%).

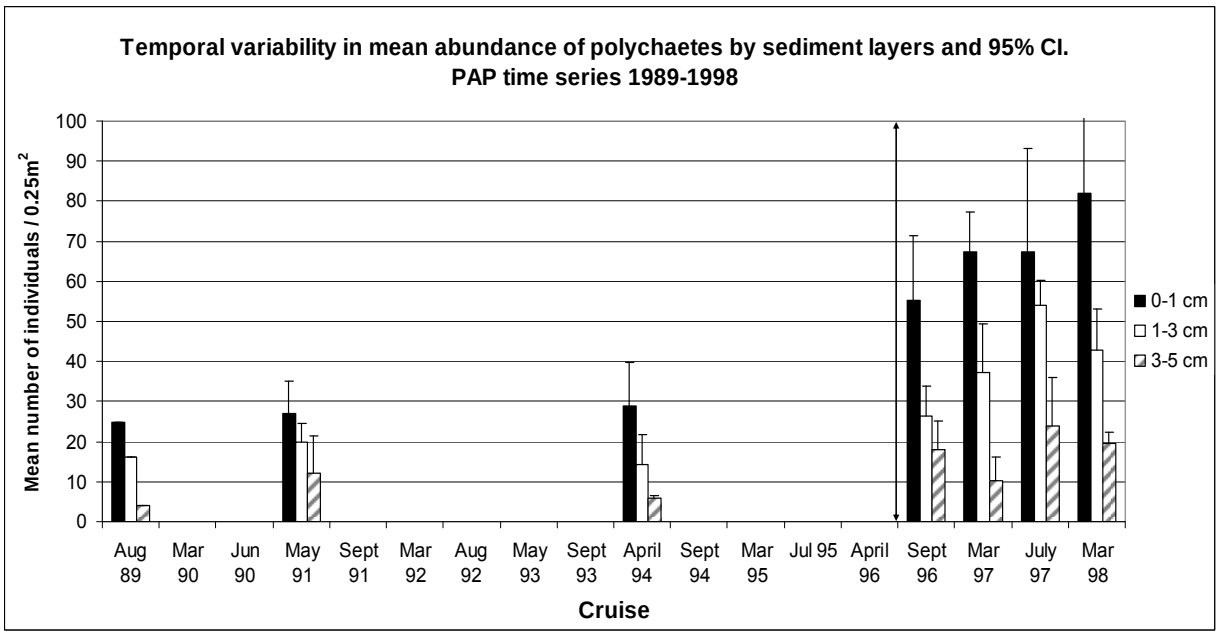

Fig 4. Temporal variability in mean abundance of polychaetes by sediment layers. The double headed arrow marks the start of the *Amperima* Event. There was no layers information in September 1998.

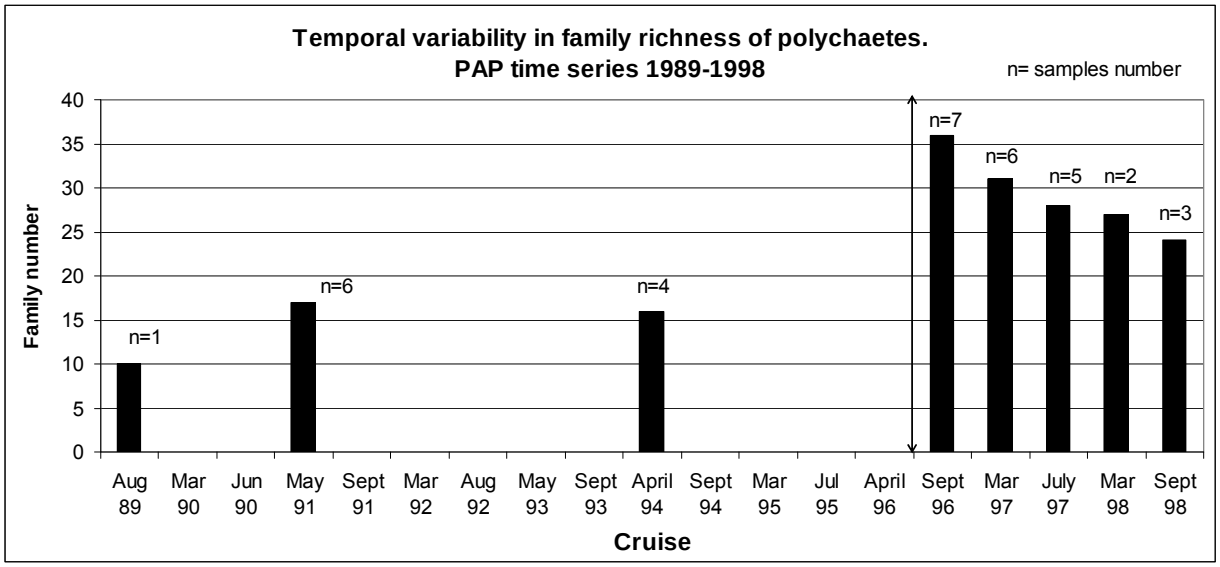

Fig 5. Temporal variability in family richness of polychaetes. The double headed arrow marks the start of the *Amperima* Event.

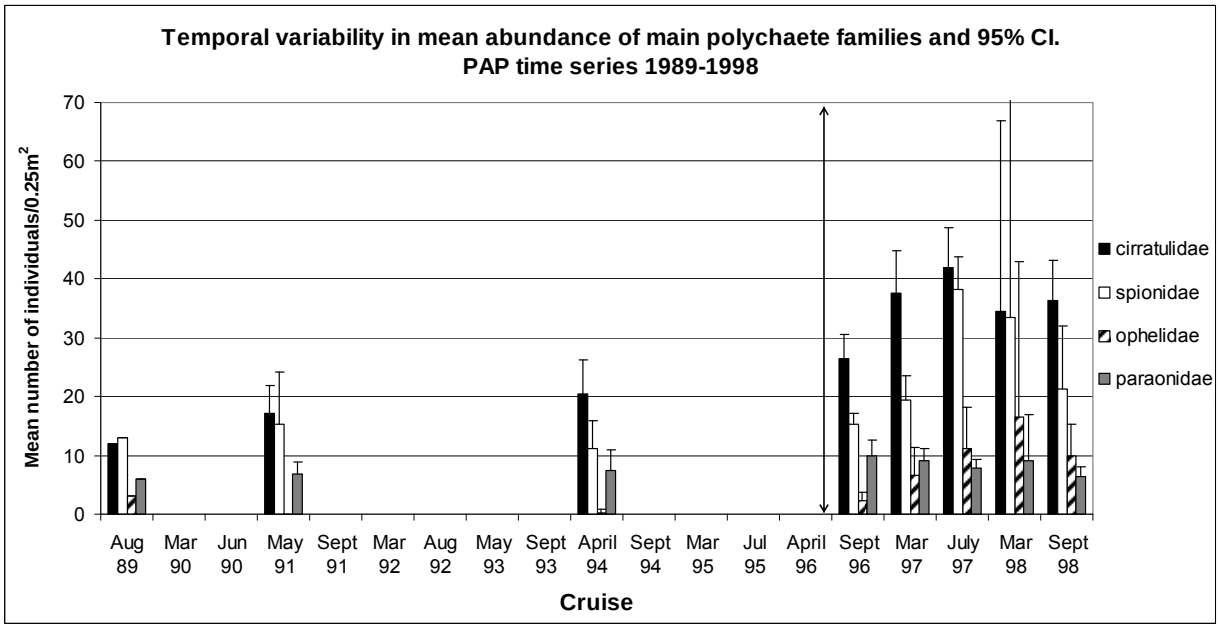

Fig 6. Temporal variability in mean abundance of main polychaete families. The double headed arrow marks the start of the *Amperima* Event.

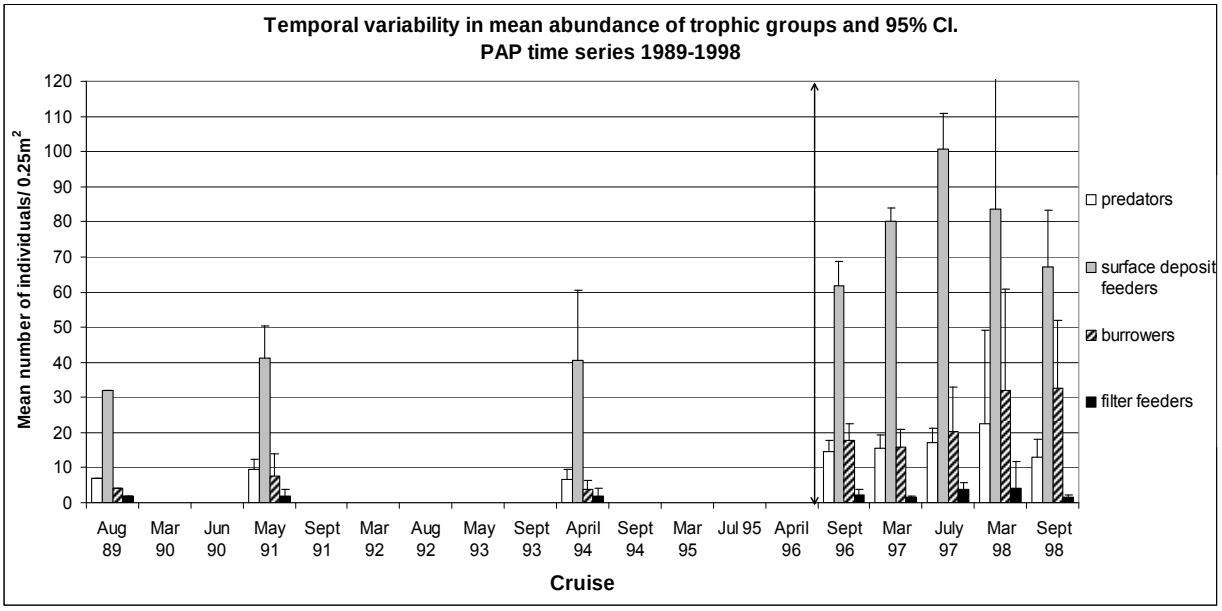

Fig 7. Temporal variability in mean abundance of polychaete trophic groups. The double headed arrow marks the start of the *Amperima* Event.

Tables

Table 1. Cruise, sampling period, station number and samples number. Samples taken in the BENGAL project denoted by *

Cruise	Date	Station	Number of box core samples
RRS *Discovery* 185	18 August – 17 September 1989	11908	1
RRS *Challenger* 79	12 May – 3 June 1991	52701	6
RRS *Challenger* 111	29 March – 25 April 1994	53201 53205	4
RRS *Discovery* 222 *	29 August – 24 September 1996	12930	7
RRS *Discovery* 226 *	12 March – 10 April 1997	13077	6
RRS *Discovery* 229 *	2-31 July 1997	13200	5
RRS *Discovery* 231 *	1-31 March 1998	13368	2
RRS *Discovery* 237 *	25 September – 8 October 1998	13627	3

* BENGAL project

Table 2. Main biogeochemical characteristics measured at PAP

Nutrient regime	Seasonal phytoplankton bloom
Sedimentation accumulation rate[a]	3.5 cm ky^{-1}
Sediment median grain size[a]	8-8.6 µm (calcareous ooze)
TOC surface sediment[b]	0.35% - 0.45%
C:N ratio[c]	4.8 – 7.8
POC flux [d]	10.6 mgC m^{-2} d^{-1} (average)

[a]Rice *et al.* (1991); [b] Rabouille *et al.*(2001); [c] Santos *et al.* (1994); [d] Lampitt *et al.* (2008)

Table 3. Site, depth, sieve fraction size, number of USNEL spade box core samples, mean number of individuals per 0.25m^2, number of species and references.

Site	Depth (m)	Sieve fraction size	No. of box cores	Abundance per 0.25m^2 (SE)	No of species	Reference
JGOFS Equatorial Pacific Study 0º N	4300	300μm	3	84 (27.9)	73	Glover *et al.* 2002
JGOFS Equatorial Pacific Study 2º N	4400	300μm	4	60 (6.4)	82	Glover *et al.* 2002
JGOFS Equatorial Pacific Study 5º N	4400	300μm	3	80 (19.1)	76	Glover *et al.* 2002
JGOFS Equatorial Pacific Study 9º N	4900	300μm	3	13 (2.3)	23	Glover *et al.* 2002
Hawaii Ocean Time Series 23º N	4800	300μm	4	9 (1.7)	14	Glover *et al.* 2002
Deep Ocean Mining Environmental Study A	5100	300μm	47	16 (0.8)	104	Glover *et al.* 2002 Paterson *et al.* 1998
Preservation Reserve Area	4800	300μm	16	65 (16.8)	100	Glover *et al.* 2002
ECHO 1	4500	300μm	15	42 (5.5)	113	Glover *et al.* 2002
CLIMAX II	5010	300μm	10	15.6 (1.7)	46	Hessler & Jumars, 1974
Cape Verde Abyssal Plain	4580-4647	250μm	5	37.8	39	Cosson-Sarradin *et al.* 1998
Cape Verde Abyssal Plain	4600	1mm, 500μm and 250μm	8	35.8 (10)	75	Glover *et al.* 2001 Sibuet *et al.* 1993
Tagus Abyssal Plain	5035	300μm	6 (Vegematic SBC 0.09m^2)	64.5 (25.8)	57	Glover *et al.* 2001 Gage *et al.* 1995
Madeira Abyssal Plain	4900	1mm, 500μm, 300μm and 250μm	5	17.5 (7.8)	29	Glover *et al.* 2001 Paterson *et al.* 1994
Porcupine Abyssal Plain	4800	1mm, 500μm, 300μm and 250μm	5	81 (20.25)	101	Glover *et al.* 2001 Paterson *et al.* 1994
Porcupine Abyssal Plain	4850	1mm, 500μm, 300μm and 250μm	23	252.00	No data	Galéron *et al.* 2001
This study (1989-1994)	4850	300μm	11	54.4 (4.4)	23 (family)	Soto *et al.* (this paper)
This study (1996-1998)	4850	300μm	23	195.7 (7.8)	43 (family)	Soto *et al.* (this paper)