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Polychaete community structure and biodiversity change in space and time at the abyssal seafloor

by

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ABSTRACT

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POLYCHAETE COMMUNITY STRUCTURE AND BIODIVERSITY CHANGE IN SPACE AND TIME AT THE ABYSSAL SEAFLOOR

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The deep sea is a dynamic environment over various spatio-temporal scales. But, the characteristics of deep-sea natural variations and underlying processes remain poorly understood, which prevents contextualising any anthropogenic impact on this environment. Long-term observations, from which inter-annual variations can be detected, as well as detailed broad-scale spatial observations, are scarce in the deep sea. In this thesis, I examined changes in both spatial (~ 0.1-10s km scale) and temporal (inter-annual scale) domains in abyssal benthic fauna at two abyssal stations in the North East Pacific (Station M, 1991 to 2011) and in the North East Atlantic (Porcupine Abyssal Plain, PAP, 1991 to 2012) using Polychaeta as study organisms. Four main results were found. **1) At intermediate scales (0.1 to 10s km), the macrofauna and polychaete family composition were related to the sediment grain size distribution (Chapter 2).** Differences in sediment grain size distribution between and among abyssal hills created habitat heterogeneity. Differences in near-bed current flows, and thus in particle size and food settling conditions, may be the primary factors influencing the sediment particle size distribution and macrofauna. Overall polychaetes and macrofauna may be more spatially variable than previously thought in abyssal areas when considering that abyssal hills might be one of the most common topographic features on Earth. **2) At inter-annual scale, polychaete families and functional groups varied in density, diversity and community structure at Sta. M and PAP (chapter 3).** Sub-surface deposit feeders, such as Paraonidae, dominated the North East Pacific, whereas surface deposit feeders, such as Cirratulidae, dominated the North East Atlantic. Differences may be related to the quantity and quality of the particulate organic carbon reaching the seafloor. Overall, changes in the dominance of functional groups imply changes in abyssal ecosystem functioning. **3) At inter-annual scale, the dynamics of polychaete abundances and body sizes suggested that migration/enhanced survivorship and recruitment events occurred (chapter 4).** The densities and median body sizes of the five density-dominant species at Sta. M were analysed over time to help elucidate population dynamics as population parameters such as reproduction or growth rate could not be directly measured. The results indicated that the density dynamics of *Paradoneis* cf. *lyr*a may have be related to enhanced survivorship or immigration of adult individuals, while the density dynamics of *Cossura* cf. *rostrata* may have be linked to individuals shifting between growth and reproduction. **4) At inter-annual scale, Sta. M polychaete changes were detected in standing stocks, rank distributions, species and functional group composition (chapter 5)**. Although a change in sampling location occurred after 2005, preventing ascribing the assemblage change unequivocally to particular environmental drivers, analyses prior to 2005 showed that the polychaete assemblage composition dynamics were primary driven by food supply variation. Overall, energetic zero-sum dynamics were not clearly observed at polychaete assemblage level, but were evident in the greater macrofauna community that includes the polychaetes. Polychaete displayed stability in body size structure in space and time, following the predictions of the metabolic theory of ecology.

In conclusion, this work highlighted that abyssal polychaete communities can change over spatial scales of tens of square kilometres and time scales of months or more; this work found a large but as yet underappreciated variability.

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Declaration of authorship

I, Claire Laguionie-Marchais, declare that this thesis entitled "Polychaete community structure and biodiversity change in space and time at the abyssal seafloor." and the work presented in it are my own and have been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;

2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;

3. Where I have consulted the published work of others, this is always clearly attributed;

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5. I have acknowledged all main sources of help;

6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;

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Chapter 1
Introduction

Long perceived as a stable environment, the deep sea is actually dynamic and heterogonous over various spatio-temporal scales (Glover et al., 2010, Rex and Etter, 2010). But, the characteristics of deep-sea natural variations and underlying processes remain poorly understood particularly in non-chemosynthetic systems (Smith et al., 2009). As the deep sea is fully integrated to the global Earth biosphere, determining natural variations is a baseline to assess the anthropogenic impact on this environment. In particular, the increasing needs for food and energy has led not only companies to exploit more deep-sea resources such as fishes, oil, gases, and chemical compounds (Thiel, 2003, Skropeta, 2008, Ramirez-Llodra et al., 2011) but also, for humanity to change the climate at unprecedented rates (Field et al., 2014). Moreover, the deep sea is not hermetic to global warming as almost its entire functioning depends on surface processes (food supply, downward current and conveyor belt).

This thesis work focused on spatio-temporal changes in soft-sedimentary abyssal plains below 3000 m unless otherwise stated. Below 3000 m, deep-sea habitats are essentially a network of abyssal plains, rolling abyssal hills, seamounts, with canyons at coastal margins, and sub-divided by mid-ocean ridges, island arcs and trenches (Smith et al., 2008). These habitats cover about 54% of the Earth’s surface and harbour a living biomass of about 55 MtC (Wei et al., 2010).

1.1 Variability in the deep sea

1.1.1 Scales and factors of variability

Natural variability is a multivariate concept observed in biotic and abiotic factors as well as any of their combinations and occurring on multiple intertwined spatio-temporal scales forming a continuum (Wiens, 1989, 2000, Levin, 1992, Shugart, 1998, Levin et al., 2001, Chapin et al., 2011). For heuristic convenience, variability is studied in practice for a subset of biotic/abiotic factors and at a given spatio-temporal scale (Ricklefs, 2004). The used spatio-temporal scales can roughly be divided into three categories thereafter used in this thesis: large scale (geographic spatial scale and geological/historical time scales), intermediate scale (landscape spatial scales and ecological/inter-annual time scales) and small scale (local to specimen spatial scale and intra-annual to daily time scale). The biotic factors comprised organisms or organisation of organisms such as population, community, meta-community as well as their interactions while abiotic factors encompasses environmental features (energy supply, physical and oceanographic heterogeneity, disturbances, e.g. Wu and Loucks, 1995, Rex and Etter, 2010).

The aim of this review is not to give an exhaustive list of all variabilities encountered in the deep sea but rather to focus on the ones relevant to the thesis work. The latter is concerned by particular spatio-temporal scales and biotic/abiotic factors. More exactly, the thesis investigated intermediate-scale variations in macrofaunal community (biotic factor) in abyssal soft-sedimentary areas. The biotic factor being macrofaunal communities, the variabilities of the following abiotic factors were considered: energy availability variation, environmental heterogeneity and disturbances. These factors are the most commonly used in community ecology in all ecosystems (Gage and Tyler, 1991, Levin et al., 2001, Morin, 2009, Mittelbach, 2012). In terms of scales, although all scales are important to our global understanding of deep-sea variations (Rex and Etter, 2010), time scale of decades are of particular interest to disentangle anthropogenically-induced climate change from natural variability. Intermediate-scale monitoring is required to assess the impact of the current climate change and resource exploitation on deep-sea systems. However, intermediate-scale data sets are harder to acquire in the deep sea as the scales are too short to be preserved in geological records but too long to be addressed in most current ecological programmes only funded at best for a few years (Glover et al., 2010).

Variability in the deep sea in terms of energy supply, environmental heterogeneity, and disturbance are presented below with an emphasis on intermediate-scale variability for abyssal benthic communities. However as local communities are a balance of processes operating at larger and smaller scales (Ricklefs, 2004, Witman et al., 2004), variability at these scales is also briefly described.

1.1.2 Variation in energy supply

In all ecosystems, fauna communities depend on energy supply, available through both thermal (solar radiation, temperature) and chemical (food supply) forms (Evans et al., 2005, Tittensor et al., 2011). At abyssal depth, the environment is virtually isothermal so that energy availability depends on food supply. Except in chemosynthetic habitats, there is no *in situ* primary production in the deep sea as the absence of light prevents photosynthesis. Most deep-sea life relies on a small percentage of the surface production that sinks to the seafloor mainly as phytodetritus (Beaulieu, 2002), faecal pellets (Pfannkuche and Lochte, 1993), remains of organisms (Stockton and DeLaca, 1982, Robinson et al., 2005, Billett et al., 2006) and less frequently as a large organic food fall such as a whale carcass (Smith and Baco, 2003). This mechanism whereby CO_2 is taken up at the ocean's surface by photosynthesis and is transferred into deep waters by sinking particles is called biological pump. Overall, as little as1% of the surface production fuels the deep sea as the particles are progressively degraded as they sink (Lampitt and Antia, 1997).

Primary production and its variability, either on land or ocean surface, are tightly linked to climate and its natural variability. The latter vary both secularly and periodically on particular scales related to orbital and other forcings. As a first approach, the variability in climate is due to two different types of processes: internal stochastic mechanisms and external forcing mechanisms that include internal mode resonant amplification (Mitchell, 1976). In terms of stochastic variability, change in climate is related to red noise processes (inversely proportional to frequency) that have been observed in atmospheric and oceanic data (Stocker, 1996, Liu, 2012). In addition, stochastic fluctuations about a well-defined mean value have been observed from decadal to millennial time scales (Hasselmann, 1976, James and James, 1992, Roebber, 1995). In terms of determinist variability, change in climate is related to variations of the Earth's position, rotation, axis inclination on scale of days to millions years. At each scale, climatic variability can occur due to self-sustained oscillations of the Earth system (Bond et al., 1992, 1993).

1.1.2.1 Large-scale variations in energy supply

Large-scale variations in energy supply results from geological time-scale and geographical spatial-scale climate variations that impact primary production (PP). In time, geological records have given evidence of climate forcing on PP and faunal communities in terrestrial (Brook and Barnosky, 2012, Saito et al., 2013), coastal (Wethey, 1985) and deep-sea ecosystems (Yasuhara et al., 2009). Over centennial, millennial and longer time scales, change in surface climate is related to variations in the Earth's eccentricity, axial tilt and precession cycles known as the Milankovitch Cycles (100 kyr-, 41 kyr-, 26 kyr-cycles). Taken in unison, variations in these three cycles create alterations in solar radiation reaching the Earth that combine with feedback mechanisms (e.g. greenhouse gases, albedo) leading to glacial/interglacial shifts (Imbrie et al., 1992, 1993). The latter have had global impacts from terrestrial (van Dam et al., 2006) to deep-sea ecosystems (Cronin and Raymo, 1997, Yasuhara et al., 2009). In particular, these climate shifts generate widespread anoxia (Kaiho, 1994a,b, Isozaki, 1997, Adkins et al., 1998, den Dulk, 2000), changes in deep-water circulation (Oppo et al., 1998, Raymo et al., 1998, Horne, 1999, Yasuhara et al., 2008), changes in bottom-water temperature (Yasuhara and Cronin, 2008), all impacting deep-sea life (Yasuhara et al., 2012).

In space, the latitudinal gradient in solar energy input induces geographical patterns in climate processes and therefore in PP (Roy et al., 1998, Huston and Wolverton, 2009). PP increases from temperate to tropical regions (Willig et al., 2003). Latitudinal change of climate is considered to be one of the main large-scale abiotic factors controlling the distribution of organisms and community composition in all ecosystems on Earth (Hawkins et al., 2003, Hillebrand, 2004, Mittelbach et al., 2007). In the deep sea, several taxa showed a latitudinal gradient likely related to variation in surface PP but knowledge remains fragmentary due to the inherent difficulty in sampling at great depths and to an uneven sampling effort in Northern and Southern Hemispheres (Rex and Etter, 2010).

1.1.2.2 Intermediate-scale variations in energy supply

At intermediate-scale, surface primary production varies with annual/decadal climate periodicities. However, the study and quantitative understanding of natural decadal/inter-decadal internal variability in the climate system is still in its infancy (Stocker, 1996, Liu, 2012). For a long time, the aim of many climate models has been to provide long-term predictions of climate change impact, while the need to predict the capabilities of forecast systems on decadal time scales has only just started to be explored (Farneti and Vallis, 2009, Taylor et al., 2011). At decadal and inter-decadal scales, the impact of periodic change in solar forcing is still highly debated (Lean and Rind, 1994, Crowley and Kim, 1996, Hegerl et al., 1997) with several studies reporting a near cycle of 30-40 years (Briffa et al., 1992, Stocker and Mysak, 1992, Kushnir, 1994, Schlesinger and Ramankutty, 1994, Mann et al., 1995). Overall, climate variability at this scale seems related to the ocean circulation, in particular the thermohaline component, the wind-driven circulation as well as the ocean/atmosphere hydrological cycle (Stocker, 2000).

The most prominent signal in year-to-year variability in the atmosphere-ocean system is ENSO, a cyclic process without a single distinct time scale (Stocker, 2000, Wolter and Timlin, 2011). ENSO originates in the atmosphere and is transmitted to the ocean via the effect of wind on horizontal currents in the tropical Pacific (Brierley and Kingsford, 2009). ENSO consists of two components:1) the first component is located in the eastern equatorial Pacific and encompasses succeeding phases of cooling, called La Niña, when more intense upwelling of warm water enters the North East Equatorial Pacific, and of warming, called El Niño, with less intense upwelling (Trenberth, 1997). 2) The second component is the Southern oscillation which is mainly an atmospheric phenomenon related to trade winds, defined by the difference in sea-level pressure at Tahiti and Darwin. When the difference is high, the pressure gradient between east and west in the tropical Pacific is large, and the trade winds are strong. When the index is negative, trades are weak (Stewart, 2004). Changes in trade winds impact the thermocline and upwelling in the North East Equatorial Pacific. Although ENSO is a regional phenomenon, its impacts are global. ENSO is considered to be the most important mode of ocean variability at the inter-annual to decadal time scale. In addition, the Pacific Decadal Oscillation (PDO) is the main mode of sea-surface temperature (SST) variability in the North Pacific and is still poorly understood (Mantua and Hare, 2002, Mantua and Mitchell, 2009). In the North Atlantic, the North Atlantic Oscillation (NAO) is the main mode of SST variability on inter-annual to inter-decadal time scales and is defined in relation to the meridional atmospheric pressure gradient over the North Atlantic (Wanner et al., 2001). Phenomena in the Arctic and Antarctic as well as in the Indian Ocean have also been detected but are currently less well known (Thompson and Wallace, 2000, Zhang et al., 2014).

All previous inter-annual to inter-decadal oscillations have an impact on terrestrial and marine ecosystems (Blenkner and Hillebrand, 2002, Stenseth et al., 2002). ENSO effects have been the most extensively studied. In terrestrial realm, ENSO modify temperature and precipitation patterns and consequently primary production with cascading effects on primary and higher consumers (Holmgren et al., 2001). In the marine realm, ENSO modifies SST, water column stratification, mixed layer depth and the frequency of deep-mixing event (Polovina et al., 1994) therefore influencing the nutricline and primary production (Limsakul et al., 2001, Behrenfeld et al., 2006, Henson et al., 2009). In turn, the latter induces changes in zooplankton, fishes and other invertebrates, marine birds and mammals (Barber and Chavez, 1983, McGowan et al., 1998, Sydeman et al., 2001, Chavez et al., 2003, Urbán and Gallardo, 2003, Lynam et al., 2004, Arntz et al., 2006, Lehodey et al., 2006, Aronés et al., 2009) and ultimately the underlying abyssal plain fauna that rely on sinking food particles via the biological pump (Smith et al., 2009).

1.1.2.3 Small-scale variations in energy supply

Primary production also changes at smaller scales as climate varies from days to seasons in relation to Earth's rotation around its axis and around the sun. Seasonal variation in light and temperature (and water on land) changes nutrient and primary production. PP seasonality has been recognised and studied for a long time in terrestrial (e.g. Chapin et al., 2011) and coastal ecosystems (e.g. Coma et al., 2000). In the deep sea, the advent of *in situ* camera deployments in the early 1980s led to the discovery of seasonal flux observed on abyssal seabed under productive waters (Deuser and Ross, 1980, Billett et al., 1983). In his review of seasonality on deep seafloor, Gooday (2002) underlined that faunal response to seasonal food pulse is not ubiquitous and still poorly characterised.

1.1.3 Environmental heterogeneity in the deep sea

1.1.3.1 Large-scale environmental heterogeneity in the deep sea

At large-scale, the bathymetric gradient is the main driver of environmental heterogeneity in the deep sea (Rex and Etter, 2010, Tittensor et al., 2011). The variability is linked to the gradual change in food supply that decreases both with depth and with distance from the nutrient-rich coastal waters (Rex and Etter, 2010). Other features such as pressure or oxygen concentration also change alongside depth as seen with elevational gradients in terrestrial ecosystems (Brown, 2001, Grytnes and McCain, 2007, Körner, 2007, McCain, 2007). Productivity may govern the bathymetric gradient on large scale but the latter is further mediated at intermediate scales by local habitat heterogeneity as described below.

1.1.3.2 Intermediate-scale environmental heterogeneity in the deep sea

At intermediate scale, the importance of habitat heterogeneity increases (McGill, 2010). The latter occurs with landscape-scale topographic features (e.g. mountains and hills on land, Haslett et al., 1997). In the deep sea, canyons (De Leo et al., 2010, McClain and Barry, 2010, Vetter et al., 2010, Ingels and Vanreusel, 2013), mid-ocean ridges (Priede et al., 2013), seamounts (McClain, 2007, McClain et al., 2010, Yesson et al., 2011) and their smaller counterpart, abyssal hills (Durden et al., 2015), increase landscape variability. Depending on their size, both deep-sea and terrestrial topographic features induced to a lesser or grater extend variations in: resource availability, oxygen concentration, substrate, depth/elevation, current/wind pattern (Levin et al., 2001, 2010, Gibson and Atkinson, 2003, Grytnes and McCain, 2007, Gallardo-Cruz et al., 2009, Rowe, 2009, McCain, 2010, Rex and Etter, 2010). Heterogeneity in depth, sediment and hydrodynamics are also important on other marine habitats such as continental shelves (e.g. Martins et al., 2013).

In abyssal sedimentary areas, seamounts and more particularly abyssal hills may be the most common topographic features with estimates of about 25×10^6 abyssal hills, knolls and seamounts away from continental margins (Turnewitsch et al., 2013). All these topographic features change the nature and density of suspended particles as well as accumulation of sediment and organic matter at the seafloor (de Stigter et al., 2007, Oliveira et al., 2007, Arzola et al., 2008, Cunha et al., 2011). In turn, increased environmental heterogeneity in current and sediment/organic matter accumulation at topographic features impact fauna biodiversity patterns compared with background environments (Tews et al., 2004) and within the feature itself. Seamount faunal density and diversity change between the summit, the flanks, the base and surrounding areas with contrasting results in terms of location of higher density/diversity within the seamount depending on its peculiar topography and location (Levin and Thomas, 1989, McClain et al., 2010, Sautya et al., 2011, Bongiorni et al., 2013, Chivers et al., 2013). Bongiorni et al. (2013) found evidence that seamount macrofauna density variance was linked to the sediment grain size and porosity whereas diversity and composition were related to food quality within sediments. At abyssal hills, Durden et al. (2015) also showed that the megafaunal assemblage and trophic composition were significantly different between hill and plain sites and linked to the percentage of coarse sediment particles.

Sediment particle size has been frequently reported as correlating with benthic deep-sea fauna distributions (Sanders 1968, Rhoads 1974, Gray, 1981, Etter and Grassle, 1992, Ellingsen, 2002), a relationship also observed in freshwater (Cummings and Lauf, 1969) and coastal ecosystems (McLachlan and Brown, 2010). As the main food resource in deep benthic system is detritus, the sediment is likely important in structuring deep-sea communities (Levin et al., 2001). The smaller size of deposit feeders in the deep sea compared to shallower habitats may favoured a macrophage deposit feeding (a selective ingestion of individual particles) to the detriment of a microphage deposit feeding (bulk sediment ingestion, Jumars et al., 1990). Such a mechanism would enhance sediment resource partitioning. However, the nature of the relationship between sediment and fauna is far from being understood (Snelgrove and Butman, 1994). Similarly the relationships between soil and its infaunal biota on land are also poorly constrained (Decaëns, 2010, Paul, 2014). In the deep sea, other factors/processes likely control both faunal and sediment distributions. The seafloor sediment mostly reflects near-bottom currents and sediment transport regimes. The latter are often modified by complex interaction with topographic features (e.g. seamounts, Turnewitsch et al., 2013; canyons, Gage, 1997).

Near bottom currents interacts with topographic features in association with other hydrographic processes such as internal tides or eddies (see details in Turnewitsch et al., 2013). Intermittently currents may become strong enough to re-suspend all or some organic/inorganic particles of sediments leading to erosion and resuspension events (similar to wind erosion effect on terrestrial systems, Pimentel and Kounang, 1998, Turbé et al., 2010, Bertin et al., 2014 and wind/current effects on coastal systems, Lawrence et al., 2004). Turnewitsch et al. (2013) highlighted that the occurrence of high frequency flows such as tidal current may be very important to locally drive the total current velocities across threshold values for non-deposition, erosion, resuspension. Details on the physical (hydrodynamical and sedimentological) processes involved in water flow/sediment dynamics and interactions can be found in the review of Paterson and Black (1999). The frequency and intensity of current transporting seafloor particles also determine the sediment stability, an important feature for infauna in particular in relation to their trophic group distribution (Rhoads, 1974, Levin et al., 1994b). Currents also induce spatial variability by horizontally moving food and larvae and by directly impacting fauna (e.g. displacement of organisms, alteration/switching of feeding modes in function of the flow, Snelgrove and Butman, 1994, Leonard et al., 1998).

1.1.3.3 Small-scale environmental heterogeneity in the deep sea

At local and smaller scales, spatial variability is induced by biogenic structures, lebensspurren, solid aggregates, mounds or constructs and pores of different shapes or sizes, substrate ripples and biotic processes as seen in coastal (Raffaelli and Hughes, 1978, Rafaelli and Hawkins, 2012, Kon et al., 2015), terrestrial (Lavelle, 2002, Wardle, 2006, Decaëns, 2010), and deep-sea systems (Jumars, 1976, Kukert and Smith, 1992, Wheatcroft et al., 1992, Snelgrove et al., 1992, 1994, Levin and Edesa, 1997, Snelgrove and Smith, 2002, Buhl-Mortensen et al., 2010).

1.1.4 Disturbances in the deep sea

1.1.4.1 Large-scale disturbances in the deep sea

Large-scale disturbances in the deep sea can be divided into human-induced and natural environmental disturbances. The latter result from catastrophic environmental perturbations such as volcanic eruptions (Hess and Kuhnt, 1996, Del Moral and Grishin, 1999), asteroid impacts (Gersonde et al., 1997, Toon et al., 1997), tectonic activity and abrupt climate variation (McGuire et al., 2002, Barash, 2011). To a greater or lesser extent, each catastrophic event can change atmospheric composition (e.g. dust, oxygen, water content), light, climate and primary production and trigger geological processes such as earthquakes and tsunamis (Toon et al., 1997). Five major mass extinctions have been reported (Benton, 1995, Jablonski and Raup, 1995, Jablonski, 2005) with impacts on terrestrial, marine (McElwain and Punyasena, 2007) and deep-sea realms. For example, the decrease in surface PP and export flux at the Cretaceous-Tertiary had lasting effects on deep-sea fauna for three million years (D'Hondt et al., 1998).

In terms of human-induced large-scale disturbances, climate change has a global impact on Earth. Climate change can be defined as a progressive trend over time due to a raise in CO_2 and other greenhouse gas emission by human activities (Glover et al., 2010, Stocker et al., 2013). The raised CO_2 emission increases the temperature in the lower atmosphere and Earth surface as radiative forcing (IPCC, 2007) and has been linked to several changes in terrestrial, freshwater and marine realms (Parmesan, 2006, see Field et al., 2007 for details of mechanisms in terrestrial ecosystems, Kunddzewicz et al., 2008). In the ocean, climate change warms upper waters (Barnett et al., 2005, IPCC, 2007), increases ocean stratification, decreases sea-ice extent, alters patterns of ocean circulation (e.g. slower thermohaline circulation), deep-water formation, ocean ventilation, salinity, precipitation and freshwater input (Joos et al., 1999, Hoegh-Guldberg and Bruno, 2010, Stocker et al., 2013). All these changes have a direct impact on marine organisms (e.g. Hofmann and Todgham, 2010) as well as on the biological pump (Falkowski and Raven, 2013). The modification in water column stratification and mixing intensity impacts nutrient quantity and quality and consequently PP (phytoplankton composition, range, geographic distribution, Gregg et al., 2003, Richardson and Schoeman, 2004, Bopp et al., 2005, Boyce et al., 2010). Overall phytoplankton biomass is declining at a global rate of about one percent of the global mean per year since 1989 (Boyce et al., 2010). In addition, intensified stratification is thought to favour smaller phytoplankton species (Tréguer and Pondaven, 2000, Bopp et al., 2005).

Because phytoplankton is at the base of all marine food web, except in chemosynthetic environments, changes in phytoplankton can spread down the water column/food web via trophic cascade (bottom-up control) as seen in freshwater systems (Winder and Schindler, 2004). Smaller and less abundant phytoplankton species may weaken the biological pump by decreasing export flux and rate with several consequences, in particular the change of carbon residence time in the deep ocean (Bopp et al., 2005) and a decrease in the amount of food reaching the ocean floor, particularly at abyssal depths (Glover et al., 2010). Recent studies have started to quantify the effect of changes in export production due to climate change on benthic biomass. In the open ocean where the carbon export is globally (but not locally) expected to diminish, the benthic biomass should decrease by ~5% (reduction of 5.2 Mt C) in the future (2091–2100) compared with contemporary conditions (2006–2015) due to climate change (Mora et al., 2013, Jones et al., 2014).

1.1.4.2 Intermediate-scale disturbances in the deep sea

At intermediate scale, disturbances can also be divided into natural and anthropogenic disturbances. In the deep sea, natural disturbance include episodic benthic storms which are important structuring force as extreme climatic events such as storms are in other ecosystems (e.g. freshwater, Leigh et al., 2014; coastal, Grémare et al., 2003; land, Chapin et al., 2011). During benthic storms, near-bottom currents can reach speeds of 15–40 $cm.s^{-1}$ and persist for several days (Hollister and McCave, 1984, Gage, 1997). The enhanced turbulent boundary layer flow both transports downward sediment in suspension and affects seafloor sediment locally on its way (erosion/deposition, Gross and Williams, 1991) with consequences for the fauna (Aller 1997). Although benthic storms mainly occur on continental margins, similar episodic high energy currents have been observed in abyssal areas (Klein 1987, Kontar et al., 1994, Levin et al., 2001). Such physical-disturbance effects have been linked to deep-sea communities (Paterson and Lambshead, 1995). Although not actively contributing, historical rare events such as landslide (most often triggered by earthquakes, Masson et al., 2006), turbidity currents, debris flows (see definition in Mulder and Alexander, 2001, Talling et al., 2007) that mobilise important quantity of sediment/substrate, have led to landscape-scale sediment variability observed nowadays (Embley, 1976, Hampton et al., 1994, Mulder, 2011). Such historical events have been suggested to reduce fauna density and biomass (Young and Richardson, 1998; Young et al., 2001, Walker and Shiels, 2012).

Intermediate-scale anthropogenic disturbances are linked to resource exploitation as seen in terrestrial ecosystems (e.g. Chapin et al., 2011) although knowledge on their impact is scarce and limited in the deep sea (Glover and Smith, 2003). However, it becomes necessary to assess the impacts of resource exploitation, all the more as it occurs with climate change and potential feedback/synergetic effects. Such interactions and synergies of anthropogenic pressures on the deep sea are still under-studied (Ramirez-Llodra et al., 2011). Industrial disturbances include or will include for example: 1) disposal of CO_2 and greenhouse gases in the deep-sea seabed or sub-seabed with potential acidification issues (Tamburri et al., 2000, Gale et al., 2001, Zweigel et al., 2004; terrestrial example: Lackner, 2003); 2) oil and gas exploration that will result in the accumulation of contaminated drill cuttings. Locally, drilling muds will generate higher total organic carbon, anoxic conditions and patchy zones of disturbed benthic communities (Ramirez-Llodra et al., 2011, Gates and Jones, 2012, terrestrial example: Osuji et al., 2004); 3) mining of deep-sea minerals, whose impacts may include destruction of the sites and fauna, sediment plume release and potential chemical pollution from equipment failure (Smith et al., 2008a, Ramirez-Llodra et al., 2011, terrestrial example: Candeias et al., 2015). The scaling up of these exploitations to industrial levels may have a major impact on benthic fauna (Ramirez-Llodra et al., 2011) all the more that serious accidents such as the Deepwater Horizon oil spill can occur with greater impacts over larger areas (Hsing et al., 2013, Fisher et al., 2014).

1.1.4.3 Small-scale disturbances in the deep sea

The combination of small-scale seafloor topography, disturbances such as seasonal or episodic food pulse and biotic interactions creates a mosaic of patches among which successional sequences are temporally out of phase (the spatial mosaic theory, Grassle and Sandler, 1973, Grassle and Morse-Porteous, 1987, Grassle and Macioleck, 1992, McClain and Barry, 2010, Rex and Etter, 2010, for marine and terrestrial ecosystems see Pickett and White, 2013, Paul, 2014). The spatial mosaic theory was investigated in the deep sea with several experiments in the 1990s that showed that only a subset of species was related to biogenic structures and that different sources of disturbances induced different responses (e.g. experiments using faecal mounds, Kukert and Smith, 1992, food trays, Snelgrove et al., 1992, 1994, 1996, reviewed in Snelgrove and Smith, 2002, Levin et al., 2013).

However, determining small-scale patchiness is important to design efficient sampling. Small-scale patchiness may be a particular issue in the remote deep sea where the sampling is fundamentally different from more accessible environments (Rex and Etter, 2010). In particular, if the sampler area is not adapted to the fauna patchiness, it can inflate the variability observed in long time-series data sets. In the late 1970s, macro-infauna small-scale spatial heterogeneity was studied in several deep-sea systems (see details in Appendix A, Hessler and Jumars, 1974, Jumars, 1975a,b, 1976, 1978, Gage, 1977, Lamont et al., 1995). Overall, these studies found a predominance of random patterns with a low degree of aggregation for the few species departing from random distribution. However, Jumars and Eckman (1983) underlined that the above studies, rather than proving spatial randomness, failed to reject the random dispersion hypothesis.

In summary, variability in the deep sea arises from multiple factors and processes operating at different and intertwined spatio-temporal scales. Of primary interest to this thesis is: 1) the characterisation of natural intermediate-scale variability (in particular energy supply and abyssal hills) impacts on deep-sea benthic communities; 2) the understanding of the mechanisms by which these variabilities structure the abyssal soft-sedimentary area fauna. To achieve these objectives, the work has been focused on two sites: the Porcupine Abyssal Plain (PAP) site in the North East Atlantic and Station M (Sta. M) in the North East Pacific where the longest time-series conducted at abyssal depths in soft-sedimentary areas were acquired. Both sites and results of their long-term monitoring programmes are presented in detail in the next section.

1.2 PAP and Sta. M long-term time series

Time-series studies have been conducted at PAP and Sta. M since 1989 to better characterise the dependence of deep-sea communities on surface water production and the potential effect of climate change on carbon cycling and deep-ocean ecosystem functions (Smith et al., 2009). Both stations are: 1) located under highly seasonal productive surface waters (Smith and Druffel, 1998, Billett and Rice, 2001); 2) relatively easily accessible to reduce time and costs (Smith and Druffel, 1998). PAP and Sta. M remain the only abyssal time-series for which water column and seabed observations have been integrated (Lampitt et al., 2010a).

1.2.1 Characteristics of PAP and Sta. M

The Porcupine Abyssal Plain is located in the North East Atlantic about 270 km southwest of Ireland. The central benthic station (48˚ 50 N, 16˚ 30 W, Fig. 1.1) is 4850 m deep and is located in a flat area with neighbouring abyssal hills about 300 mab and one rising about 1000 mab (Klein and Mittelstaed, 1992, Turnewitsch and Springer, 2001) and so is unlikely to be influenced by strong downslope or advective processes (Billett and Rice, 2001). The sediment at the PAP central location is a calcareous ooze with a median grain size of 8 to 8.6 µm (Rice et al., 1991). The currents within 150 m of the seafloor are generally less than 15 $cm.s^{-1}$ (not exceeding 20 $cm.s^{-1}$) with no evidence of benthic storms (Lampitt et al., 2001, Vangriesheim et al., 2001). In addition, Billett and Rice (2001) highlighted PAP lies between two other important sampling localities in the NE Atlantic: JGOFS North Atlantic Bloom Experiment, NABE (Ducklow and Harris, 1993, Lampitt et al., 2001) and EU-funded Ocean Margin EXchange programmes, OMEX (van Weering et al., 1998, Joint and Wassmann, 2001). PAP also lies under temperate seasonally-productive waters generating spring phytoplankton bloom with inter-annual variability (Rice et al., 1994). Several research programmes have been conducted at PAP whose details can be found in Billett and Rice (2001) and Lampitt et al. (2010a).

Figure 1.1 PAP and Sta. M location (Google Map, 2015).

Sta. M is located in the North East Pacific, 220 km west of Point Conception off the central California coast (Smith and Druffel, 1998). Sta. M sampling location changed from 34^{o} 50´ N, 123˚00´ W, 4100 m depth (Fig. 1.1) to 35^{o} 10´ N, 122^{o} 59´ W, 4000 m depth after 2006 to accommodate water depth limitations of the remotely operated vehicles (Kuhnz et al., 2014). Sta. M sediment is a silty-clay. Although Sta. M lies 75 km southwards of the base of the Monterey Deep-Sea Fan and 100 km westwards of the continental slope, it has little topographic relief (0.2 % SSW slope equivalent to 100 m over 1600 km^{2}) with no recent evidence of turbidity flows or slumping (Beaulieu and Baldwin, 1998, Smith and Druffel, 1998). The highest flow has been measured at 50 mab with an average speed of 3.8 cm.s^{-1} (not exceeding 20 cm s^{-1}, Beaulieu and Baldwin, 1998). In addition, Sta. M lies within an important sampling locality in the NE Pacific: the California Current Ecosystem Long-Term Research (CCE LTER, Ohman and Hsieh, 2008). Sta. M lies under an upwelling area generating a spring phytoplankton bloom with inter-annual variability.

1.2.2 Particulate organic carbon flux variation

The Particulate Organic Carbon (POC) flux is a measurement of the pelagic-benthic coupling, the translation of surface production patterns down through the water column to the seabed (Rex and Etter, 2010). The pelagic-benthic coupling was studied with a focus more on surface processes at PAP and more on benthic boundary layer processes at Sta. M. The sediment traps used at the beginning of the time series to assess POC flux (Smith et al., 2006, Lampitt et al., 2010b) have been replaced by more advanced technologies: full-depth mooring at PAP with autonomous sensors measuring (Hartman et al., 2013), a sedimentation sensor combining the traditional sediment traps with a digital-imaging system and fluorometer to document hourly changes in sedimentation events at Sta. M (Sherman and Smith, 2009).

Overall results at both stations indicated that POC flux displayed seasonal variability in quantity and quality (Baldwin et al., 1998, Kiriakoulakis et al., 2001, Fabiano et al., 2001, Lampitt et al., 2001, 2010b, Wilson et al., 2013). Intra-annual variations in POC quantity have been related to the occurrence of surface-water spring blooms (Smith et al., 1994, 2006, Beaulieu and Smith, 1998, Gooday, 2002, Lampitt et al., 2010b). Variations in POC flux quality are introduced by change in phytoplankton species during the bloom (Fabiano et al., 2001, Kiriakoulakis et al., 2001). Diatoms dominate the early spring bloom before being progressively replaced by smaller and/or more gelatinous species (e.g. coccolithophores, small dinoflagellates and cyanobacteria, Gooday, 2002). Spatial processes in surface also bring intra-annual variations in phytoplankton. At PAP, cyclonic eddies with filamentous structures modify phytoplankton quantity and quality (Hartman et al., 2010, Martin et al., 2010a,b, Painter et al., 2010, Smythe-Wright et al., 2010). Such sub- to mesoscale features have also been observed in the California Current (Strub and James, 2000). Exactly how eddies might influence the POC flux reaching abyssal seafloor remains to be understood. Indeed, material reaching the abyssal seafloor at a given sampling location is a temporal and spatial integration of surface processes albeit a distorted and fainter signal (Rex and Etter, 2010). Spatio-temporal integration has been termed a statistical funnel (Siegel and Deuser, 1997, Siegel and Armstrong, 2002, Smith. et al., 2008) associated with a surface catchment area (Rex and Etter, 2010). Lampitt et al., (2001) proposed a 200 km radius catchment area at PAP site and Smith et al. (2006) a 50 km radius catchment area at St. M.

POC flux also displayed inter-annual changes in quantity and quality (Lampitt et al., 2010b, Smith et al., 2013, 2014). At PAP, POC flux was different in magnitude and timing from one year to another but without exhibiting a long-term trend (Lampitt et al., 2010b). No clear relationship was found between these POC flux variations at abyssal depths and surface chlorophyll-a or primary production (Lampitt et al., 2010b). However, climate variation is hypothesised to be a key factor. Using models developed for Sta. M, Smith et al. (2006) found a significant positive correlation between POC flux and NAO index with a five month time lag over 1989-2000. In addition, the timing of the spring bloom could be important (with effect on the biogeochemistry of the remainder of the productive season) and has been delayed over certain periods (Lampitt et al., 2010b). Linking surface production and abyssal POC flux remains complicated by the lack of knowledge on mid-water column processes and their variability (Smith et al., 2009). Lampitt et al. (2010b) The proportion of total production supported by new nutrients (f ratio) and the proportion of export flux at the base of the euphotic zone, which reaches 3000 m (transfer efficiency) could be important parameter to target to advance the understanding of pelagic-benthic coupling (Lampitt et al., 2010b).

Inter-annual changes in POC flux also occurred at Sta. M. Until recently, results indicated a long-term decrease in POC flux reaching Sta. M seafloor over 1989-2006 (Smith and Kaufmann, 1999, Smith et al., 2006, 2009). Over this period, abyssal POC flux variations were linked with climate indices on ocean basin and regional scales: 6 month lagged correlation with NOI (Northern Oscillation Index, related to climate in the North Pacific), 1-3 month lagged correlation with the Bakun Upwelling Index (related to coastal upwelling intensity, Smith et al., 2009). However, new time points (2007-2013) in the time series showed that POC flux exhibited both inter-annual and episodic variations. Major POC flux peaks occurred in the last 18 months of the time series: one flux of diatom *Rhizosolenia* in summer 2011 (highest POC flux on record at the site) and one of salp in spring 2012 and September 2012 (Smith et al., 2013, 2014). The latter led to the highest seafloor coverage with salp detritus going from less than one percent cover in early March to a high of 98% cover in early July 2012. By combining POC flux and carbon input from detrital aggregates, Smith et al. (2013) obtained the highest estimates of carbon supply to Sta. M seafloor over the time-series. Such episodic supply of food resulting in the rapid vertical transport of surface planktonic organisms containing chlorophyll pigments have increased in frequency and magnitude over the last several years maybe in relation with increased upwelling (Kahru et al., 2009, 2012). However, the detailed mechanisms behind these episodic events remain unknown (Smith et al., 2013, 2014). The changes may be only part of multi-decadal variations, unrelated to global climate change (Smith et al., 2013). Overall, at both PAP and Sta. M, a better characterisation of pelagic-benthic coupling remains a primary objective.

1.2.3 Faunal variation

At both stations, megafauna communities have been the most extensively studied and are dominated by mobile echinoderms, mostly holothurians, but also echinoids and ophiuroids

(Billett et al., 2001, 2010, Ruhl and Smith, 2004, Kuhnz et al., 2014). At PAP, a dramatic change in megafauna density and dominance occurred around 1996, mainly driven by one holothurian species, *Amperima rosea*, whose density increased by 3 orders of magnitude within a 2-year period, the so-called "*Amperima* event" (Billett et al., 2001, Wigham et al., 2003). Concomitantly, several megafauna taxa were found to increase (*Ellipinion molle, Ophiocten hastatum*) or decrease (*Oneirophanta mutabilis*) in density (Billett et al., 2001). A second "*Amperima* event" occurred in 2002-2005 albeit with lower magnitude (Billett et al., 2010). The peaks in *A. rosea* density corresponded with decreased body size suggesting that a recruitment event occurred. The faunal changes were also observed in a wider area around PAP (Billett et al., 2001) as well as in macro- and meio-fauna, indicating that environmental factors rather than stochastic population imbalance were driving the dynamics (Billett et al., 2010). Evidences point to inter-annual variations in POC flux quantity and quality as an important factor: 1) during the second "*Amperima* event" (2001), a large-scale change in POC flux occurred (Lampitt et al., 2010b). And, both "*Amperima* events" were associated with negative NAO index in 1997 and 2002 (Smith et al., 2009). 2) Pigment variations were linked to some holothurian species dynamics (Hudson et al., 2003, FitzGeorge-Balfour et al., 2010). As holothurians cannot synthesise phyto-pigments and some other compounds, species selectively feeding or digesting these pigments from POC flux can be advantaged (e.g. *A. rosea* with carotenoid, Ginger et al., 2001, Witbaard et al., 2001, Wigham et al., 2003, Hudson et al., 2004). So far, the time-series remains too short and low frequency to draw firm conclusions about the nature of the "*Amperima* event" (cyclic, episodic …) and its link to climate (Smith et al., 2009).

Significant changes in megafauna density and dominance also occurred at Sta. M. From 1989 to 2004, several Echinodermata species densities varied by up to three orders of magnitude (Ruhl and Smith, 2004, Ruhl, 2007). Species increasing in density had decreasing body size suggesting that reproduction and recruitment events occurred, while species decreasing in density may have had less favourable competitive interactions and higher mortality rates (Ruhl, 2007). The variation in megafauna species densities were significantly correlated to the NOI lagged by 14 to 18 months highlighting the influence of El Niño/La Niña events and climate on abyssal fauna (Ruhl and Smith, 2004, Ruhl, 2008). New time points (2007-2013) in the time-series showed that another shift occurred in megafauna community in 2011-2012 (Kuhnz et al., 2014): before 2011, the megafauna assemblage was high in diversity, low in density (compared to 1989-2004) and dominated by sessile, suspension-feeding sponges. After 2011, the megafauna assemblage was low in diversity, high in density and dominated by mobile, detritus-feeding holothurians (Kuhnz et al., 2014). The densities of some holothurians were the highest recorded since 1989 with some increasing by nearly an order of magnitude. The megafauna community composition after 2009 seemed close to that of 1991-1992 suggesting a putative long-term cycle spanning two decades. As at PAP, mechanisms behind the variations remain unclear but likely were linked to inter-annual variations in POC flux quantity and quality (Ruhl et al., 2014). The 2011 shift observed in Sta. M megafauna community concomitantly occurred with the two major POC flux peaks of diatom *Rhizosolenia* and of salps (Smith et al., 2013).

Other fauna have been less extensively studied at both stations: 1) macrofauna. During the first PAP “*Amperima* Event” (1996-1998), several taxa also displayed concomitant temporal variations in density (Galéron et al., 2001). Infaunal polychaetes density increased by a factor three from 1989-1994 to1996-1998 although the assemblage composition did not vary (Soto et al., 2010). This suggested that POC quantity rather than quality may be the main driver of polychaete dynamics. Some polychaete species (Opheliidae) had an opportunistic recruitment event in 1996 (Vanreusel et al., 2001). At Sta. M, nematodes, crustaceans, and annelids dominated the meio- and macro-fauna. From 1989 to 1998, Ruhl et al. (2008) found significant correlations between total macrofauna and meiofauna biomass and POC flux with a decrease in body size when POC flux increased. However, the response was not consistent across phyla. At annual scale, Annelida were significantly correlated to NOI with a 7 month lag; 2) other faunal groups studied include: meiofauna (Gooday et al., 2010, Kalogeropoulou et al., 2010), fishes (e.g. Bailey et al., 2006, 2009, Drazen et al., 2008), sponges (e.g. Kahn et al., 2012, Laguionie-Marchais et al., 2015) and bacteria (e.g. Eardly et al., 2001) and are not detailed here.

1.2.4 Benthic carbon process and ecosystem function variation

Variations in POC flux and benthic communities have important consequences for carbon processes at abyssal seafloor. Many of these processes are due to or mediated by faunal activities such as: 1) remineralisation after consumption by epifaunal/infaunal organisms for respiration, reproductive and somatic growth; 2) incorporation into sediments by bioturbation (e.g. Biles et al., 2002). At Sta. M, changes in the Sediment Community Oxygen Consumption (SCOC, a measure of carbon use at the seafloor) have been measured since 1989 (Drazen et al., 1998, Smith et al., 2001, McGill et al., 2009, Sherman and Smith, 2009). SCOC fluctuated substantially from year to year in synchrony with POC flux but with less variance (Smith et al., 2013). The POC flux:SCOC ratio was mostly less than unity over 1989-1998 and 2005-2007 suggesting that the sediment community was food deprived (Smith et al., 2009). But recent data indicated a major increase in SCOC coinciding with the peak in of salp detritus deposition in spring 2012 (Smith et al., 2013). Since 2011, POC flux:SCOC ratio has been above unity four times highlighting food utilization by the benthic community tracks POC flux. Therefore Smith et al. (2013) hypothesised that over long periods of time, the deep sea can be sustained by large episodic supplies of food from surface waters. Organic carbon not readily consumed by the benthic community provides an oversupply available for remineralisation during subsequent periods of low food supply.

Variations in megafauna density have also been shown to impact carbon processes at seafloor at both stations. At PAP, the "*Amperima* event" period was marked by an increased activity of mobile epibenthic fauna that led to a decreased in the time required for megafauna to process the entire sediment surface: from 2.5 years to 6 weeks after 1996 with potential impacts on bioturbation, diagenetic, and other biogeochemical processes (Bett et al., 2001, Rabouille et al., 2001). In addition, the selective feeding of holothurian species may alter labile food resource available to other organisms (Ginger et al., 2001, Iken et al., 2001, Witbaard et al., 2001, Billett et al., 2010). At Sta. M, variations in food supply also have been linked to megafaunal behaviour (Kaufmann and Smith, 1997). In particular megafauna bioturbation rates have been significantly and positively correlated to POC flux and climate indexes (Vardaro et al., 2009). Using data of both PAP and Sta. M megafauna, Ruhl et al. (2014) found a fourfold variation in echinoderm respiration over inter-annual time scales at both sites, which were linked to shifts in species composition and structure. At Sta. M, the mobile surface deposit-feeding echinoderm respiration was estimated to re-mineralise about 1-6% of the annual POC flux.

1.2.5 Need for macrofauna studies

Sta. M and PAP time-series have given invaluable baseline information on the relationship between surface processes, POC flux, abyssal benthic fauna and carbon processes at inter-annual scale. However, discerning long-term trends from inter-annual to decadal changes has remained challenging in part because processes behind these dynamics need to be mechanistically better understood. In addition, Sta. M and PAP studies of abyssal benthic fauna have been mainly focused on megafauna. Yet, under climate change condition, benthic megafaunal organisms are not projected to experience as large a decline as for macrofauna, particular sediment-dwelling infauna (Jones et al., 2014). Macrofauna are important for carbon processes at the abyssal seafloor and has been shown to respond to changes in surface conditions (Ruhl et al., 2008). *In situ* enrichment experiments conducted at Sta. M and PAP have proven that macrofauna can ingest carbon quickly and mix it into deeper sediment layers with taxa displaying differential responses in terms of their selection and uptake of labelled POC (Aberle and Witte, 2003, Sweetman and Witte, 2008). Therefore, a better characterisation of macrofauna temporal variations at a finer taxonomic resolution could provide important insights in assessing abyssal benthic carbon flow dynamics and macrofauna functional role.

Macrofauna species-level studies have not yet been conducted at St. M and PAP. However, conducting species-level studies with deep-sea specimens is a laborious task. Therefore it is important to study taxa that are most likely to be able to provide data to address key questions. Sta. M and PAP benthic macrofauna are dominated by Polychaeta (Ruhl et al., 2008, Soto et al., 2010). Therefore polychaetes have been selected as the model organism for this thesis work to achieve a better mechanistic understanding of macrofauna intermediate-scale variations at the abyssal seafloor. General features of polychaetes and wherever possible of deep-sea polychaetes are presented in details in the next section.

1.3 Polychaetes

Polychaetes are annelid segmented worms found from freshwater (Glasby and Timm, 2008) to almost any benthic marine habitats at all latitudes and depths (Grassle and Macioleck, 1992, Paterson et al., 2009). In the deep sea, the polychaetes often dominate the infaunal macrofauna from chemosynthetic environments to sedimentary abyssal areas, both in terms of density and species richness (Gage and Tyler, 1991, Van Dover, 2000, Young, 2003, Ruhl et al., 2008, Soto et al., 2010). Due to this diversity, the following review of polychaete phylogeny, morphology, life history and functionality is not detailed for each family but rather is a general overview of the class features.

1.3.1 Polychaete phylogeny

The evolution of Polychaeta and Annelida in general is still poorly understood (Struck et al., 2011, Struck, 2013, Weigert et al., 2014). Non-segmented taxa such as Echiura, Pogonophora and Sipuncula have been recently placed within the Annelida phylum and the clitellates within polychaetes, making polychaete a paraphyletic group (Struck et al., 2007, Zrzavý et al., 2009, Parry et al., 2014). The Polychaeta fossil record dates back to the lower Cambrian (Conway Morris and Peel, 2008, Vinther et al., 2011) and suggests that most major family clades were present prior to the Pangea break up at the end of the Permian. Polychaetes appeared to have survived each of the known major extinction events (Reuscher, 2013). Rouse and Fauchald (1997) distinguished two major clades of polychaetes based on their morphology: the Palpata comprising the order Aciculata and Canalipalpata, and the Scolecida. Struck et al. (2011) phylogenomic analyses were in accordance with the morphological hypotheses of polychaete relationships with Acicula and Orbiniidae forming a monophyletic clade and Canalipalpata with clitellates forming a paraphyletic clade. However, in the Struck et al. (2011) classification, taxa at the base of the tree are unstable and other analyses are needed to clarify polychaete phylogeny (Struck, 2013, Weigert et al., 2014).

Until future molecular analyses resolve the current uncertainties, the polychaete group is still an accepted group of annelid worms widely used in ecological studies (Fauchald et al., 2009, Reusher, 2013). About 85 families of polychaetes have been described (Read, 2014) likely comprising more than 12 000 taxonomically valid species with an additional 6000 species yet to be discovered (Appeltans et al., 2012a). More phylogenetic analyses of species, genus and family relationships are however needed to unravel the true diversity of Polychaeta (Reusher, 2013). In the deep sea, 768 species were recorded in 2009 belonging to 52 families (Paterson et al., 2009). The origin and radiation of deep-sea polychaete species is also under investigation. One of the favoured hypotheses is that as periodic mass extinctions occurred in the deep-sea and that species re-invaded the deep sea from shallower slope and shelf depths (Rogers, 2000, Rex and Etter, 2010, but see Danovaro et al., 2014). Few polychaete families are only found in the deep sea and most genera have shallower counterparts supporting the multiple invasion hypothesis (Glover, 2000). Overall polychaete deep-sea species diversity is considered to be high (Grassle and Macioleck, 1992) and its origin is an active research area.

1.3.2 Polychaete morphology

Although current state-of-the-art taxonomy is based on molecular analysis and specialised microscopy techniques, polychaete identification has mostly been based on their external morphological features (e.g. Fauchald, 1977). Such features are also indicators of life style and ecosystem function. As annelid worms, polychaetes have an elongated, bilaterally symmetrical soft body, with two pre-segmented regions, the prostomium and the peristomium, fused in some families, a segmented trunk and a post-segmental pygidium (Fig. 1.2, Beesley et al., 2000). The overall polychaete body shape, segmentation and flexibility may be indicative of the mobility and burrowing ability of the species.

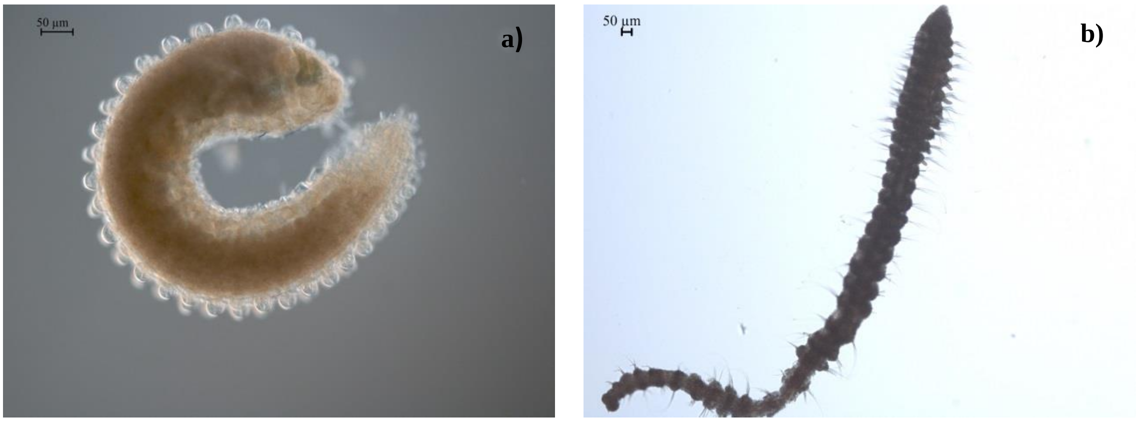

Figure 1.2 Polychaete body shape variations illustrated with Sta. M specimens (a) *Sphaerodoropsi*s sp. A, (b) *Paraonella rubriceps*.

Among the main morphological features used for polychaete identification are the head and related appendages. The head is composed of the prostomium, peristomium and, in some families, of cephalised segments (Beesley et al., 2000). The appendages may include sensory antenna, sensory palps, tentacular crown, tentacular cirri (Fig. 1.3). In many species, the anterior part of the buccal organ is an eversible non-muscular proboscis. The presence of jaws, teeth and other chitinized structures is not only an important for identification but also an indicator of the feeding group (Fauchald and Jumars, 1979, Fig. 1.3). The proboscis and prostomium shape have also been linked to the burrowing ability of some polychaetes (Che and Dorgan, 2010a,b, Murphy and Dorgan, 2011).

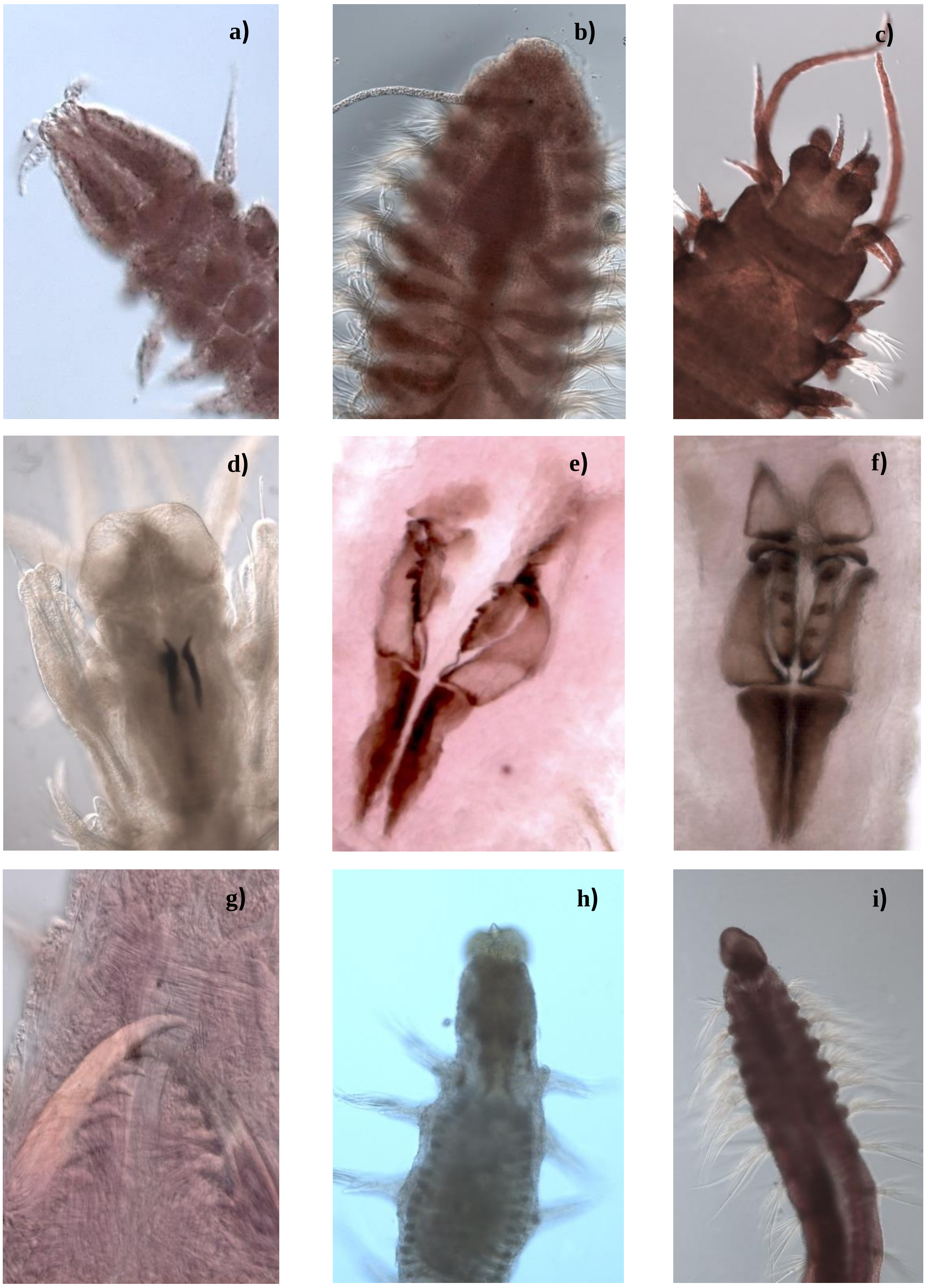

Figure 1.3 Polychaete prostomium and related appendages illustrated with Sta. M specimens (a) Phyllodocidae sp. A with terminal palps and tentacular cirri, (b) *Aricidea* sp. C with antenna, (c) Nereididae sp. C with antennae, palps, tentacular cirri, (d) *Paraonuphis* sp. A, ventral side with mandible seen by transparency (after several day immersion in ethanol-glycerol solution) and palps in the background, (e) *Abyssoninoe* sp. A, dorsal view, jaws seen by transparency, (f) *Augeneri*a sp. A, dorsal view, jaws seen by transparency, (g) *Ceratocephale* sp. A, jaws seen by transparency, (h) *Sphaerosyllis* sp. A, dorsal view, with extended proboscis and mid-dorsal tooth, (i) *Ammotrypanella* sp. B, ventral view, non-armed proboscis extended.

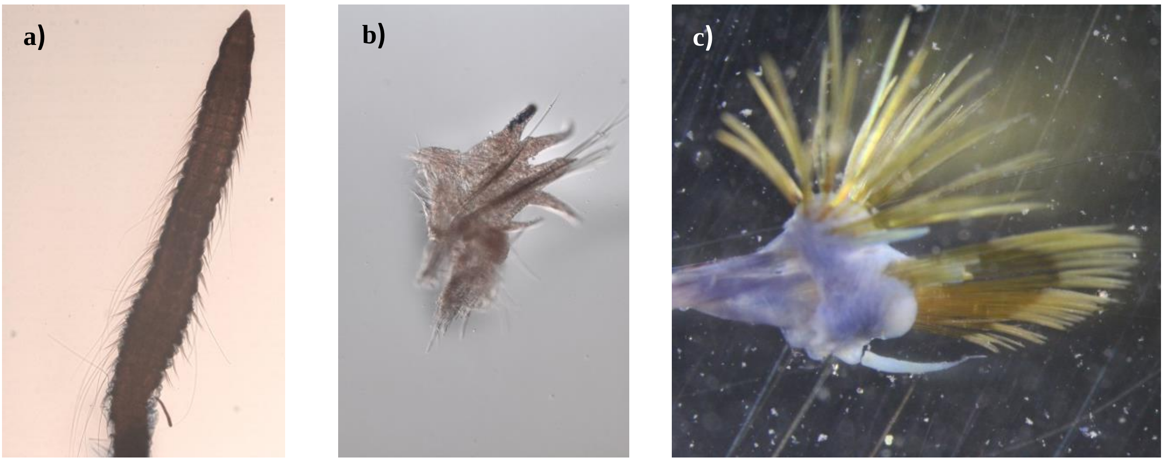

Figure 1.4 Polychaete parapodia illustrated with Sta. M specimens (a) *Chaetozone* sp. A, undeveloped parapodia, (b) Nereididae sp. D, developed parapodia, (c) *Harmathoe* sp. A, developed parapodia.

Other important morphological features are related to the segments. Segments usually bear unjointed appendages called parapodia on both sides (Fig. 1.4).The parapodia can be extremely reduced in some families (mostly burrowing and sedentary families), be biramous or uniramous. The chaetae projecting from the parapodia are bundles of chitinous, thin-walled cylinders held together by a sclerotinised protein, whose shapes are extremely diverse (Beesley et al., 2000, Fig. 1.5). Parapodia and chaetae are indicator of the species mobility, protection ability and anchorage. The segments can also bear branchiae that are indicator of gas exchange ability (Beesley et al., 2000, Lamont and Gage, 2000).

Deep-sea and shallower polychaete morphologies are not fundamentally different. The specimen size reduction is the main conspicuous feature of abyssal polychaetes (Hartman and Fauchald, 1971). Despite these similarities, the identification of deep-sea specimens remains challenging (Paterson et al., 2009). The smaller specimens are easily damaged by the sampling processes, in particular sieving, leading to fragmentation and loss of important morphological features (e.g. antennae). Therefore few species have been described and few taxonomic papers are available to compare specimens. Many ecological quantitative studies used morphotype (sp. A, B, C, etc.) rather than named species, with their description being not publicly available (Paterson et al., 2009).

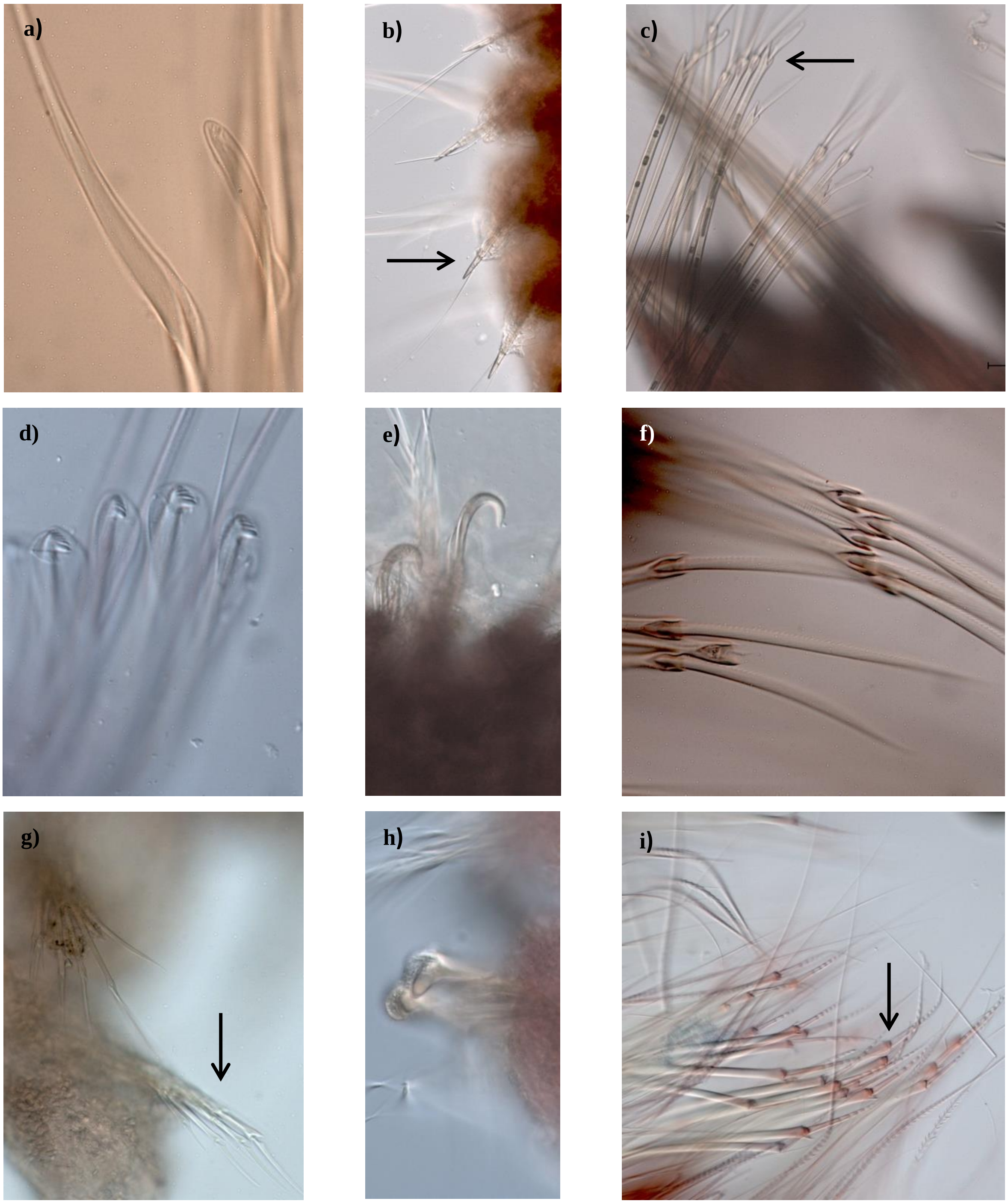

Figure 1.5 Polychaete chaetae illustrated with Sta. M specimens (a) *Abyssoninoe* sp. A, limbate chaetae and hook, (b) *Cirrophorus branchiatus*, bayonet chaetae, (c) Nereididae indet., compound falcigers, (d) *Prionospio* sp. H, hooded hooks, (e) *Sigambra* sp. A, curved hooks, (f) Nereididae sp. C, compound spinigers (g) *Sphaerosyllis* sp. A, compound chaetae, (h) *Dipolydora* sp. A, modified hooks in chaetiger 5, (i) *Leanira* sp. A, pseudo-compound chaetae.

1.3.3 Polychaete life histories and functions

Overall, polychaete life histories are poorly known. Giangrande (1997) estimated that only about three percent of polychaete species had their life histories described, among which very few inhabit the deep sea (Gage and Tyler, 1991, Wilson, 1991, Young, 2003, Mercier et al., 2014). In terms of reproduction, polychaete strategies are diverse even for congeneric species and can be sexual or asexual. Seventeen modes of reproduction were identified but the relative occurrence of each mode is still uncertain (Beesley et al., 2000). Both larval development (direct or planktotrophic/lecithotrophic larvae) and the fate of female gametes (e.g. free spawning, internal brooding, external brooding inside a tube or not, Wilson, 1991) are used in the reproduction mode classification. In the deep-sea, Young (2003) reviewed 16 non-chemosynthetic polychaetes species for which there was some life-history knowledge but only four lived deeper than 3000 m. Since this review, only a few more species have been added in dedicated papers (Eckelbarger et al., 2005, Mincks et al., 2009, Paxton and Arias, 2014, Mercier et al., 2014). Young (2003) found that most of these studied deep-sea species had separate sexes, continuously reproduced (but see Blake, 1993, Vanreusel et al., 2001, Mercier et al., 2014), and were brooders (Levin et al., 1994a, Paxton and Arias, 2014). However, the lack of seasonal reproduction may be an artefact as there are few deep-sea sampling time-series programmes. In the same way, brooding is easier to document than other developmental modes. Consequently, it is not yet clear if brooding and aseasonality are true features of deep-sea polychaetes or a sampling bias (Young, 2003). Most deep-sea polychaete life-history data come from fortuitous observations.

Polychaetes are mainly associated with benthic habitats from intertidal to trench systems in rocky, sandy, muddy or coral reef substrates Polychaetes either live at the water-sediment interface (e.g. under rocks, crevices) or buried within the sediment, directly or in tubes, mostly in the top 10 cm. Burrowing is related to protection against predation, search for food and/or establishment of a steady place to live in an unstable or shifting environment. Tubes can be either carried out by the worm while searching for food or fixed in a position. Polychaete position on/within sediment reflects their feeding activity (Blake, 1994). Polychaete feeding guilds as defined by Fauchald and Jumars (1979) were based on: 1) the feeding mode: predator, filter feeder, surface deposit feeder, sub-surface deposit feeder; 2) the motility associated with feeding activity: motile, discretely motile and sessile specimens; 3) the morphology of the mouthpart: jaws, tentacles, or unarmed pharynx.

Based on observations of shallow-water species, each polychaete family was assigned one or several functional groups (FG), i.e. groups that utilise the same resource in similar ways (Jumars et al., 2015). The Fauchald and Jumars’ classification has long been the only unified classification of polychaete FG and consequently has been extensively used in studies on polychaetes (> 1600 citations). However, since 1979, the knowledge on polychaete morphology, life habits, and phylogeny has improved (e.g. Penry and Jumars, 1990, Lindsay and Woodin, 1995, Mistri et al., 2002, Guieb et al., 2004, Tzetlin and Purschke 2005, Struck et al., 2011, Würzberg et al., 2011). Evidence now suggests that many polychaetes may be multimodal and may adapt to utilize what resources are available. Recently, Jumars et al. (2015) proposed a revised definition of polychaete functional groups to include this knowledge.

Except in chemosynthetic environments, deep-sea polychaete FG are not thought to be different from the shallower ones. As almost all deep-sea polychaete families occur in shallower ecosystems, Fauchald and Jumars ’classification has been used in the deep sea (e.g. Soto et al., 2010). Until advanced techniques such as isotope, fatty acid analyses, or feeding experiments become more frequent in the deep sea (Levin et al., 1999, Witte et al., 2003, Sweetman and Witte, 2008, Jeffreys et al., 2013), the analogy with shallower species remain the most relevant. Deep-sea polychaetes are dominated by deposit feeders (Hessler and Jumars, 1974, Paterson et al., 1998, Glover et al., 2001, Aberle and Witte, 2003, Sweetman and Witte, 2008) that more or less continuously ingest dilute food whose principal content by weight is mineral material (Jumars et al., 2015). In addition to the sediment horizon in which they feed, the degree of food item selection is thought to be an important resource partitioning mechanism. Smaller deposit feeders are thought to be macrophagous, selecting food items one at a time and larger ones are thought to be microphagous, mechanically feeding of bulk sediment (Penry and Jumars, 1987, Jumars et al., 1990, Etter and Grassle, 1992, Hentschel, 1996, Paterson et al., 2006 but see Jumars et al., 2015).

Through feeding, respiration, locomotion and burrowing activities, polychaetes are important bioturbators. Polychaetes impact organic matter redistribution and take part to gating the entry of organic material into deep burial that removes carbon from the active biosphere on geological time scales (Jumars et al., 2015). Such function is important in the context of current climate change. In addition polychaetes modify sediment ventilation, redox condition, microbial metabolic processes and exchanges of sediment-water fluxes of solutes (Aller, 1982, Lopez and Levinton, 1987, Kristensen, 1988, Kristensen et al., 1992, Levin et al., 1997, Hutchings, 1998, Jumars et al., 2015). By altering the physical and geochemical qualities of sediment, polychaetes also influence the species composition of their habitats and therefore are considered as ecosystem engineers (Herringshaw et al., 2010). Polychaetes also directly interact with infaunal meiofauna, protists and bacteria *via* competition, predation and facilitation process (Levin and Edesa, 1997, Levin et al., 1997, Van Nugteren et al., 2009) and are an integral part of their habitat food chain.

1.3.4 Polychaetes as model organisms for abyssal ecological studies

In this study polychaetes were selected to address a series of ecological questions on abyssal macrofauna assemblage. Although no perfect surrogate exists, targeting a taxon was relevant due to the limited time-frame of the project and complexity of deep-sea macrofauna taxonomy. Such approach is frequently used in marine ecological studies (e.g. Olsgard et al., 2003, Thistle, 2003, Danovaro et al., 2004, Arvanitidis et al., 2009). Several reasons justify the choice of polychaetes. First, abyssal macrofauna densities are low compared to shallower systems. Polychaetes being density dominant in a majority of deep soft-bottom macrofauna (Gage and Tyler, 1991, Grassle and Macioleck, 1992, Glover et al., 2001, 2002, Ruhl et al., 2008, Paterson et al., 2009, Soto et al., 2010), they offer the highest number of specimens per sample unit. More specimens offer higher degrees of freedom in statistical analyses. Second, within limits, knowledge of ecology of shallow-water polychaete species can be inferred as applicable to deep-water species. Few polychaetes (44 species from 15 families) have been reported as being exclusively abyssal (Paterson et al., 2009). Third, polychaetes are diverse in terms of life histories, functional groups and are considered as ecosystem engineers. Investigating ecological questions across such functional diversity is an advantage when comparing results with other ecosystems and identifying common ecological patterns. Lastly, polychaetes appeared responsive to changes that occurred at Sta. M and PAP (Aberle and Witte, 2003, Ruhl et al., 2008, Sweetman and Witte, 2008, Soto et al., 2010).

1.4 Thesis aims and objectives

Although long-term time series conducted at PAP and Sta. M have provided invaluable baseline information on the dynamics and relationships between surface processes, POC flux, abyssal benthic megafauna and carbon processes, discerning long-term trends from inter-annual to decadal changes has remained a challenge. In addition to pursuing the time-series, a better characterisation of benthic fauna dynamics across a wider range of faunal size group could provide important insights in ecosystem dynamics and driving processes. Therefore, my PhD work examined changes at spatial and temporal intermediate scales in abyssal benthic macrofauna at PAP and Sta. M using polychaetes as model organisms.

In chapter 2, the influence of intermediate-scale topographic features, namely abyssal hills, on macrofauna assemblage is assessed at PAP. Assessing spatial heterogeneity is important in order to adequately sample populations and to unravel the mechanisms regulating spatio-temporal patterns. The assessment of habitat heterogeneity defined by depth, slope and percentage of coarse sediment particles has shown significant differences between hills and plains at PAP and influences on megafauna (Durden et al., 2015). On seamounts, the bigger counterpart of abyssal hills, faunal distributions have been related to sediment grain size distribution although not as a primary structuring factor but rather as a factor indicative of driving forces such as hydrodynamics (currents) and sediment transport regime (particle settling pattern, Snelgrove and Butman, 1994). The review of the background knowledge suggests the following hypothesis **Hc2: abyssal macrofauna assemblage (density, diversity, composition, structure) changes at scales of 0.1-10s km with topographic features, namely abyssal hills, in relation to the sediment grain size distribution spatial variation and its position with respect to topographical features.**
This main hypothesis can be divided into three more specific hypotheses to test. Firstly, the sediment grain size distribution has been shown to be the main factor correlating with megafauna distribution at PAP (Durden et al., 2015) and is known to correlate with infauna invertebrate distributions (Etter and Grassle, 1992, Snelgrove and Butman, 1994). This support the existence of a relationship between sediment grain size distribution and macrofauna assemblage features:
Hc21: The polychaete/macrofauna assemblage features (density, diversity, composition, structure) are related to the sediment grain size distribution within and surrounding a single hill as well as between and among hills.
Secondly, the change in depth and sediment grain size distributions alongside a single hill is expected to impact the fauna distribution as seen on seamounts (McClain, 2007, McClain et al., 2009, 2010, Yesson et al., 2011, Chivers et al., 2013):
Hc22: The polychaete/macrofauna assemblage features (density, diversity, composition, structure) change within and surrounding a single hill.

Thirdly, the occurrence of abyssal hills within an abyssal plain has already been shown to generate habitat heterogeneity for megafaunal assemblages at PAP (Durden et al., 2015) at scales of 1-10s km. Abyssal hills are also expected to increase habitat heterogeneity for macrofauna at these scales:
Hc23: The polychaete/macrofauna assemblage features (density, diversity, composition, structure) change between and among hills.

In chapter 3, the inter-annual dynamics of polychaete assemblages at PAP and Sta. M are described and compared. Results obtained with megafauna at Sta. M (Ruhl and Smith, 2004) and PAP (Billett et al., 2010) showed inter-annual variations in terms of density and diversity in relation to POC flux and climate index variations. In addition, preliminary studies conducted on macrofauna at PAP (Soto et al., 2010) and Sta. M (Ruhl et al., 2008) showed that macrofauna changed in terms of density between years. So the review of the background knowledge suggests the following hypothesis **Hc3: at abyssal depths, the macrofauna communities change at inter-annual scale in relation with megafauna and environmental factors as observed in terrestrial and shallower marine ecosystems.**
The main hypothesis can be divided into three specific hypotheses to test. Firstly, significant inter-annual variations are expected in the overall polychaete assemblages as suggested by preliminary studies at Sta. M and PAP (Ruhl et al., 2008, Soto et al., 2010):
Hc31: The polychaete assemblage density and composition are statistically different over the time-series both at PAP and at Sta. M.
Secondly, long-terms studies of various community dynamics (e.g. desert rodents, Thibault et al., 2004; holothurians, Ruhl, 2008) have indicated the role of resource partitioning and niche-based mechanisms. The rank abundance distributions (RADs) that describe the abundance and dominance of each taxon relative to the others are thought to be biodiversity indicator of resource use by each rank (MacArthur, 1957, Sugihara et al., 2003). Both Thibault et al. (2004) and Ruhl (2008) found that RAD was a dynamic property. So switches in polychaete rank composition are expected to occur at inter-annual scale:
Hc32: The polychaete rank abundance distributions are statistically different at inter-annual scales both at PAP and Sta. M.
Thirdly, at both Sta. M and PAP, the megafauna seemed to readily respond to climate-driven change in abyssal food supply. As polychaetes largely rely on the same detrital resource and have been shown to quickly respond during *in situ* feeding experiments

(Witte et al., 2003, Sweetman and Witte, 2008, Jeffreys et al., 2013), the polychaete assemblage dynamics are expected to be related to the megafauna dynamics and its drivers (POC flux, climate indexes):
Hc33: Inter-annual changes in polychaete family/functional group assemblages are correlated with megafauna assemblage and environmental factors (climate indexes and POC flux) dynamics.

In chapter 4, the density and body-size dynamics of Sta. M density-dominant species are analysed. In the deep sea, population parameters such as reproduction or growth rate can not be directly measured for numerous species. Detailed abundance and size frequency distribution data provide some of the best information available to help elucidate the population dynamics of abyssal benthic species (Ruhl, 2007). The conjoint study of density and body size can give evidence of life-history events: recruitment corresponds with an increased density of smaller individuals; migration and enhanced survivorship correspond with an increased density of larger individuals; reproduction may correspond with smaller individuals without changes in density if individuals stop their growth to reproduce; mortality and competitive interactions correspond with a decrease in density. Such life-history events were evident for the density-dominant megafauna species at Sta. M and PAP and were related to change in food supply quantity and quality (Ruhl, 2007, Billett et al., 2010). So a review of the background knowledge suggests the following hypothesis **Hc4: when population parameters can not be directly observed, the inter-annual density and body size dynamics of macrofaunal species can reveal life-history events (e.g. reproduction, recruitment, migration, enhanced survivorship) linked to environmental variations**.
The main hypothesis can be divided into three specific hypotheses to test. Firstly, the changes in polychaete family density (Laguionie-Marchais et al., 2013, Chapter 3) as well as the changes in macrofaunal phyla (Ruhl et al., 2008) observed over 1991-2005 at Sta. M suggest that variations in polychaete species density and body size occurred and are statistically significant at inter-annual scale:
Hc41: For each species, the density and body size statistically change at inter-annual scale.
Secondly, the correlations found between the density and body size dynamics of the density-dominant megafauna species at Sta. M over time (Ruhl, 2007) suggest that polychaete species density and body size dynamics may be correlated at inter-annual scale:
Hc42: The density and body size dynamics of each species are correlated, being indicative of life-history events.

Thirdly, the Sta. M polychaete family study (Laguionie-Marchais et al., 2013, Chapter 3) showed that polychaetes dynamics were linked to megafauna dynamics. In addition the work conducted on megafauna showed that changes in POC flux quantity and quality were influential in the reproduction of some holothurians (Wigham et al., 2003, Hudson et al., 2004). So polychaete life-history events are expected to be linked to environmental variations:
Hc43: The density and body size dynamics of each species are related to megafauna and food supply dynamics.

In chapter 5, long-term variations (1991-2011) in the polychaete species assemblage and energetic use are assessed to provide insights into the mechanisms driving the polychaete structure, dynamics, and biogeochemical function. The objective is to use species-level time-series data to investigate generic ecology theories on community structure: niche partitioning (Hutchinson, 1957), energetic compensation (Ernest et al., 2008) and body-size (Brown et al., 2004). By using such data, Ruhl et al. (2014) found evidence of change in megafauna energy use, resource use, community structure and composition that met the specific assumptions of climate-driven community variation via niche-based and energetic abundance mechanisms. So a review of the background knowledge suggests the following hypothesis **Hc5: in a resource limited environment, niche, energetic, and body-size related mechanisms control species assemblage dynamics**.
The main hypothesis can be divided into five specific hypotheses to test. Firstly, results of megafauna assemblage dynamics (Ruhl et al., 2014) showed change in biodiversity and energy use rate. In combination with the results of the polychaete family assemblage dynamics (Laguionie-Marchais et al., 2013), significant changes in polychaete species assemblage biodiversity and energy use rate are expected:
Hc51: Polychaete assemblage features (density, biomass, diversity, composition) and its energetics (rate of energy use) statistically change at inter-annual scale.
Secondly, the study at family level Laguionie-Marchais et al., 2013) have given evidence that potential relationships between POC flux and polychaete assemblage were complex at Sta. M. However, polychaete family and functional group changes occurred in correlation with changes in the megafauna assemblage, suggesting that common external factors may be driving dynamics across the different faunal groups. The longer data set of species-level polychaete assemblage may clarify the relationship between polychaete assemblage and POC flux dynamics and support the following hypothesis:

Hc52: Polychaete assemblage features and energetics dynamics are correlated to food supply dynamics.

Thirdly, ecological theories based on resource partitioning posit that communities are structured by compensatory dynamics, i.e. for fixed resource levels, the total abundance is constant, and increases in the abundance of a taxon are compensated for by decreases in abundance of others (Hubbell, 2001, Ernest and Brown, 2001). In real systems, however, evidence for such interspecific compensatory dynamics of abundances is limited (Houlahan et al., 2007, Ruhl et al., 2014) suggesting the following hypothesis:

Hc53: There are no compensatory dynamics in polychaete assemblage at inter-annual scale (an increase in the density of a species does not systematically relate to the decrease in the densities in other(s)).

Fourthly, abundance is not directly related to the rate of resource consumption and therefore allows questions about zero-sum dynamics to be addressed only indirectly and imprecisely. The same rate of resource supply can support either fewer organisms with higher per capita rates of consumption or more organisms with a lower per capita rate of consumption. Under the zero-sum dynamics theory, the total number of individuals is inversely related to the mean individual metabolic rate. This relationship has been observed in tropical forest data (Ernest et al., 2009) and for megafauna at Sta. M (Ruhl et al., 2014) suggesting the following hypothesis:

Hc54: There is energetic zero-sum dynamics in polychaete assemblage at inter-annual scale (the mean individual respiration rate is inversely related to total density.

Fifthly, other ecology theories are based on the primary role of body size in structuring communities. Body size is a key predictor of individual energy use rate. For a constant limiting resource, a lower total biomass of small organisms can be supported relative to larger organisms. Given a central assumption of equitable resource use across geometric body mass classes (e.g. Savage et al., 2004) and “energetic equivalence rule” (Damuth, 1987) the metabolic theory of ecology (Brown et al., 2004) predicts that faunal density should decrease with -3/4 power with increasing geometric size class, and that biomass should increase with 1/4 power, while total metabolism should remain approximately constant. Such relationships have been previously found in the deep sea (McClain, 2004), which suggests the following hypothesis:

Hc55: Body size is a structuring factor of the Sta. M polychaete assemblage at inter-annual scale (following the equivalent energy rule predicted by the metabolic theory).

In chapter 6, the main conclusions of the thesis are presented with an emphasis on their broader implications, future important lines of research in the deep sea and the global relevance of the latter to human kind.

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Chapter 2

Influence of intermediate-scale habitat heterogeneity on abyssal polychaete and macrofauna distributions

This chapter is a modified version of a paper in preparation:
- Laguionie-Marchais, C., Bett, B.J., Durden, J.M., Robert, K., Morris, K., Paterson, G.L.D., Jones, D.O.B., Ruhl, H.A. Influence of intermediate-scale habitat heterogeneity on abyssal polychaete and macrofauna distributions. Progress in Oceanography.

Abstract

Topography is a major driver of spatial variation in ecosystems. Understanding such spatial heterogeneity is important to adequately sample populations and unravel the mechanisms regulating biodiversity. In the deep sea, large-scale topographic features such as canyons and seamounts influence the sedimentary conditions and resource availability. Less is known about the influence of abyssal hills, the smaller analogues of seamounts, which are globally common. This study examined the macrofauna density, diversity and composition patterns in relation to abyssal hills: 1) within and surrounding a single abyssal hill sampled in 2012 (~0.1-1s km scale); 2) between and among abyssal hills sampled in 2011 (~1-10s km scale). Both sampling regimes were conducted in the North East Atlantic at the Porcupine Abyssal Plain. Abyssal hills created spatial heterogeneity with variation in the physical variables such as depth and sediment particle size distribution both within and surrounding a single abyssal hill and between and among abyssal hills. Abyssal hills were characterised by a greater percent of coarse particle fractions. The within and surrounding single abyssal hill analysis showed that macrofauna density could be significantly different over 50 m depth changes. The between and among hill analysis showed that polychaete and macrofauna compositions were related to the sediment particle size distributions. Differences in near-bed current flows, and thus in sedimentary and food settling conditions, may be the primary factors influencing the macrofauna. Further work is now required to assess the degree of faunal differences in and among abyssal hills as the latter are one of the most common topographic features on Earth and have been rarely sampled in the past.

2.1 Introduction

Spatial heterogeneity is a key factor both in sampling design and theoretical ecology (Currie and Paquin, 1987, Rex and Etter, 2010). Identifying biotic and abiotic spatial distributions and their variability is a prerequisite to unravel the mechanisms regulating patterns in an ecosystem (Levin, 1992). In the deep sea, large-scale topographic features such as canyons (De Leo et al., 2010, McClain and Barry, 2010, Vetter et al., 2010, Ingels and Vanreusel, 2013), seamounts (McClain, 2007, McClain et al., 2010, Yesson et al., 2011), mid-ocean ridges (Priede et al., 2013) influence faunal distributions by inducing environmental gradients and variations in depth, productivity, oxygen, current, sediment, and lateral transport of particulate organic carbon (food supply) along the seabed (Levin et al., 2001, 2010, Rex and Etter, 2010). Less is known about habitat heterogeneity produced by topographic features at the scale of abyssal hills. Jumars (1976) suggested that such features, with their varying sediment particle size distribution (Johnson, 1972) may provide a structural heterogeneity that may relate to the distributions of some species. Because abyssal hills are thought to be one of the most common topographic features on Earth, their influence is likely to be pervasive (Macdonald et al., 1996, Wessel et al., 2010, Turnewitsch et al., 2013). Here I examined the influence of abyssal hills on a scale of a few kilometres (~0.1-10s km) by comparing the macrofauna and in particular the polychaete assemblages on abyssal plains and neighbouring abyssal hills.

Understanding abyssal hill influence is critical for assessing anthropogenic impacts such as climate change (Smith et al., 2009, Mora et al., 2013, Jones et al., 2014) and resource exploitation on abyssal systems (Glover and Smith, 2003, Ramirez-Llodra et al., 2011). Unresolved habitat heterogeneity and associated sampling error may reduce the ability to understand links between climate, surface processes and deep-sea communities (Godbold et al., 2011). Understanding such links has been the focus of time-series studies conducted at the Porcupine Abyssal Plain (PAP) station in the North East Atlantic since 1989 (Billett et al., 2010). However, at PAP, the influence of features such as hills is not well resolved. Therefore, two research cruises were conducted to survey the region around the PAP-Sustained Observatory (PAP-SO) in 2011 and 2012 to understand how the topography of the seabed, in particular abyssal hills, alters benthic faunal abundances and distributions.

Previous research has found significant differences between megafaunal assemblages on abyssal hills and surrounding plains at PAP (Durden et al., 2015). The differences in environmental factors and megafauna were assessed between four abyssal hill and four abyssal plain sites. The hills encompassed several elevations and slopes ranging from 2.2 to 8.6° based on shipboard multibeam data. At all sites, the sediment particle size distribution was bimodal, but there was a greater fraction of coarse particles on the hills. Overall habitat heterogeneity, defined by depth, slope and percentage of coarse sediment particles was significantly different between hills and plains, whereas the phytodetrital cover and median phytodetrital clump size visually determined from videos were not. Durden et al. (2015) found that the megafaunal assemblage and trophic composition were significantly different between hill and plain sites and linked to percentage of coarse sediment particles.

Here I consider macrofauna, which were also sampled at the same general sites as the megafauna to examine how macrofaunal density as well as assemblage structure and composition may differ between abyssal hills and plains. A two-stage approach was conducted: 1) the first stage consisted in characterising polychaete/macrofauna assemblages within and surrounding a single hill (thereafter referred as WH, ~0.1-1km scale). 2) The second stage consisted in characterising polychaete/macrofauna assemblages between and among hills (thereafter referred as BH, ~1-10s km scale). Differences between hill and plain sites were tested at two taxonomic levels: for different macrofauna taxa and for different families of the dominant class, the Polychaeta. As higher taxonomic groupings include a broader range of evolutionary adaptations to environmental variations (Narayanaswamy et al., 2003), detecting different responses at different taxonomic levels may help in unravelling different processes. Spatial distributions and their underlying mechanisms have been shown to vary with taxa (Jumars and Eckman, 1983, Snelgrove and Smith, 2002). For Polychaeta, I also used functional groups as there is evidence that small-scales polychaete distribution patterns are partly related to feeding modes (Reise, 1979).

Macrofauna and polychaete assemblages have been shown to be influenced by topographic features such as mid-ocean ridges (Priede et al., 2013, Shields and Blanco-Perez, 2013), canyons (Paterson et al., 2011, Gunton et al., 2015a,b) and seamounts (Gillet and Dauvin, 2000, Surugiu et al., 2008, Bongiorni et al., 2013, Chivers et al., 2013) and therefore are expected to be influenced by abyssal hills. All these topographic features change the nature and density of suspended particles as well as accumulation of sediment and organic matter (de Stigter et al., 2007, Oliveira et al., 2007, Samadi et al., 2007, Arzola et al., 2008, Cunha et al., 2011). In turn the increased environmental heterogeneity impacts macrofauna density and diversity compared with background environments (Tews et al., 2004). In particular, at seamounts (the most comparable topographic feature to abyssal hills), macrofauna density and diversity change between the summit, the flanks, the base and surrounding areas with contrasting results in terms of the location of higher density/diversity within the seamount (Levin and Thomas, 1989, Bongiorni et al., 2013, Chivers et al., 2013). Bongiorni et al. (2013) found evidence that the macrofauna density variance was linked to the sediment particle size and porosity whereas diversity and composition were related to food quality within sediments.

Overall, results of seamount macrofauna and abyssal hill megafauna studies suggest the following hypotheses: 1) at PAP, the macrofauna/polychaete assemblages (density, diversity, composition, structure) are related to the sediment particle size distribution within and surrounding a single hill (WH ~0.1- 1km scale) as well as between and among hills (BH ~1- 10s km scale). 2) The macrofauna/polychaete assemblage (density, diversity, composition, structure) change within and surrounding a single hill (WH). 3) The macrofauna/polychaete assemblage (density, diversity, composition, structure) change between and among hills (BH).

2.2 Materials and Methods

In the North East Atlantic, two research cruises were conducted at the Porcupine Abyssal Plain, PAP, (48˚ 50 N, 16˚ 30 W, 4850 m depth, Billett and Rice, 2001). PAP is characterised by a flat area with abyssal hills rising about 300 mab (metres above bottom) and one rising about 1000 mab (Klein and Mittelstaed, 1992, Turnewitsch and Springer, 2001).

2.2.1 Within and surrounding a single hill (WH) data

2.2.1.1 Sampling sites

The RRS Discovery cruise 377/8 (Ruhl, 2013) was conducted in July 2012. Habitat heterogeneity and macrofauna were studied within and surrounding a single abyssal hill H3 (Fig. 2.1, 2.2 and Table 2.1). Overall 24 stations were sampled within and surrounding the hill using three to six cores from each megacorer deployment for macrofauna analysis. One core of each megacorer was also used at each station to determine sediment characteristics as detailed below. The investigated stations were distributed by even 50-m depth bands: shallower than (<) 4690 m, 4740-4690 m, 4790-4740 m, 4840-4790 m and deeper than (>) 4840 m (Table 2.1).

Table 2.1 Within and surrounding a single hill (WH) sampling details: date of sampling, station (corresponding with a megacorer drop each time), coordinates, number of cores collected, sampled area (m^2), depth (m), depth band (m).

Date	Station	N	W	Number of cores	Sampled area (m^2)	Depth (m)	Depth band (m)
13/07/2012	A1	48.956	-16.545	6	0.047	4633	< 4690
13/07/2012	A2	48.963	-16.548	5	0.039	4668	< 4690
14/07/2012	A3	48.954	-16.546	5	0.039	4674	< 4690
15/07/2012	AA1	48.960	-16.545	6	0.047	4693	4740-4690
12/07/2012	B1	48.963	-16.553	4	0.03	4715	4740-4690
12/07/2012	B2	48.951	-16.550	6	0.047	4718	4740-4690
13/07/2012	B3	48.967	-16.545	6	0.047	4695	4740-4690
15/07/2012	BB1	48.951	-16.542	4	0.031	4691	4740-4690
10/07/2012	C1	48.982	-16.547	3	0.024	4779	4790-4740
10/07/2012	C2	48.980	-16.547	4	0.031	4773	4790-4740
11/07/2012	C3	48.952	-16.534	3	0.024	4845	> 4840
12/07/2012	C4	48.977	-16.548	4	0.031	4773	4790-4740
16/07/2012	CC1	48.963	-16.559	5	0.039	4787	4790-4740
09/07/2012	D1	48.992	-16.527	4	0.031	4820	4840-4790
09/07/2012	D2	48.939	-16.546	4	0.031	4832	4840-4790
11/07/2012	D3	48.938	-16.603	4	0.031	4844	> 4840
11/07/2012	D4	48.937	-16.613	4	0.031	4844	> 4840
11/07/2012	D5	48.950	-16.585	4	0.031	4845	> 4840
17/07/2012	DD2	48.998	-16.586	6	0.047	4828	4840-4790
11/07/2012	E2	49.014	-16.586	4	0.031	4847	> 4840
10/07/2012	E3	49.020	-16.606	4	0.031	4847	> 4840

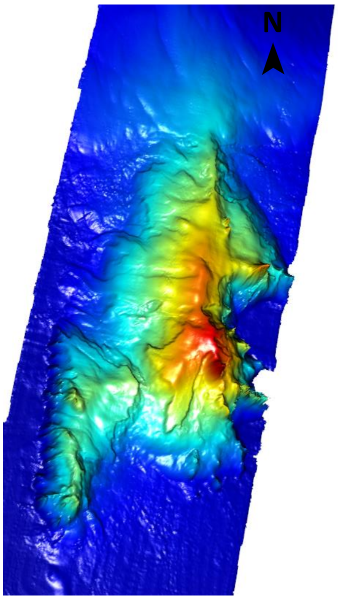

Figure 2.1 Within and surrounding a single hill (WH) sampling map (courtesy of Dr. Robert) at the Porcupine Abyssal Plain in the North East Atlantic (abyssal hill 'H3', Fig. 2.2, from Ruhl, 2013). Twenty four stations were sampled belonging to five 50-m depth bands: < 4690 m in red, 4740-4690 m in yellow, 4790-4740 m in green, 48490-4790 m in light blue, > 4840 m in dark blue.

2.2.1.2 Habitat heterogeneity data

To test if the physical habitat differed within the single hill H3, environmental data (depth and sediment particle size) were collected. Elevated topography is expected to cause enhanced bottom currents, impacting the sedimentation of both organic and inorganic (sand/mud) particles. Depth can be used as a proxy for this effect and was obtained with a hull-mounted Simrad EM12 hydrographic multibeam echo sounder that collected the bathymetric data during the research cruise JC071 (Lampitt, 2013). The sediment percent of sand (i.e. coarse particle fraction) can be used as a direct measure of effect on local environment. The sediment cores from the megacorer were analysed for particle size distributions. The sediment particles were measured by laser diffraction using a Malvern Mastersizer in five near-surface layers (0-1 cm, 1-3 cm, 3-5 cm, 5-10 cm and 10-15 cm, see details in Durden et al., 2015). Sediments from each layer were weighed and combined to obtain the sediment particle size distribution of the 0-15 cm sediment. The percent of sand particles (%sand, percentage of particles larger than 63 µm) were determined and used as a summary univariate parameter of sediment particle distributions.

2.2.1.3 Macrofauna processing and identification

Once on board, the macrofauna cores were put into a cold room (~4˚C). The surface water of the cores was siphoned off and sieved through a 300 µm-mesh sieve and added to the 0-1 cm sediment layer. The sediment cores were sliced into five layers: 0-1 cm, 1-3 cm, 3-5 cm, 5-10 cm and 10-15 cm. Each layer was bulk preserved in a 10% borate-buffered formalin solution and stored prior to sieving and sorting.

Samples were stained for 24-h in Rose Bengal, rinsed in distilled water, elutriated using a 300-µm sieve, transferred to a 70% isopropyl alcohol solution. Two levels of taxonomic identification were performed on the macrofauna: family level for polychaete specimens and the best available taxonomic resolution for the rest of the macrofauna (order level at best). Taxonomic identification was done under high power microscopes (Zeiss Discovery v20 Stereo and high power Leica DM 5000 B) by comparing the external morphology of specimens with published identification keys (e.g. Fauchald, 1977). Only specimens with a head were used, leading to a conservative assessment of density and diversity (Paterson et al., 2009). Polychaete families were assigned to a single functional group (Table 2.2, Fauchald and Jumars, 1979) as detailed in Laguionie-Marchais et al. (2013).

Table 2.2 Three-letter code key of polychaete functional groups as defined by Fauchald and Jumars (1979).

First Letter Feeding Mode	Second Letter Mobility	Third Letter Feeding Apparatus
B – Subsurface deposit feeder	D – Discretely motile	J – Jaw
F – Filter feeder	M – Motile	T – Tentacle
P - Predator	S - Sessile	X – non-armed structure
S –Surface deposit feeder		

2.2.2 Between and among hill (BH) data

2.2.2.1 Sampling sites

The RRS James Cook cruise 062 (Ruhl, 2012) was carried out in July-August 2011 to study between and among hill habitat heterogeneity and macrofauna. Three sites were located on the abyssal plain (P1, P3, P4) and four sites on abyssal hills in the same area (H1, H2, H3, H4 see details in Durden et al., 2015). The hill 'H3' corresponded with the WH analysis. P1 corresponded to the PAP Central locality sampled as part of the PAP-SO long-term time series since 1989. Each site was sampled at random for infaunal macrofauna (Fig. 2.2). Five replicates (from five separate megacorer drops, hereafter referred to as stations) were taken at each site. Each megacorer deployment had up to 12 cores on the coring head (10-cm diameter core). Sample sizes for macrofauna varied between one and height cores (Table 2.3). One core of each megacorer was also used to determine sediment characteristics as detailed above.

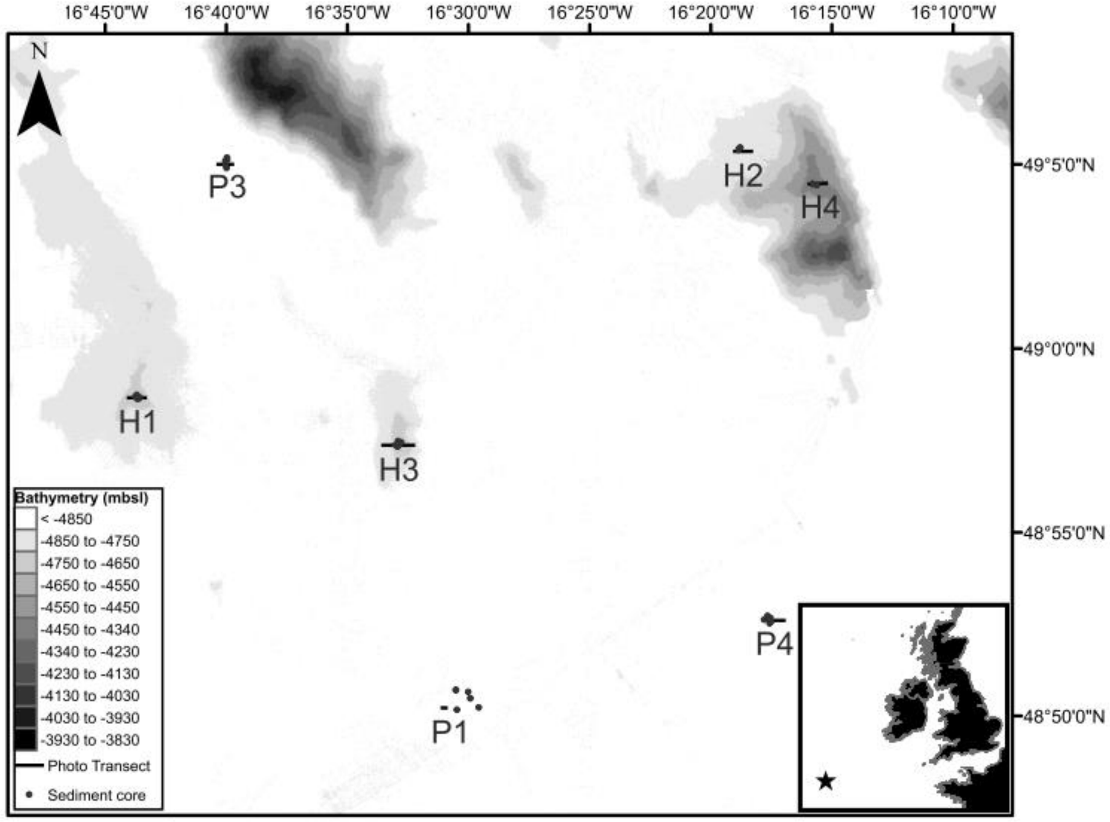

Figure 2.2 Between and among hill (BH) sampling map at the Porcupine Abyssal Plain in the North East Atlantic (insert). Bathymetry is indicated by the grey scale. Three abyssal plain sites: P1 (Cent.), P3, P4 and four abyssal hill sites were sampled: H1, H2, H3, H4 (from Durden et al. 2015). Five replicates were collected at each site.

Table 2.3 Between and among hill (BH) sampling details: date of sampling, site with abyssal plain areas demoted as P and abyssal hill denoted as H, station (with corresponding number of megacorer drops), number of cores collected and amalgamated, coordinates, depth (m), and sampled area (m^2).

Site	Depth (m)	Date	Station (number of deployment)	Number of cores	N	W	Sampled area (m^2)
P1	4814	27/07/2011	P1-1 (2)	8	48.841	-16.499	0.063
		28/07/2011	P1-2 (1)	4	48.836	-16.508	0.031
		30/07/2011	P1-3 (1)	4	48.837	-16.493	0.031
		31/07/2011	P1-4 (1)	4	48.844	-16.500	0.031
		31/07/2011	P1-5 (2)	4	48.845	-16.509	0.031
P3	4819	08/08/2011	P3-1 (2)	4	49.085	-16.667	0.031
		17/08/2011	P3-2 (1)	4	49.086	-16.667	0.031
		09/08/2011	P3-3 (2)	5	49.083	-16.667	0.039
		09/08/2011	P3-4 (1)	4	49.085	-16.666	0.031
		09/08/2011	P3-5 (2)	4	49.082	-16.666	0.031
P4	4815	10/08/2011	P4-1 (2)	6	48.879	-16.294	0.047
		18/08/2011	P4-2 (1)	5	48.878	-16.292	0.039
		10/08/2011	P4-3 (2)	8	48.877	-16.297	0.063
		11/08/2011	P4-4 (1)	1	48.876	-16.292	0.008
		11/08/2011	P4-5 (1)	2	48.875	-16.293	0.016
H1	4653	05/08/2011	H1-1 (2)	5	48.978	-16.729	0.039
		05/08/2011	H1-2 (1)	1	48.977	-16.727	0.008
		20/08/2011	H1-3 (2)	6	48.978	-16.726	0.047
		07/08/2011	H1-4 (1)	3	48.977	-16.728	0.024
		08/08/2011	H1-5 (1)	1	48.979	-16.728	0.008
H2	4743	14/08/2011	H2-1 (1)	2	49.090	-16.316	0.016
		15/08/2011	H2-2 (1)	2	49.090	-16.314	0.016
		14/08/2011	H2-3 (2)	5	49.090	-16.314	0.039
		14/08/2011	H2-4 (2)	6	49.091	-16.313	0.047
		14/08/2011	H2-5 (1)	4	49.091	-16.315	0.031
H3	4618	17/08/2011	H3-1 (1)	2	48.956	-16.549	0.016
		17/08/2011	H3-2 (2)	6	48.958	-16.548	0.047
		18/08/2011	H3-3 (1)	2	48.956	-16.550	0.016
		18/08/2011	H3-4 (1)	3	48.957	-16.546	0.024
		18/08/2011	H3-5 (1)	3	48.956	-16.549	0.024
H4	4314	21/08/2011	H4-1 (1)	2	49.074	-16.260	0.016
		23/08/2011	H4-2 (1)	2	49.076	-16.264	0.016
		22/08/2011	H4-3 (1)	2	49.074	-16.260	0.016
		22/08/2011	H4-4 (1)	2	49.074	-16.264	0.016
		22/08/2011	H4-5 (2)	4	49.075	-16.263	0.031

2.2.2.2 Habitat heterogeneity data

To test if the physical habitat differed between abyssal hills and plains, environmental data (depth, slope as well as sediment particle size and total organic carbon) were collected. A hull-mounted Simrad EM12 hydrographic multibeam echo sounder was used to collect bathymetric data during the research cruise 158 on the RRS Charles Darwin in June 2004 (Lampitt, 2010). The slope associated to each site was obtained using photographic transect, bathymetric data and a native function in ArcMAP (v10.0, esri) using a 100 m buffer around each photographic transect (see details in Durden et al., 2015).

The sediment particle size was measured by laser diffraction using a Malvern Mastersizer following the procedure described in paragraph 2.2.1.2. The sediment was also analysed for total organic content using a Yanaco MT-5 CHN analyzer after removing carbonate by acidification of samples in ceramic sample boats with HCI vapour (method of Yamamuro and Kayanne, 1995). The enhanced bottom currents caused by elevated topography are expected to impact the sedimentation of organic material. The sediment %TOC is a direct measure of this effect on local resource availability.

2.2.2.3 Macrofauna processing and identification

The BH macrofauna cores were processed and identified as described in section 2.2.1.3.

2.2.3 Analytical approach

2.2.3.1 Within and surrounding a single hill (WH) habitat heterogeneity

The difference in sediment %sand between stations and between depth bands was tested with an ANalysis Of VAriance after arcsin transformation (ANOVA, Minitab v.17, Sokal and Rohlf, 2012). Correlation between the two physical variables (depth, %sand) was tested with a Spearman’s Rank correlation (r_s, Minitab v.17, Sokal and Rohlf, 2012).

The normalised environmental factors (depth, sediment %sand) were combined for multivariate analyses. An Euclidian ‘distance’ matrix was computed to create an environmental similarity matrix. The latter was tested for differences between stations and depth bands with an ANalysis Of SIMilarity (ANOSIM [R], Primer v.6, Clarke, 1993, Clarke and Gorley, 2006, 999 permutations employed).

The sediment size particle distributions were also used as multivariate data. The sediment similarity matrix was obtained with the DOMDIS routine (Primer v.6, Clarke, 1990) applied to the ranked cumulative sediment particle size distributions. The matrix was tested for differences between stations and depth bands with an ANOSIM.

2.2.3.2 Between and among hill (BH) habitat heterogeneity

The difference in depth and sediment %sand between sites and between abyssal hill and abyssal plain sites were tested with an ANOVA after arcsin transformation of the percent data. Similarly %TOC and slope were tested for differences between abyssal hill and abyssal plain sites. Correlation between the four physical variables (depth, slope, %sand, %TOC) was tested with a Spearman's Rank correlation.

The normalised environmental factors (depth, slope, sediment %sand, %TOC) were combined for multivariate analyses. An Euclidian 'distance' matrix was computed to create an environmental similarity matrix. The environmental similarity matrix represented the habitat heterogeneity and was tested for differences between abyssal hills plains with an ANOSIM.

The sediment similarity matrix was obtained with the DOMDIS routine applied to the ranked cumulative sediment particle size distributions. Difference in sediment particle size distribution between abyssal hill and abyssal plain sites was tested with an ANOSIM test.

2.2.3.3 Fauna within and surrounding a single hill (WH)

The fauna was investigated for differences within and surrounding a single hill and potential factors driving differences. Statistical analyses were conducted on three different data groupings: polychaete family (P), polychaete functional group (FG), and macrofauna (M). The total densities of polychaete and macrofauna (D_P for polychaetes, D_M for macrofauna) were standardised to unit area (ind.m^2) and log(x+1) transformed prior to statistical analyses. Data were checked for Normality using the Shapiro-Wilk normality test (Sokal and Rohlf, 2012). Differences in polychaete and macrofauna densities between depth bands were tested using an ANOVA with Tukey pairwise comparisons (Sokal and Rohlf, 2012). A General Linear Model analysis using depth bands as a replicated treatment (factor) and depth and %sand as continuous covariates was also conducted after log transformation of the continuous variables (GLM, Minitab v.17, Sokal and Rohlf, 2012). Diversities were assessed with estimated (rarefied) species richness (S_{est}), Chao1, the

Shannon's index, and Simpson's index (Magurran, 2004) using individual-based rarefaction (EstimateS, v.9.1.0, Colwell et al., 2012). Diversity of macrofauna taxa and polychaete families were respectively rarefied at 79 individuals and 35 individuals.

The P, FG, and M rank abundance distributions were obtained by ranking respective densities for each depth band (rank 1 being the most abundant). The dominant Ps, FGs and Ms were individually tested for density differences between depth bands using an ANOVA.

The assemblage composition was analysed using multivariate techniques. The Bray-Curtis similarity of the squared-root transformed density data was computed for P, FG, and M. Non-metric multi-dimensional scaling (MDS, Kruskal and Wish, 1978) was applied to examine the faunal similarity matrices. An ANOSIM was performed to test composition differences between depth bands.

The relationship between WH fauna and habitat heterogeneity was investigated both with univariate techniques as Spearman correlations between density data and physical variables (depth, sediment %sand) and with multivariate techniques. The relationships between faunal similarity matrices and the environmental Euclidian matrix were investigated using the RELATE routine (Mantel test, ρ, Primer v.6, Mantel, 1967). The relationships between faunal similarity matrices and the sediment similarity matrix were also investigated using the RELATE routine.

2.2.3.4 Fauna between and among hills (BH)

The fauna was investigated for differences between and among hill and for potential factors driving these differences. Statistical analyses were conducted on three different data groupings: P, FG and M. The total densities of polychaetes and macrofauna (D_P for polychaetes, D_M for macrofauna) were standardised to unit area (ind.m^2) and were log(x+1) transformed prior to statistical analyses. Data were checked for Normality using the Shapiro-Wilk normality test. Differences in polychaete and macrofauna densities between sites (P1, P3, P4, H1, H2, H3, H4) were tested using an ANOVA and differences between abyssal hill and plain sites were tested using a t-test. A General Linear Model analysis using site as a replicated treatment (factor) and depth and %sand as continuous covariates was also conducted after log transformation of the continuous variables.

Diversities were assessed with estimated (rarefied) species richness (S_{est}), an asymptotic richness estimator (Chao1), the Shannon's index, and Simpson's index using individual-based rarefaction. Diversity of macrofauna and polychaete families were respectively rarefied at: 1) 93 individuals for macrofauna and 45 individuals for polychaetes at site level; 2) 422 individuals for macrofauna and 174 individuals for polychaetes at abyssal hill/plain site level.

The P, FG, and M rank abundance distributions were obtained by ranking respective densities for abyssal plain and hill sites. The dominant polychaete families, FGs and macrofauna taxa were individually tested for density differences between abyssal hill and plain sites using a t-test

The assemblage composition at each site and between abyssal hill and plain sites was analysed using multivariate techniques. The Bray-Curtis similarity of the squared root transformed density data was computed for P, FG, M. 2d non-metric MDS were applied to examine the faunal similarity matrices and an ANOSIM was performed to test composition differences between abyssal hill and abyssal plain area.

The relationship between BH fauna and habitat heterogeneity was investigated both with univariate techniques as spearman correlations between density data and physical variables (depth, slope, sediment %sand, %TOC) and with multivariate techniques. The relationships between faunal similarity matrices and the environmental Euclidian matrix were investigated using the RELATE routine (Mantel test, ρ, Primer v.6, Mantel, 1967). The relationships between faunal similarity matrices and the sediment similarity matrix were also investigated using the RELATE routine.

2.3 Results

2.3.1 Habitat heterogeneity

2.3.1.1 Within and surrounding a single hill (WH) habitat heterogeneity

The WH sediment distributions were bimodal (Fig.2.3) with consistent separation between modes at 22.9 μm and peaks at approximately 4 and 200 μm, likely attributable to coccoliths and foraminiferan tests, respectively. The sediment %sand was significantly different between depth bands (ANOVA, F = 29.1, p = 0.001). The sediment %sand decreased from the top of the abyssal hill out onto the abyssal plain, apart from the depth band 4840-4790 m around the base of the abyssal hill (Fig. 2.3). Both variables, depth and %sand, were significantly correlated (r_s = -0.900, p = 0.037).

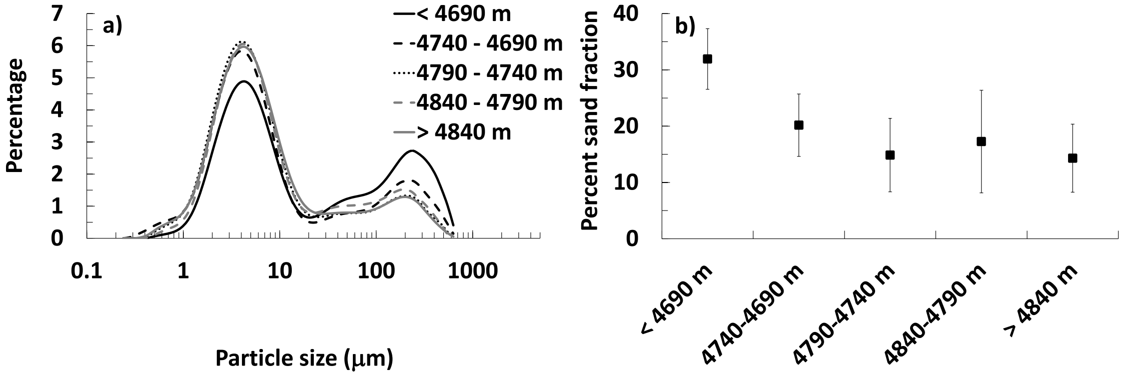

Figure 2.3 Within and surrounding a single hill (WH) sediment features (a) particle size distributions of surface sediments (0-15 cm) at each depth band with %sand increasing inversely with depth, (b) sediment %sand with standard deviation at each depth band with significant differences (< 4690 m different from 4740-4690 m/4840-4790 m, different from 4790-4740 m/> 4840 m).

The habitat heterogeneity (defined by the multivariate similarity matrix of environmental factors, i.e. all physical factors assessed simultaneously) were also significantly different between depth bands (ANOSIM, R = 0.749, p = 0.001). Overall, the sediment distributions were significantly different among depth bands (ANOSIM, R = 0.275, p = 0.010).

2.3.1.2 Between and among hill (BH) habitat heterogeneity

The BH sediment distributions were bimodal with peaks at approximately 4 and 200 μm, as observed in the WH study (Fig. 2.4). The sediment %sand was significantly different between sites (ANOVA, F = 41.14, p < 0.001). The depth, slope and %sand were significantly different between abyssal hill and plain sites (ANOVA, respectively F = 29.76, p < 0.001, F = 7.68, p = 0.039, and F = 8, p = 0.037). In particular, the sediment %sand was significantly greater on abyssal hills than on abyssal plain sites (Fig. 2.4) whereas the sediment total organic carbon content was higher on abyssal plains (37.0 ± 1.8%) than on abyssal hills (31.0 ± 3.6%, Fig. 2.4). All variables, depth, slope, %sand and %TOC were correlated (depth-%sand: r_s = -0.929, p = 0.003; depth-%TOC: r_s = 0.821, p = 0.023; %sand-%TOC: r_s = -0.893, p = 0.007; slope-depth: r_s = -0.857, p = 0.014; slope-%sand: r_s = 0.857, p = 0.014; slope-%TOC: r_s = -0.964, p < 0.001).

The habitat heterogeneity (depth, slope, sediment %sand, sediment %TOC simultaneously assessed) was also significantly different between abyssal hill and plain sites (R = 0.537, p = 0.048).

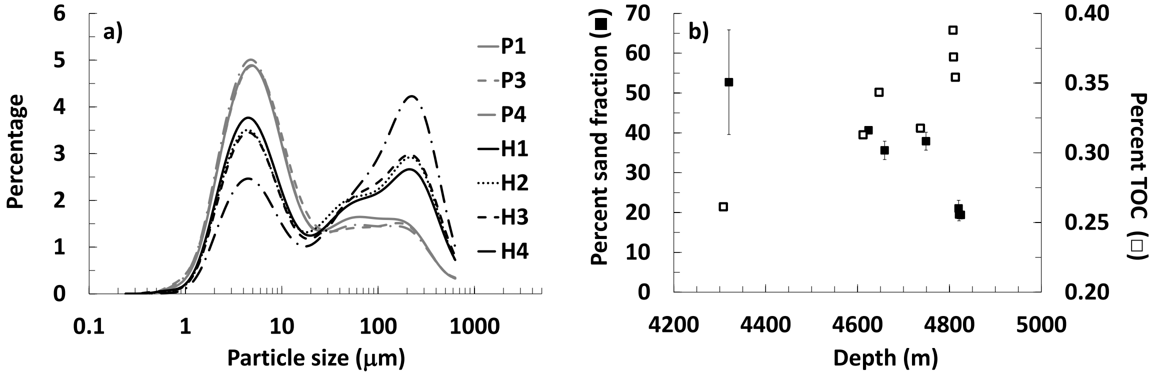

Figure 2.4 Between and among hill (BH) sediment features (a) particle size distributions of surface sediments (0-15 cm) at each site with abyssal hill sites in black and abyssal plain site in grey. The percent %mud (< 63 μm size fraction) increased with depth whereas the %sand decreased with depth, (b) sediment %sand with standard deviation (■) and %TOC (□) *versus* depth. Note that these variables have an inverse relationship with depth and were significantly different between abyssal hill and plain sites.

Overall, the sediment distributions were significantly different between abyssal hill and plain sites (ANOSIM, R = 0.944, p = 0.029). The difference in sediment particle size distributions was greater in BH than WH (ANOSIM, R = 0.944, p = 0.029 *vs.* R = 0.418, p = 0.001).

2.3.2 Macrofauna patterns

2.3.2.1 Macrofauna within and surrounding a single hill (WH)

Overall 725 specimens were collected among which 320 were polychaetes (see Appendix B.1). The macrofauna total densities were significantly different among the sampled stations (ANOVA, F = 2.09, p = 0.012) and among depth bands (ANOVA, F = 2.79, p = 0.031, Table 2.4) with higher density in > 4840 m depth band and lower density in 4840-4790 m depth band. The General Linear Model detected significant (p < 0.05) effects for depth band and %sand for the macrofauna density. By contrast, polychaete total densities were not significantly different between sampled stations or depth bands (ANOVA, F < 2, p > 0.05).

Seventeen macrofauna taxa among which were 26 polychaete families were collected. In terms of diversity, no index was significantly different between depth bands for macrofauna or polychaetes (Table 2.4, Appendix B.2) except in terms of polychaete family Inverse Simpson's index that was lower at the 4840-4790 m depth band suggesting an increase in dominance.

Table 2.4 Within and surrounding a single hill (WH) densities of polychaetes (D_P) and macrofauna (D_M), number of polychaete family (S_P) and macrofauna taxa (S_M), Inverse Simpson's Index of polychaete family (I_P) and macrofauna taxa and Inverse Simpson Index (I_M) with standard deviations related to depth bands. Densities are given in ind.m^{-2}. Diversity indices were estimated using individual-based rarefaction with 79 (for macrofauna) and with 35 (for polychaete family) individuals.

Grouping	D_P	S_P	I_P	D_M	S_M	I_M
< 4690 m	371.1 ± 92.5	14.7 ± 1.9	7.15 ± 1.03	935.1 ± 71.9	21.1 ± 2.5	6.66 ± 0.89
4740-4690 m	344.3 ± 85.8	12.5 ± 2.7	6.10 ± 1.03	760.6 ± 75.4	19.9 ± 2.8	7.29 ± 0.91
4790-4740 m	377.7 ± 104.8	12.9 ± 2.2	5.43 ± 0.73	952.9 ± 55.7	20.9 ± 2.8	6.44 ± 0.86
4840-4790 m	307.8 ± 83.1	10.0 ± 1.9	3.75 ± 0.16	630.0 ± 90.8	18.0 ± 2.6	6.30 ± 0.12
> 4840 m	403.5 ± 76.2	13.4 ± 2.7	6.11 ± 1.05	1054.1 ± 66.2	23.1 ± 2.3	7.60 ± 1.36

The rank abundance distributions by density had similar level and shape across all depth bands (Fig. 2.5). In terms of macrofaunal taxa, Haparcticoida occupied rank one at all depths whereas Isopoda, Cirratulidae and Spionidae switched between rank 2 and 4. In terms of polychaetes, the Cirratulidae dominated the deeper depths (4790-4740 m, 4840-4790 m and > 4840 m) whereas the Spionidae dominated the shallower depths (< 4690 m, 4740-4690 m, Appendix B.3-B.4). Note that at all depths, Spionidae and Cirratulidae were close in density except at 4840-4790 m where Cirratulidae density was three times higher. SDT was the dominant functional group at the top and base of the hill (< 4690 m, 4740-4690 and > 4840 m) whereas SMT was dominant at the intermediate depths (4790-4740 m and 4840-4790 m).

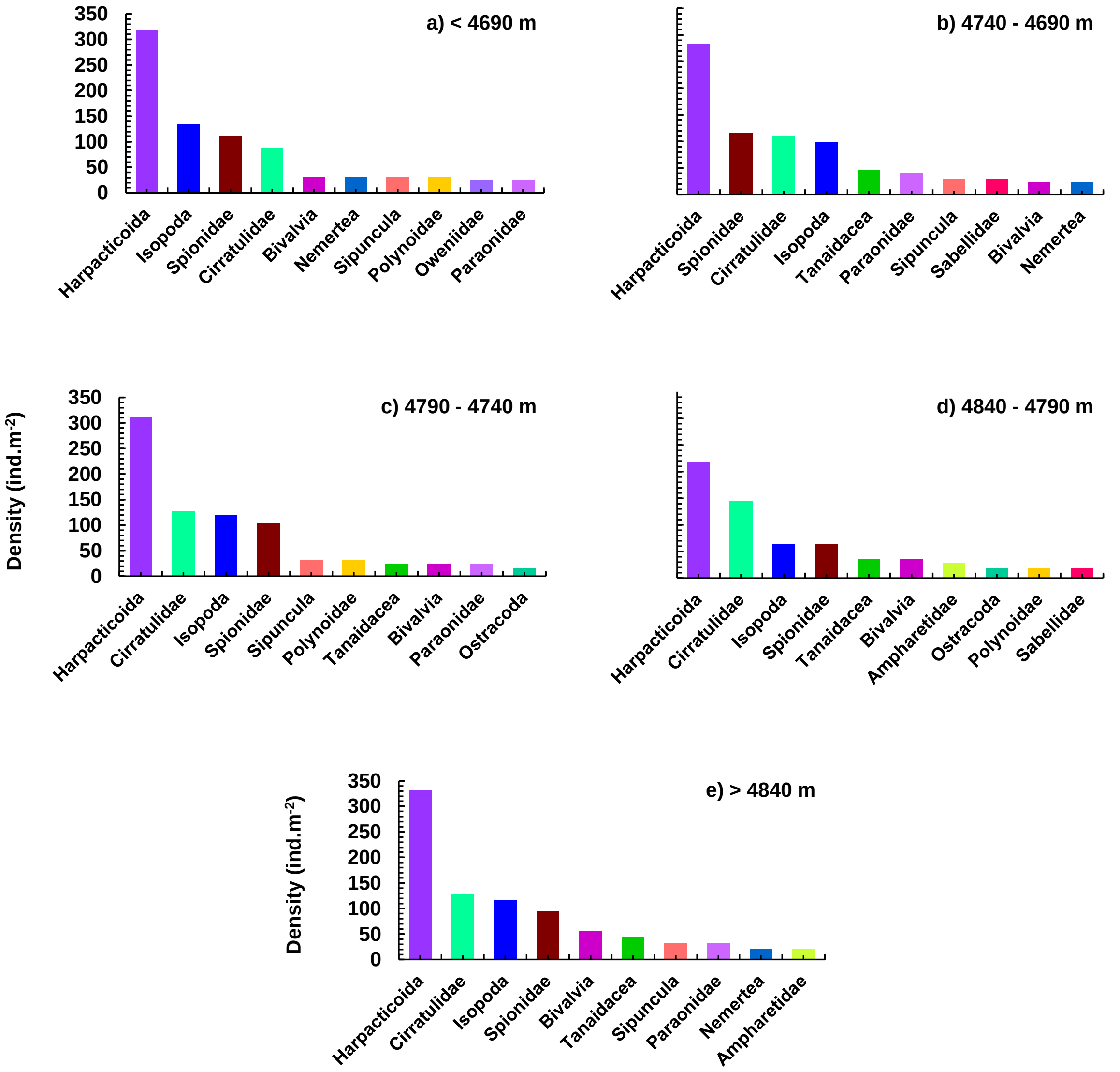

Figure 2.5 Within and surrounding a single hill (WH) rank abundance distribution for macrofauna taxa at each depth band. The most dominant taxa (rank 1) are on the left side and the 10$^{\text{Th}}$ dominant taxa (rank 10) are on the right side. Note that the same four taxa dominated the assemblages at all depths. Cirratulidae and Spionidae had similar density levels except in the depth band 4840-4790 m.

Overall, there was no statistical difference in macrofauna/polychaete composition similarity matrix by sampled sites or by depth bands (ANOSIM, $R < 0.02$, $p > 0.05$, Appendix B.5-B.7).

In terms of relationship between the fauna and the physical environment, there was no significant correlation between the total macrofauna/polychaete densities and depth or %sand ($r_s < 0.2$, $p > 0.05$). Some taxa were significantly correlated with the sediment %sand by depth bands but, none were among the most abundant (Appendix B.8). No correlation was found either for the faunal similarity matrices (macrofauna and polychaetes) and the sediment similarity matrix or the environmental factor similarity matrix (RELATE, $\rho < 0.5$, $p > 0.05$).

2.3.2.2 Macrofauna between and among hills (BH)

Overall 917 specimens were collected among which 453 were polychaetes (see Appendix B.1). Macrofauna total densities were not significantly different between sites (ANOVA, $F = 0.63$, $p = 0.707$) or between abyssal hill and plain sites ($t = 0.46$, $p = 0.652$, see Table 2.5). Similar results were found for the polychaetes between sites (ANOVA, $F = 1.37$, $p = 0.262$) or between abyssal hill and plain sites ($t = 1.65$, $p = 0.109$, see Table 2.5). The General Linear Model detected no significant effects for site, depth and %sand on macrofauna or polychaete total density.

Nineteen macrofauna taxa among which were 31 polychaete families were collected. On abyssal hills, 14 macrofauna taxa were recorded with four only found on hills and 28 polychaete families were recorded with five only found on hills. On abyssal plains, 14 macrofauna taxa were recorded with three only found at plain sites and 26 polychaete families were recorded with three only found at plain sites. In terms of diversity, no index was significantly different between the abyssal hill and plain sites either for macrofauna or polychaetes (ANOVA, $p > 0.05$, Appendix B.9).

Table 2.5 Between and among hill (BH) densities of polychaetes (D_P) and macrofauna (D_M), number of polychaete family (S_P) and macrofauna taxa (S_M), Inverse Simpson's Index of polychaete family (I_P) and macrofauna taxa and Inverse Simpson Index (I_M) with standard deviations related to sites and abyssal plain/hill sites. Densities are given in ind.m^{-2}. Diversity indices were estimated using individual-based rarefaction with 93 (for the site analysis) and 422 (for the hill/plain analysis) individuals for macrofauna and with 45 (for the site analysis) and 174 (for the hill/plain analysis) individuals for polychaete family.

Grouping	D_P	S_P	I_P	D_M	S_M	I_M
P1	436.5 ± 126.6	17.4 ± 2.7	6.52 ± 0.97	899 ± 473	27.1 ± 3.0	9.92 ± 0.82
P3	538.0 ±280.5	15.7 ± 1.1	7.33 ± 0.82	962 ± 527	21.4 ± 1.6	7.35 ± 0.78
P4	458.6 ± 208.3	16.6 ± 2.6	5.79 ± 0.24	955 ± 414	21.9 ± 2.4	5.88 ± 0.49
H1	617.8 ± 148.7	14.0 ± 2.7	7.33 ± 0.55	1121 ± 301	22.4 ± 3.2	10.77 ± 0.37
H2	369.4 ± 172.4	13.8 ± 1.4	5.40 ± 0.64	742 ± 248	22.5 ± 1.8	9.15 ± 0.59
H3	500.6 ± 155.7	17.1 ± 2.4	7.66 ± 0.51	1122 ± 229	24.4 ± 2.7	8.87 ± 0.47
H4	317.2 ± 119.2	16.4 ± 2.3	4.87 ± 0.32	859 ± 409	24.8 ± 2.8	7.34 ± 0.20
Plain sites	513.0 ± 199.0	25.0 ± 1.9	7.02 ± 0.09	948 ± 410	39.0 ± 2.1	7.83 ± 0.05
Hill sites	396.0 ± 161.0	25.9 ± 1.6	6.82 ± 0.35	908 ± 328	38.9 ± 2.1	9.84 ± 0.06

The rank abundance distributions had similar levels of density but differences in shape between hill and plain sites (Fig. 2.6). In terms of macrofaunal taxa, Haparcticoida occupied rank one and Isopoda rank 3 at both hill and plain sites. In terms of polychaetes, the Cirratulidae dominated on hill sites (rank 2) and the Spionidae on plain sites (rank 2). Overall, the Spionidae and Cirratulidae were the two most abundant families on both plains and hills (Fig. 2.6). Surface deposit feeders (SDT, SMT) dominated both abyssal hills and plains but the proportion of SMT, 'mobile' polychaetes, compared to SDT, 'sedentary' polychaetes was higher on hills (Fig. 2.6) with the ratio SMT:SDT being marginally different between abyssal hill and plain sites ($t = 1.82$, $p = 0.079$).

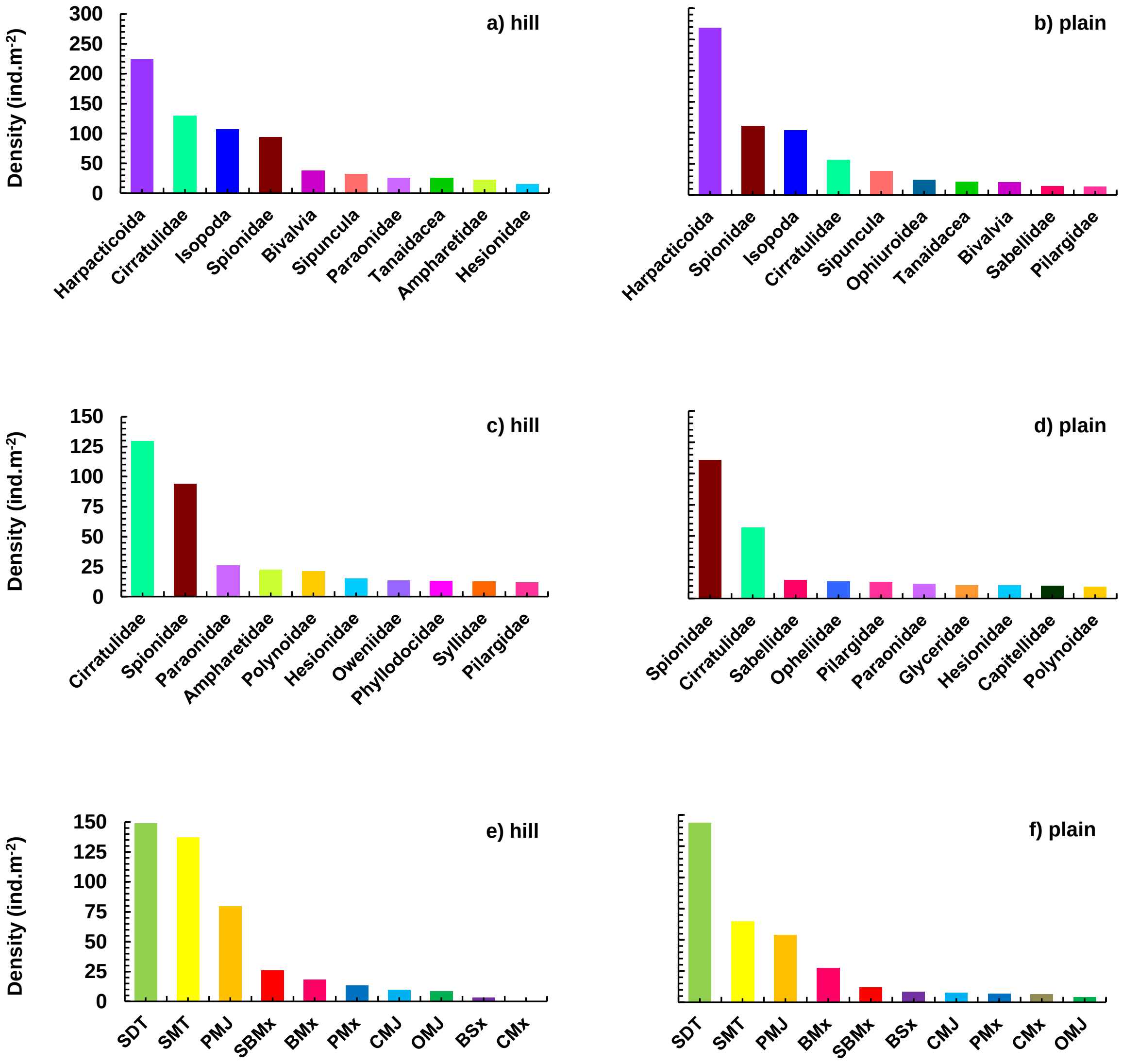

Figure 2.6 Between and among hill (BH) rank distributions, top ten taxa for abyssal hill sites on the left and abyssal plain sites on the right for (a-b) macrofauna taxa. Macrofauna RADs had similar shape with the plain RAD rank 1 displaying higher density than hill RAD rank 1, (c-d) polychaete families, with Spionidae and Cirratulidae switching in dominance between hill and plain sites, (e-f) polychaete functional groups with the plain sites dominated by SDT and the hill sites dominated by SDT and SMT. The most dominant taxa (rank 1) are on the left side and the 10th dominant taxa (rank 10) are on the right side.

Overall, there was no significant difference in macrofauna/polychaete composition similarity matrix between sites or between abyssal hill and plain sites (ANOSIM, $R < 0.1$, $p > 0.050$, Fig. 2.7).

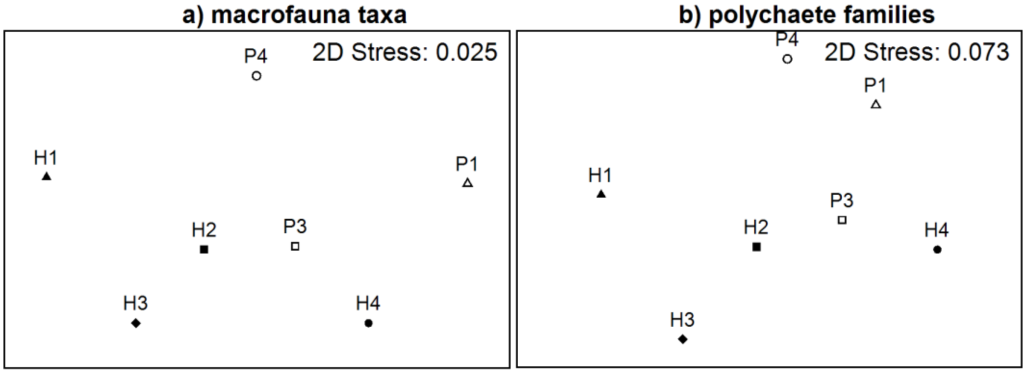

Figure 2.7 Between and among hill (BH) multi-dimensional scaling ordination of (a) macrofauna taxa composition, (b) polychaete family composition. Note that the hill and plain sites are not separated.

In terms of relationships between the fauna and the physical environment, the total macrofauna density was not correlated to any factor whereas the polychaete total density was correlated to %sand ($r_s = 0.378$, $p = 0.025$ by deployment) and to %TOC ($r_s = -0.786$, $p = 0.036$ by site). Only some polychaete families and functional groups were significantly correlated with sediment %sand and %TOC (Appendix B.10). In particular, the Cirratulidae family and the SMT functional group were positively correlated with sediment %sand and negatively with %TOC. By contrast, the Spionidae were negatively correlated to sediment %sand, but positively correlated to %TOC.

Significant relationships were found between the sediment particle size distribution similarity matrix and: 1) the macrofaunal composition similarity matrix (RELATE, $\rho = 0.280$, $p = 0.048$); 2) the polychaete family composition similarity matrix (RELATE, $\rho = 0.346$, $p = 0.019$). However, there was no significant relationship between the macrofauna/polychaete composition similarity matrix and the similarity matrix of environmental factors (RELATE, $\rho < 0.1$, $p > 0.050$).

2.4 Discussion

2.4.1 Macrofauna assemblage in relation to abyssal hills

The physical differences between and among hills, in particular in relation to sediment character, was related to macrofauna and polychaete assemblages. The compositions of the latter were related to the sediment particle size distribution. However, these changes in composition were not accompanied by changes in macrofauna/polychaete density or diversity, although polychaete total density was correlated to %sand and %TOC of sediment. Durden et al. (2015) also reported differences in megafaunal composition in relation to sediment features between abyssal hill and plain sites. However, megafauna was also significantly different in terms of biomass and diversity (albeit not total density).

The lack of difference for BH macrofauna/polychaete density/diversity may be real or apparent due to several factors: 1) the number of macrofaunal specimens per core was low and variable, which greatly lowered the power of the statistical tests. The low number of specimens was related to a small total area sampled. Despite an intensive megacoring programme (48 megacorer deployments for a total of 130 cores sampled) during the BH analysis, the total sampled area for macrofauna was about 1 m^2. In proportion, this area is much lower than the one studied for megafauna. Small sample sizes under-sample rare species leading to a likely underestimation of differences among sites (Cao et al., 1998). Sampling abyssal macrofauna to obtain enough individuals for robust statistical analyses remains a challenge (Dr. Billett, pers. com. see also Blomqvist, 1991, Gage, 1996, 2000, Levin et al., 2001, Rumohr et al., 2001, Hilbig, 2004, Magurran, 2004). 2) The classification of sites as abyssal hill or plain may be too simplistic. For example, the observations of the cores from the three plain sites, P1, P3 and P4 suggested that different physical disturbances (resulting from sediment movements due to local hydrodynamics) occurred at each site. P1 and P4 cores displayed dark bands and sediment stratification whereas P3 cores did not. The latter differed possibly due to the run out of slope failures from the adjacent steep hill (Durden et al., 2015). 3) The detailed study of macrofauna on one hill (H3, WH analysis) showed that the total macrofauna density and polychaete family diversity varied along the hill, with higher density in > 4840 m depth band and lower density in the 4840-4790 m depth band. So, within hill spatial heterogeneity may increase the data variance between hill sites making the distinction between hill and plain less clear (an issue that the present data did not allow to properly investigate).

Overall the presence of abyssal hills still increased the number of macrofauna taxa found in the PAP area. Five polychaete families Chaetopteridae, Euphrosynidae, Onuphidae, Poecilochaetidae and Trichobranchidae, had not been sampled on the Porcupine Abyssal Plain (PAP) before. So, abyssal benthic spatial variations as well as diversity of macrofauna/polychaete are likely to be greater than hitherto known as abyssal hills may be the most common topographic features on Earth (Macdonald et al., 1996, Wessel et al., 2010, Turnewitsch et al., 2013). As noted with seamounts (Bongiorni et al., 2013, Chivers et al., 2013), abyssal hills are not more diverse than surrounding areas but contribute to an enhanced regional biodiversity.

2.4.2 Relationship between macrofauna and sediment particle size

The link between polychaete and macrofauna compositions and the sediment particle size distribution suggests that they are affected by common processes (BH analysis). The megafauna assemblage was also linked to the sediment coarse particle fraction (Durden et al., 2015). Overall, the sediment particle size has been frequently reported as correlating with macrofauna distribution (Levin et al., 2001, Ellingsen, 2002). The species diversity increases with sediment particle size diversity (Etter and Grassle, 1992). Three non-mutually exclusive scenarios have been proposed: 1) the sediment particle size directly influences the macrofauna distribution. So far, evidence of such a scenario is rare (see review in Snelgrove and Butman, 1994). 2) The macrofauna diversity enhances the sediment particle size diversity via feeding and bioturbation activities (Rhoads and Young, 1970, Rhoads, 1974, Jumars et al., 1981, 1990, Luckenbach et al., 1988). Some species have been shown to ingest or retain specific particle sizes during feeding modifying the availability of this particle size for other fauna (Self and Jumars, 1988, Taghon, 1982). 3) Other factors/processes control both faunal and sediment distributions. The latter hypothesis was favoured by Snelgrove and Butman (1994) as the sediment-fauna relationships are sometimes weak or variable supporting the hypothesis that other correlates may be more important.

Food availability (%TOC) was correlated to sediment particle size distribution (%sand) among and between hills (BH analysis) suggesting that the same local processes may drive both variables. The percent TOC was significantly different between abyssal hill and plain sites with higher values occurring at sites of lower %sand. Polychaete total density was correlated to both %TOC and %sand but not macrofauna. However, TOC is not considered to be the best estimate of food available to the benthos as the organic compounds resistant to biological degradation accumulate in sediments (Danovaro et al., 2001). Future analyses, such as sediment lipid content, would be better in determining nutrient availability and its influence on fauna distributions. Organic matter quality variation has been related to macrofauna composition variation in seamounts (Bongiorni et al., 2013)

2.4.3 Influence of local hydrodynamic processes

At PAP, the flow conditions may be the primary factor influencing the sedimentary conditions and food availability. The increased %sand fraction and lower %TOC at hill compared to plain sites are consistent with the elevated topography of abyssal hills causing enhanced bottom currents, impacting the sedimentation of both inorganic (mud/ sand, Turnewitsch et al., 2004) and organic (food, bacteria, larvae) material (Rhoads, 1974, Levin and Thomas, 1989, Klein and Mittelstaetd, 1992, Snelgrove and Butman, 1994, Consalvey et al., 2010, Lavelle and Mohn, 2010). Based on observations of sediment cores, Durden et al. (2015) highlighted the most likely hydrodynamical processes generating differences in sediment particle size distributions between hill and plain sites. On abyssal plains, contemporary currents and historical turbidity events might be the dominant hydrodynamical processes while on abyssal hills, enhanced flow velocities lead to deposition and sorting of sediment particles with subsequent erosion. However, fluid-flow interaction with hills are more complex as several processes may interact to generate the distribution of sediments and as the geometries of abyssal hills have been shown to generate asymmetrical flow fields around these topographic features, a phenomenon also observed on larger seamounts (Turnewitsch et al., 2013). The unique geometry of each hill implies uniqueness of hydrodynamic processes and sediment conditions generating spatial heterogeneity in abyssal sediment at scale of 0.1-10s km.

At the scale of one hill, the within and surrounding a single hill (WH) analysis showed that different parts of a hill were likely affected by different hydrodynamic activities. As observed within single seamounts (Levin and Nitrouer, 1987, Cacchione et al., 1988), contrasting hydrodynamics and sedimentary settings are found within a single hill. In WH analysis, the sediment %sand diminished from the summit of the hill to the abyssal plain except at the depth band 4840-4790 m that had higher value than the depth band 4790-4740 m. The greater sediment %sand at 4840-4790 m suggests a higher current activity at this depth as observed on some seamounts with moats forming around their base (Roberts et al., 1974). However, phytodetritus was observed in the 4840-4790 m depth band. At this depth, the currents may be less strong than at the summit and remove finer sediment particles but not fully re-suspend phytodetritus (current speeds of approximately 6-8 cm s^{-1} at 1 m above the seafloor can be sufficient to re-suspend phytodetritus, Lampitt, 1985, Klein, 1987). The review of Turnewitsch et al. (2013) also highlighted that variability in both current speed and direction was important controls of the sediment dynamics. Overall, topographically-induced currents along hill slope seemed to modulate not only the sediment particle size distribution but also (sometimes differentially) the phytodetritus capture rate of the seafloor.

Topographically-induced currents modulating sediment particle size distribution may also directly influence the macrofauna. Flow conditions have been shown to be important in structuring communities in canyons (McClain and Barry, 2010, Paterson et al., 2011) and seamounts (Levin and Thomas, 1989, Levin et al., 1994, Chivers et al., 2013). In particular, Levin and Thomas (1989) found that infaunal lifestyle reflected the variations in hydrodynamic conditions. Cirratulidae and Spionidae dominated polychaetes across PAP abyssal hill and plain sites, often at similar densities (note that both families are often among the dominant families on seamounts, Bongiorni et al., 2013, Chivers et al., 2013). Both Cirratulidae and Spionidae are opportunistic deposit feeders and have been shown to select for particle size (Shimeta, 1996, Shull and Yasuda, 2001). Spionidae tend to select smaller size particles during feeding (Luckenbach et al., 1988, Shimeta, 1996, Hentschel, 1996, 1998, Shimeta and Koehl, 1997, Bock and Miller, 1999, Guieb et al., 2004) according to the optimal foraging theory (Taghon et al., 1978, Taghon, 1982, Self and Jumars, 1988). In the between and among hill analysis, Spionidae were negatively correlated to the coarse particle fraction whereas Cirratulidae were positively correlated. Preference in particle size has been thought to be an important resource partitioning mechanism among deep-sea deposit feeders (Jumars et al., 1990, Etter and Grassle, 1992, Hentschel, 1996, Paterson et al., 2006). Other differences in terms of burrowing ability (Levin and Thomas, 1989) and degree of mobility (e.g. enhanced particle size selectivity in deposit feeders with greater mobility in unstable sediment conditions, Levin et al., 1994, Bongiorni et al., 2013) may explain the local dominance of Spionidae/Cirratulidae. Species-level studies may help to better understand how the Cirratulidae and Spionidae modulate their responses in relation to flow conditions. In variable currents, spionid species have been shown to switch between deposit and suspension feeding (Taghon and Green, 1992, Hentschel, 1996, 1998, 2004). Taghon and Greene (1992) showed that some species of Spionidae favoured deposit feeding in low energetic flows, while others favoured suspension feeding in high energy flows. Species able to deposit and suspension feed likely have an advantage over strictly suspension-feeding species. Species-level studies may reveal that different Spionidae and Cirratulidae species inhabit hill and plain sites.

2.5 Conclusions

Variation in depth and sediment particle size distribution linked to abyssal hills created spatial heterogeneity among the surrounding abyssal plains. The within and surrounding single abyssal hill analysis showed that macrofauna density was significantly different between depth bands. The larger scale analysis between and among hill showed that macrofauna and polychaete assemblage compositions were related to the sediment particle size distribution. Historical and contemporary differences in local flow conditions may be the primary factor influencing sediment particle size distribution (%sand), food availability and therefore the fauna. Overall polychaetes and macrofauna may be more spatially variable than previously thought in abyssal areas when considering that abyssal hills might be one of the most common topographic features on Earth. Future work should now: 1) study the variation in macrofauna biomass to compare with the megafauna biomass spatial variations; 2) determine the flow conditions around each PAP abyssal hill and their variabilities; 3) modify macrofauna sampling to collect more specimens and improve the power of statistical tests.

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Chapter 3

Inter-annual dynamics of abyssal polychaete communities in the North East Pacific and North East Atlantic – A family-level study

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Abstract

Characterising how deep-sea communities change on contemporary time scales and understanding underlying ecosystem processes has become important under changing climate and the rise in the exploitation of deep-sea resources. However, little is known about these dynamics and processes. Long-term observations from which inter-annual variations can be detected are scarce in the deep sea. This study examines inter-annual changes in density, family richness and evenness, family and functional group rank abundance distributions of infaunal polychaetes at two abyssal stations in the North East Pacific (Station M, 1991 to 2005) and in the North East Atlantic (Porcupine Abyssal Plain, 1991 to 1999). The two long-term data sets were used to investigate not only if polychaete assemblage structure and composition varied at inter-annual scales in terms of diversity and rank abundance distributions but also if any changes were related to previous observations in megafauna and environmental factors at each locality. The polychaete assemblage structure at each locality was analysed using univariate statistics as well as multivariate ordination techniques based on Bray Curtis similarity of the yearly family density. Sub-surface deposit feeders, such as Paraonidae, dominated the North East Pacific, whereas surface deposit feeders, such as Cirratulidae, dominated the North East Atlantic. Both stations showed inter-annual variations in density, family evenness and rank abundance distributions. The greatest changes occurred in 1998 in both time series when polychaete densities peaked, and switches in the rank abundance of the most abundant families and functional groups took place. Inter-annual variations in the polychaete assemblage were correlated with a limited number of holothurian species changes, but no correlation was found with particulate organic matter flux or climate indices. Ecological and environmental factors behind the family-level changes remain elusive. Overall, changes in the dominance of functional groups imply changes in abyssal ecosystem functioning with potential consequences on carbon cycling at the seabed.

3.1 Introduction

Understanding temporal variations in deep-sea system is becoming more important because of the increasing exploitation of deep-sea resources such as fisheries, hydrocarbons and minerals (Glover and Smith, 2003, Thiel, 2003). In addition, global warming is likely to impact ocean conditions with consequences on primary and export of that production to the deep ocean (Bopp et al., 2005, Sarmiento and Gruber, 2006, Richardson, 2008, Steinarcher et al., 2010). Most deep-sea fauna depend on such export production as sinking particulate organic carbon (POC) flux for food through pelagic-benthic coupling (Smith, 1987). In a food-limited environment, such as the deep sea, the supply of food is important in structuring deep-sea communities (Billett, 1991) and has links to many long-term carbon processes such as bioturbation, remineralisation, and burial (Smith et al., 1997, Witte and Pfannkuche, 2000, Bett et al., 2001, Smith et al., 2001, Ruhl et al., 2008, Smith et al., 2009). Characterising deep-sea system temporal variations is important to assess how ecosystem processes are linked to climatic variations, stochastic events and long-term trends (Smith et al., 2009, Glover et al., 2010). In recent years, significant inter-annual changes have been found in abyssal macro-infaunal communities in the North-East Pacific (Ruhl et al., 2008) and North-East Atlantic (Soto et al., 2010), including changes in polychaete densities, the dominant macrofaunal taxon in many areas of the ocean. In order to achieve a mechanistic understanding of processes shaping abyssal communities in time, the inter-annual variations of macrofauna assemblage structure defined as density, family richness, evenness, family and functional group (FG) compositions have been characterised.

To date, only two abyssal (> 4,000 m) soft-bottom habitats have been studied for a period greater than 20 years: Station M (Sta. M) in the North East Pacific and the Porcupine Abyssal Plain Sustained Observatory (PAP) in the North East Atlantic. Previous research has characterised pelagic-benthic coupling and abyssal fauna ecology, especially in terms of temporal patterns (Smith and Druffel, 1998, Billett and Rice, 2001, Lampitt et al., 2010a). Results from sediment traps have shown that POC flux has intra- and inter-annual variations in quantity and quality at both stations (Baldwin et al., 1998, Smith et al., 2006, Lampitt et al., 2010b). Climate has been proposed as a key factor generating inter-annual variations in POC flux, in particular the variations of the El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO). Changes in POC flux at Sta. M were significantly and positively correlated with the North Oscillation Index (NOI, an ENSO indicator) where changes in POC flux lagged NOI variations by 6 months. Similar correlations also found that POC flux at PAP lagged variations in the NAO by 5 months (Smith et al., 2006). At Sta. M, POC flux variations appeared to impact megafauna species in different ways: some increased in density during periods of high food supply whereas others decreased. The most striking examples include the holothurians *Elpidia minutissima,* the echinoid *Echinocrepis rostrata* as well as less dominant species like holothurians *Scotoplanes globosa* a at Sta. M (Ruhl and Smith, 2004). At PAP, the densities of the holothurians *Amperima rosea*, *Ellipinion molle,* and the ophiuroid *Ophiocten hastatum* varied by several orders of magnitude between 1989 and 2005 (Billett et al., 2010, Bett et al., 2001).

Less is known about sediment macrofauna assemblage temporal variations. From 1989 to 1998, Ruhl et al. (2008) found significant correlations between POC flux, the NOI and some macrofauna phyla densities at monthly and inter-annual scales at Sta. M. At PAP, during the first *'Amperima* Event' (1996-1998), macrofauna also displayed taxon-specific temporal variations in density (Galéron et al., 2001). Focusing on infaunal polychaetes, Soto et al. (2010) showed that density and total family number changed between 1989-1994 and 1996-1998, the latter period coinciding with the first *'Amperima* Event'. *In situ* enrichment experiments conducted at Sta. M and PAP have shown that macrofauna can ingest carbon quickly and mix it into deeper sediment layers (Aberle and Witte, 2003, Sweetman and Witte, 2008). Therefore, macrofauna temporal variations could provide important insights in assessing deep-sea carbon flow dynamics (Ruhl et al., 2008). However, a better mechanistic understanding of macrofauna inter-annual variations is needed to make such insights.

Examining macrofauna assemblage structure variation at a finer taxonomic resolution than has been done previously will provide greater knowledge of the functional role of macrofauna at Sta. M and PAP. Intra-annual variations in POC flux are related to seasonality with both stations located at temperate latitudes, where seasonality influences food quantity and quality. While there is evidence to suggest that intra-annual changes in polychaete assemblage structure and composition occur (e.g. Drazen et al., 1998), our study focuses on longer term change. In this study, polychaetes were examined at the family-level because: 1) polychaetes dominate a majority of deep-benthic soft-bottom macrofaunal communities in terms of density and species number (Olsgard et al., 2003, Paterson et al., 2009); 2) few polychaete families have been reported as being exclusively abyssal and those families have apparently limited adaptations compared to shallow-water forms (Glover, 2000, Paterson et al., 2009); 3) polychaetes have varied life-histories and perform important ecological functions such as sediment reworking, bioturbation and carbon recycling (Rouse and Pleijel, 2001, Olsgard et al., 2003); 4) polychaetes are clearly responsive to changes in organic matter supply (*e.g.* Ruhl et al., 2008, Soto et al., 2010).

In addition to finer taxonomic level, a better characterisation of Sta. M and PAP macrofauna assemblage inter-annual variations requires the use of various ecological descriptors. Based on niche theories, Rank Abundance Distribution (RAD) provides a useful way to describe resource division among a community (MacArthur, 1957, Hubbell, 1979, Magurran, 2004). In time series research, the investigation of RAD variation can facilitate mechanistic insights into community inter-annual variations. Analysing switches in rank composition over time can investigate the potential role of biological or environmental processes in community temporal variations (Thibault et al., 2004, Magurran, 2007, Ruhl, 2008). When used with more classical indexes such as density, richness and evenness, RADs can provide an informative description of change (Magurran and McGill, 2011). Ruhl (2008) used temporal RAD analyses to show that benthic community-level megafauna changes at Sta. M from 1989 to 2004 were modulated by climate-driven resource variations rather than random ecological drift.

This study examines inter-annual variations in polychaete density, family richness and evenness, family RAD (RAD_F) and functional group RAD (RAD_G) at Sta. M from 1991 to 2005 and PAP from 1991 to 1999. Using the two long time-series polychaete data sets, three main questions were addressed: 1) Did polychaete assemblage structure and composition change at inter-annual scales in terms of diversity both as family richness and as Pielou’s Evenness Index? 2) Did polychaete assemblage structure and composition change in terms of RAD_F and RAD_G at inter-annual scales? 3) Did inter-annual changes in polychaete family assemblage composition or structure relate to previous observations in megafauna and environmental factors at each locality?

3.2 Materials and Methods

3.2.1 Study areas and macrofauna sampling

From 1991 to 2005, twenty-two of the research cruises to Sta. M (50˚00 N, 123˚00 W, in the North East Pacific, 4100 m depth, see details in Smith and Druffel, 1998) included macrofauna sampling using a Free-Vehicle Grab Respirometer (FVGR, Smith et al., 2001). The FVGR is a sampling system comprised of four 413-cm^2 grabs separated by 25 cm (square design) collecting the top 15 cm of sediment (Table 3.1).

Table 3.1 Stations, dates, number of chamber grab and drops (Sta. M) or box-corer (PAP) and locations of macrofauna samplings at Sta. M and PAP.

Station	Year	Month	Chamber grab (drop) or **Box-corer**	Latitude ˚N	Longitude ˚W
Sta. M	1991	February	1 (1)	34.84	122.93
		June	7 (2)	34.90	123.05
		July	2 (2)	34.89	123.07
		October	3 (1)	34.88	123.11
	1992	February	5 (2)	34.88	123.12
		June	5 (2)	34.91	123.11
		July	3 (1)	34.78	122.95
		October	6 (2)	34.85	123.15
	1993	February	3 (1)	34.79	122.92
		July	3 (1)	34.82	123.07
		November	5 (2)	34.80	122.93
	1994	February	2 (2)	34.78	122.92
	1995	February	5 (2)	34.93	123.12
		June	1 (1)	34.95	123.13
	1996	February	4 (2)	34.72	122.98
		June	3 (1)	34.68	122.94
		October	5 (2)	34.69	122.90
	1998	April	2 (1)	34.93	123.03
		August	3 (2)	34.78	123.03
		December	2 (1)	34.78	123.00
	2005	February	3 (1)	34.853	123.20
		June	3 (1)	34.93	123.25
PAP	1991	May	**6**	48.85	16.50
	1994	April	**4**	41.85	16.50
	1996	September	**7**	48.85	16.48
	1997	March	**6**	48.83	16.50
		July	**5**	48.83	16.48
	1998	March	**2**	48.84	16.49
		September	**3**	48.83	16.50
	1999	May	**3**		

After recovery, material was sieved through a 300 µm mesh and preserved in 10% borate-buffered formalin solution (Drazen et al., 1998). While FVGR samples were collected from 1989-1990, these were no longer available for further analysis.

From 1991 to 1999, ten research cruises to PAP, (48˚ 50 N, 16˚ 30 W, in the North East Atlantic, 4850 m depth, Billett and Rice, 2001) sampled macrofauna using a 0.25 m^2 USNEL box-corer (Table 3.1). Overlying water and five top centimetres of sediment were sieved using a 300 µm mesh and retained material was similarly preserved in a 10% formalin solution (Soto et al., 2010).

Before identification, Sta. M samples were sorted to phylum level at the Scripps Institution of Oceanography prior to 2006, and thereafter at the Monterey Bay Aquarium Research Institute. Samples for PAP were sorted at the Natural History Museum (NHM) of London. In both cases, samples were stained for 24-h in Rose Bengal, rinsed in distilled water, transferred to a 70% isopropyl alcohol solution and sorted at phylum-level. Sta. M annelids were then sent to NHM for taxonomic identification. PAP polychaetes sampled prior to 1999 were identified to family level by E. Soto.

3.2.2 Taxonomic identification

Taxonomic identification was undertaken under high power microscopes (Zeiss Discovery v20 Stereo and high power Leica DM 5000 B) by comparing the external morphology of specimens with published identification keys (Fauchald, 1977, Rouse and Pleijel, 2001). Dr.Soto identified PAP specimens until 1998 and I identified PAP specimens in 1999 as well as all Sta. M specimens. Family-level identification was a first step before a more detailed taxonomic analysis. For family identification, only specimens with a head were used leading to a conservative assessment of density and diversity (Paterson et al., 2009). Overall, only 2% and 5% of fauna were unknowns at Sta. M and PAP respectively.

Each family was assigned to a single functional group among those defined by Fauchald and Jumars (1979) and amended by subsequent authors (*e.g.* Pagliosa, 2005). The choice of the retained functional group was based on the feeding strategy most likely to be encountered in an abyssal environment, e.g. direct herbivory was not meaningful in abyssal systems. Fauchald and Jumars’ classification was mainly derived from shallow-water specimen observations; such a classification must therefore be used with caution in an abyssal context. However, as few polychaete families have been reported as being exclusively abyssal (Glover, 2000), analogy with shallower species is not unreasonable. Polychaete functional group research is still ongoing (e.g. Lindsay and Woodin, 1995, Mistri et al., 2002, Würzberg et al., 2011) with evidence suggesting that many polychaetes may be multimodal and may adapt to utilize what resources are available (Dr. L. Lovell, pers. com.). However, so far, Fauchald and Jumars (1979) FG classification remains the only unified classification, based on polychaete morphological traits and appeared the most relevant for this analysis (Table 3.2).

Table 3.2 Three-letter code key of polychaete functional groups as defined by Fauchald and Jumars (1979).

First Letter Feeding Mode	Second Letter Mobility	Third Letter Feeding Apparatus
B – Subsurface deposit feeder	D – Discretely motile	J – Jaw
F – Filter feeder	M – Motile	T – Tentacle
P - Predator	S - Sessile	X – non-armed structure
S –Surface deposit feeder		

3.2.3 Statistical analysis of polychaete assemblage diversity at inter-annual scale

After identification, persistence over time defined as percentage of occurrence over the time-series was computed for each family and functional group. Only data from three or more FVGR chamber grabs at Sta. M and box-corers at PAP for each sampled month (Table 3.1) were used. Data were averaged by year for further analyses. Because the sampling methods were different at Sta. M and PAP any comparisons between them must be undertaken with caution. Firstly, Sta. M was sampled over a greater range of seasons than PAP (respectively February-December vs. March-October). Sta. M data statistical analyses were therefore computed for both the full range of samples across months February-December and the range which overlaps with samples at PAP, March-October. The results were not dependant on seasonal range, and therefore only results of the full data set are presented here. Secondly, although using a common analytical treatment is an asset to compare stations, we acknowledge there are important limits to quantitative comparison between Sta. M and PAP because different sampling technologies were employed. For example, the box corer samples a larger continuous area than the FVGR grabs and the two systems have different so-called bow-wave effects (Bett et al., 1994). These bow-wave effects can cause systematic differences in the level of disturbance to the seafloor sample as the coring device operates. The main results rely on examining the variations at each site rather than direct quantitative comparison.

Polychaete mean densities were computed for each sampling year, as well as Pielou's evenness Index (Primer V.6, Magurran, 2004, Clarke and Gorley, 2006). Family numbers were estimated by rarefaction technique to account for uneven sampling effort in each time-series (Coleman technique, EstimateS, Colwell et al., 2012). Rarefaction curves were computed for each sampling year and tested for differences by Kruskal-Wallis rank test (SigmaPlot v.11, Sokal and Rohlf, 2012). Family richness at each locality was compared by using family accumulation curves (Estimate S, Magurran, 2004) and Mann-Whitney Rank Sum Test (SigmaPlot v.11, Sokal and Rohlf, 2012). Relationships between univariate indexes were investigated with Spearman correlation ($r_{s,}$ SigmaPlot v.11, Sokal and Rohlf, 2012).

The polychaete assemblage structure at each locality was analysed using multivariate ordination techniques (Primer v.6). Family composition as Bray-Curtis Similarity of the 4th root-transformed yearly family density data was computed. Prior to further temporal analyses, the effects of spatial heterogeneity were tested. Two similarity matrices were created, one with spatial distances and one with linear temporal distances between each sample. Using the RELATE routine (Mantel test, ρ, Primer v.6, Mantel, 1967) relationships between polychaete assemblage similarity matrix and these two matrices were investigated. A non-parametric Multi-Dimensional Scaling (MDS, Kruskal and Wish, 1978) method was then applied to polychaete similarity matrices. Inter-annual changes were assessed using multivariate Analysis Of SIMilarity (ANOSIM [R], Primer v.6, Clarke, 1993), which uses randomisation testing of significance with 999 permutations. Also, the MDS x-ordinate was used as a summary univariate parameter to characterise assemblage structure and composition over time.

3.2.4 Statistical analysis of polychaete assemblage structure as RAD_F and RAD_G at an inter-annual scale

Family and functional rank abundance distributions (RAD_F and RAD_G) were obtained by ranking respectively family and functional group densities for each year (rank 1 being the most abundant). In each case, the density values were retained and the distributions were only re-order by ranking these densities without applying any transformation on the data. Ranked composition as Bray-Curtis similarities of the 4th root-transformed yearly ranked data were computed (Primer v.6). A RELATE test was performed with a matrix of linear temporal time between each sample and RAD_F, RAD_G matrices. In other words we examined if the similarity of various RAD distributions was more similar when the samples were taken closer together in time. Similarity data were also used for hierarchical clustering (group average linkage, Primer v.6, McGarigal et al., 2000) and MDS. For FG analysis, the ratio between surface and sub-surface feeder density was examined. Spearman correlations (r_s, SigmaPlot v.11) were computed between families and between FG variables to assess potential compensatory effects as defined by negative co-variation (*sensu* Houlahan et al., 2007).

3.2.5 Statistical analysis of relationships with megafauna and environmental factors

Spearman correlations were used to investigate potential relationships between polychaete assemblage and megafauna/environmental factors (SigmaPlot v.11). Several polychaete assemblage descriptors were tested: mean density, rarefied family number, MDS-x ordinate of the Bray Curtis similarity, family, functional group and rank densities. For family, FG and rank densities, only those with a coefficient of variation (CV, standard deviation to mean ratio) less than one were used: 15 most abundant families and 7 functional groups. Also, for megafauna, only species or indicators representative of marked temporal changes were used. At Sta. M, *Elpidia minutissima*, *Echinocrepis* sp., *Scotoplanes globosa*, total echinoderm biomass and density at Sta. M were examined (Ruhl and Smith, 2004, Ruhl, 2007). At PAP, *Amperima rosea*, *Peniagone diaphana*, *Oneirophanta mutabilis*, total echinoderm biomass and density, total holothurian surface deposit-feeder biomass and density, total holothurian sub-surface deposit-feeder biomass and density were used (Iken et al., 2001, Billett et al., 2010). A distinction between surface and sub-surface deposit-feeding megafauna was applied at PAP only because the Sta. M data did not include sub-surface deposit feeders (cf. photography data were used to quantify megafauna at Sta. M while trawl data were obtained at PAP).

In terms of environmental factors, the climate indicators NAO at PAP and NOI at Sta. M were tested, as well as site-specific records of POC flux to the seafloor. At Sta. M, a near-continuous monthly data record of POC flux was made possible by a composite measure of POC flux integrated from sediment trap data at 50 and 600 mab and a model based on satellite data to fill in the gaps in the record (Ruhl et al., 2008). No such gap filling data are available for PAP, where much of the need for gap filling pre-dates the availability of suitable satellite colour data. Monthly and yearly cross-correlations were used to test relationships over a distribution of monthly and yearly temporal lags between the environmental factors (climate and food supply) and polychaete assemblage features. Because data sets were highly gapped, serial autocorrelation was not tested. Significance was assessed with several criteria regarding correlation sign, p-value and involved time lags. These tests were aimed to understand if climate processes, productivity and POC fluxes had a direct but lagged impact on the abyssal polychaete communities at both stations.

3.3 Results

3.3.1 Taxonomic results

At Sta. M, a total of 3000 specimens were identified, belonging to 39 families and 10 FG. At PAP, a total of 4984 specimens were identified representing 41 families and 9 FG. Three families were present at all sampled times at Sta. M: Capitellidae, Lumbrineridae, Paraonidae and eight families were present at least 80% of the sampled time: Cirratulidae, Cossuridae, Opheliidae, Orbiniidae, Phyllodocidae, Pilargidae, Spionidae, Syllidae. At PAP, six families were found 100% of the sampled times: Ampharetidae, Cirratulidae, Paraonidae, Pilargidae, Sabellidae, Spionidae and seven families occurred 80% or more of the sampled times: Capitellidae, Chrysopetalidae, Fauveliopsidae, Flabelligeridae, Opheliidae, Phyllodocidae, and Scalibregmatidae. In terms of functional groups, BMx, OMJ, PMJ, PMx, SBMx, SMT and SDT (see Table 3.2) occurred at least 80% of the sampled times at both Sta. M and PAP. Overall, the two localities shared 34 families, among which seven were present in at least 80% of the samples. One family, the Paraonidae, was present in all samples. At Sta. M, oligochaetes (Phylum Annelida) occurred in substantial and variant numbers, but were notably absent from PAP.

3.3.2 Polychaete assemblage density and diversity

Polychaete density varied inter-annually at both stations (Fig. 3.1a, b). The highest densities were found in 1998 at both sites with 1893 ± 393 ind. m^{-2} at Sta. M and 839 ± 285 ind. m^{-2} at PAP. The lowest densities were approximately four times less and were recorded in 2005 at Sta. M with 490 ± 219 ind. m^{-2} and in 1994 at PAP with 203 ± 52 ind. m^{-2}.

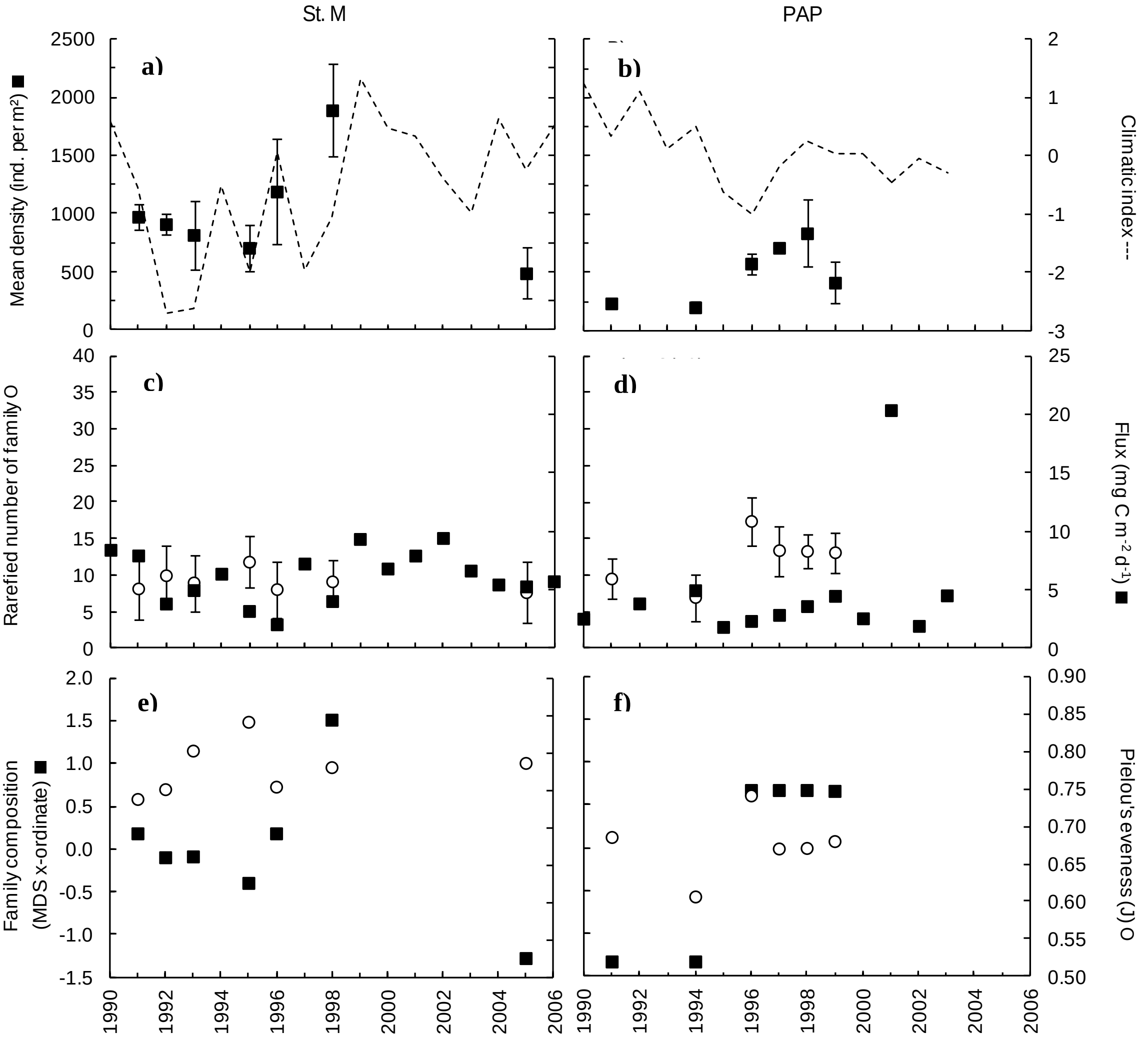

Figure 3.1 Polychaete assemblage structure univariate indexes at Sta. M and PAP over 1991-2005 (a) Sta. M mean polychaete density as individuals per m^{-2} (ind. m^{-2}) (■) with associated standard error and yearly-averaged NOI index (dashed line) with 1998 and 2005 driving temporal difference (b) PAP mean polychaete density as ind. m^{-2} (■)with associated standard error and yearly-averaged NAO index with 1996-1998 driving the difference (c) Sta. M rarefied family number with 18 individuals (○) with associated standard error and mean annual POC flux (d) PAP rarefied family number with 50 individuals (○) with associated standard error and mean annual POC flux (e) Sta. M MDS x-ordinate (■) and Pielou's evenness Index (○) (f) PAP MDS x-ordinate (■) and Pielou's evenness Index (○).

In terms of diversity, rarefied family number changed between years (Fig. 3.1c, d) but without significant statistical difference at Sta. M ($p > 0.05$). In contrast, significant differences occurred at PAP between the periods 1991-1994 and 1996-1999, the '*Amperima* Event' ($p = 0.022$) with rarefied family numbers higher during the '*Amperima* Event'. Pielou's evenness index also varied inter-annually at both stations (Fig. 3.1e, f) albeit without correlation to density or rarefied family number over the whole time-series

(Spearman Correlation, $p > 0.05$). Greater evenness occurred in 1995 at Sta. M and 1996 at PAP. The highest dominance was found in 1991 at Sta. M and 1994 at PAP.
Overall family composition changed at inter-annual scale ($R = 0.151$, $p = 0.01$ at St M, $R = 0.636$, $p < 0.001$ at PAP with year as a factor). As no relationship was found between the spatial distance between samples and their similarity ($\rho < 0.1$, $p > 0.1$) at either locality, these changes were not found to be linked to spatial variations among sampling. However, a significant relationship was obtained between the temporal distance between samples and their similarity: samples taken further apart in time were less similar to each other than samples taken near in time ($\rho = 0.303$, $p < 0.001$ for Sta. M and $\rho = 0.582$, $p = 0.061$ for PAP). The inter-annual variations in family composition were thus linked to temporal rather than spatial processes. Family composition MDS-x ordinate had an opposite sign in 1991, 1996 and 1998 compared to 1992, 1993, 1995 and 2005 at Sta. M (Fig. 3.1e, 0.063 stress value) with a marginally significant difference among the two groups of years (ANOSIM, $R = 0.463$, $p = 0.029$). At PAP, MDS-x ordinate (0.001 stress value) also had different signs between 1991, 1994 compared to the '*Amperima* Event' period (Fig. 3.1f). These two groups of years were significantly different (ANOSIM, $R = 1$, $p = 0.069$). In other words, family composition was different over periods of time rather than from year to year.

Comparing the two stations, allowing for different sampling methodologies, Sta. M had twice the standardised density of PAP. However, both stations had similar density trends over years: decreasing from 1991 to 1995 and increasing from 1996 to 1998. In terms of family numbers, Sta. M and PAP had similar accumulation rates (Fig. 3.2, Mann Whitney, $U = 21$, $p > 0.05$).

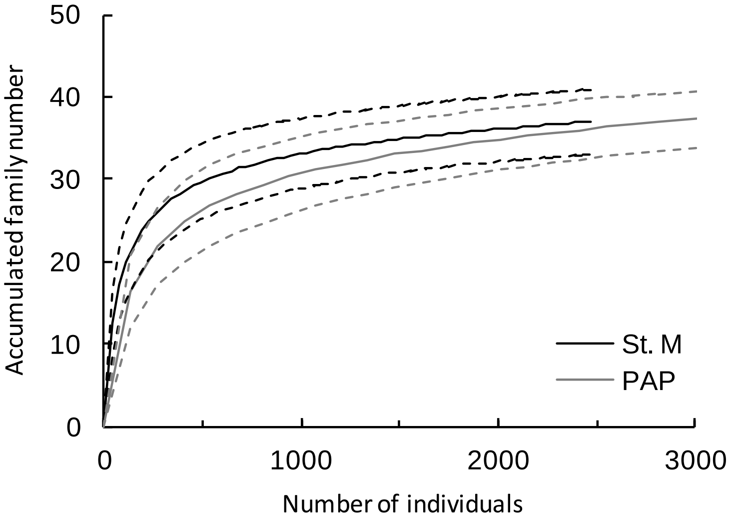

Figure 3.2 Family accumulation curves for Sta. M (black line) with 95% confidence interval (black dashed line) and PAP (grey line) with 95% confidence interval (grey dashed line). Note that both stations had similar accumulation rate.

3.3.3 Polychaete assemblage structure as RAD_F

Directional changes in family rank abundance distribution (RAD_F) occurred at both stations at inter-annual scales (Fig. 3.3a, b).

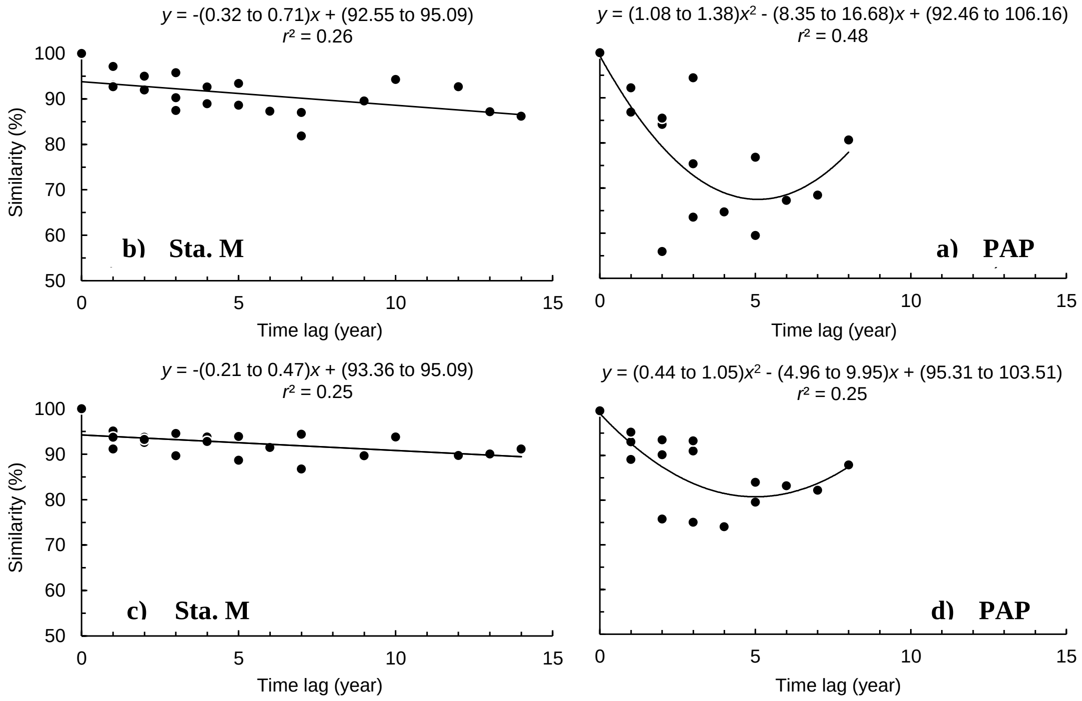

Figure 3.3 Scatter-plots of Bray-Curtis Similarity (%) for (a) all possible RAD$_{\mathrm{F}}$ pairs in 1991-2005 at Sta. M and (b) 1991-1999 at PAP and for (c) all possible RAD$_{\mathrm{G}}$ pairs in 1991-2005 at Sta. M and (d) 1991-1999 at PAP. The regression lines are best fit only shown for visual purposes (the statistical results of the Mantel test are given in sections 3.3.3 and 3.3.4). Note that samples taken closer together in time were generally more similar to those taken with longer time intervals.

Samples taken closer together in time were generally more similar to those taken with longer time intervals between samples: $\rho = 0.269$, $p = 0.051$ at Sta. M and $\rho = 0.780$, $p < 0.001$ at PAP.

The RAD$_{\mathrm{F}}$ similarity dendrogram showed three clusters at Sta. M: 1998, 2005 and 1991-1996 (Fig. 3.4a). At Sta. M, no significant clustering was found with family composition dendrograms (Fig. 3.4b). At PAP, two clusters were found in both cases: 1991-1994 and 1996 to 1999, the '*Amperima* Event' period (Fig. 3.4c, d).

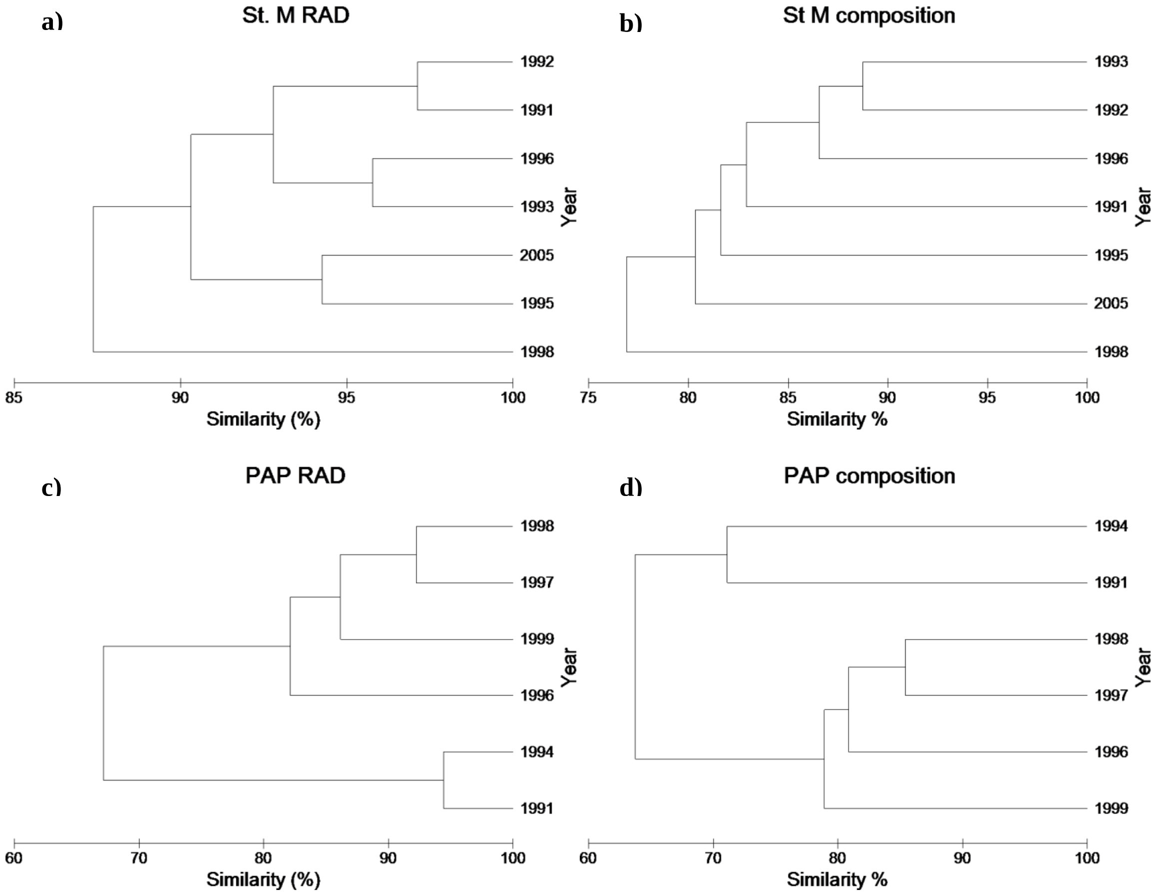

Figure 3.4 Bray-Curtis dendrograms of (a) Sta. M yearly RADF (b) Sta. M yearly composition (c) PAP yearly RADF (d) PAP yearly composition. Note that year of greatest and least densities belonged to different clusters at both stations.

At each locality, year of greatest and least densities belonged to different clusters and their corresponding rank abundance distribution (RAD_F) varied in density level, shape and composition (Fig. 3.5). Sta. M rank 1 was occupied by Paraonidae, except in 1998 when oligochaetes became dominant, whereas other ranks had four or more switches. From 1991 to 1999, PAP rank 1 to 3 only switched once or twice and lower ranks five or six-times. Cirratulidae, Spionidae and Paraonidae occupied the first three density ranks at PAP, with relative density changes over time, except in 1998 when Opheliidae became the most dominant family. Spearman correlations between family densities (CV < 1) at both stations were only positive, if significant.

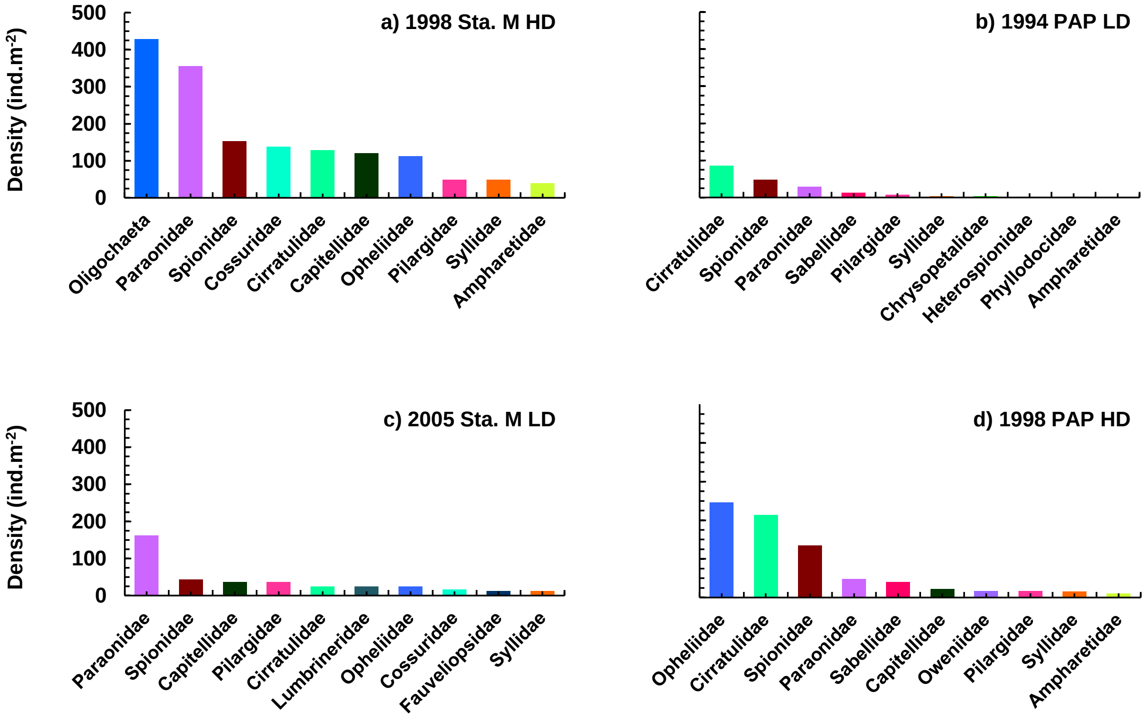

Figure 3.5 Family rank abundance for (a) Sta. M in 1998, year of high polychaete mean density (HD) (b) PAP in 1994, year of low polychaete mean density (LD) (c) Sta. M in 2005, year of low polychaete mean density (LD) (d) PAP in 1998, year of high polychaete mean density (HD). Rank 1 on the left is the most abundant. Families occupying each rank are given below. Rank densities are given in individuals per m^{-2} (ind. m^{-2}). The RAD differed in shape between stations and over time at each station.

3.3.4 Polychaete assemblage structure as RAD_G

Polychaete communities also had directional changes in yearly RAD_G (Fig. 3.3c, d). Samples closer together in time were generally more similar to those with longer time intervals between them: $\rho = 0.353$, $p = 0.006$ at Sta. M and $\rho = 0.654$, $p = 0.031$ at PAP. RAD_G dendrograms of both stations gave similar clusters to RAD_F plots. The FG rank abundance distributions (RAD_G) changed in terms of composition, shape and level at both stations (Fig. 3.6). At Sta. M, rank 1 and 2 switched four times between 1991 and 2005, Rank 3 switched only once. Surface deposit feeders as BMx occupied rank 1 in 1991, 1992, 1995 and 2005. Sub-surface deposit feeders as BMx dominated in 1993, 1996, 1998. Some predators such as PMJ or tentaculate surface feeders such as SMT and SDT were mainly in ranks 3 to 5 albeit with different positions over time.

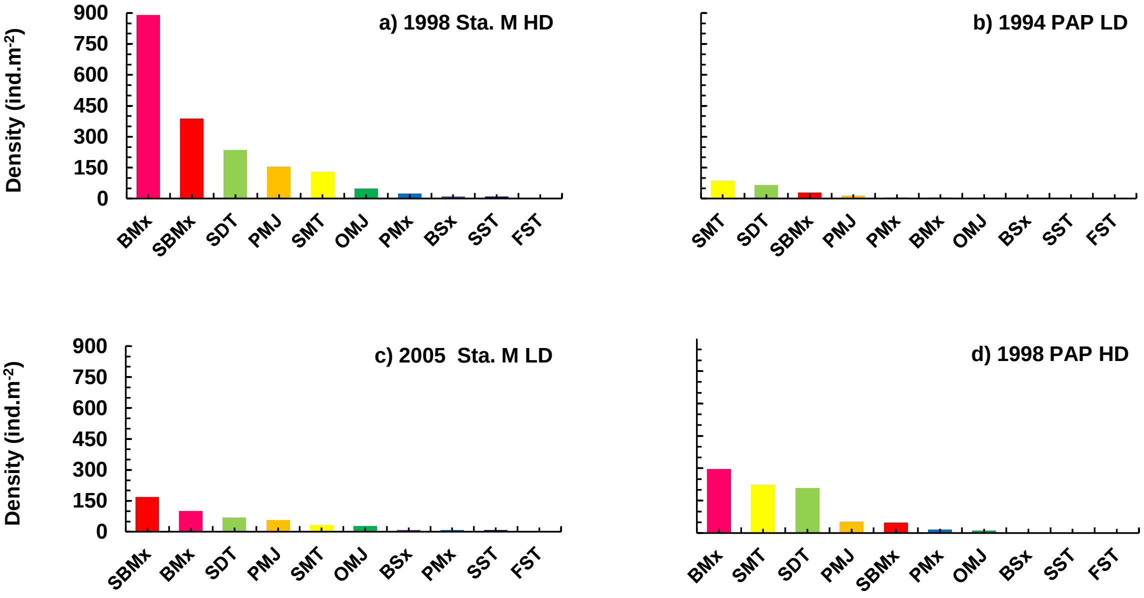

Figure 3.6 Functional group rank abundance for (a) Sta. M in 1998, year of high polychaete mean density (HD) (b) PAP in 1994, year of low polychaete mean density (LD) (c) Sta. M in 2005, year of low polychaete mean density (LD) (d) PAP in 1998, year of high polychaete mean density (HD). Rank 1 on the left is the most abundant. Functional groups occupying each rank are given below. Rank densities are given in individuals per m^{-2} (ind. m^{-2}). The RAD differed in shape between stations and over time at each station.

At PAP, family rank 1 and 3 switched four times and family rank 2 changed three-times. In terms of functional groups, rank 1 was occupied by surface deposit feeders as SMT in 1991, 1994, 1996, 1997, 2002 and SDT in 1989 and 1999. Only in 1998, sub-surface deposit feeders as BMx became the most dominant FG (due mainly to the influx of one family: the Opheliidae). Between rank 3 and 5, the functional groups the two types of deposit feeders (SBMx, BMx) and predators as PMJ were found most of the time. Both stations were dominated by deposit feeders but the relative proportion of surface and sub-surface deposit feeders was different: surface (S) dominated at PAP and sub-surface (B) deposit feeders at Sta. M. The surface to sub-surface ratio (SB ratio) had inter-annual variations also relating to RAD_G changes (Fig. 3.7). Correlations (Spearman) between FG (CV < 1) at both stations were only positive, if significant.

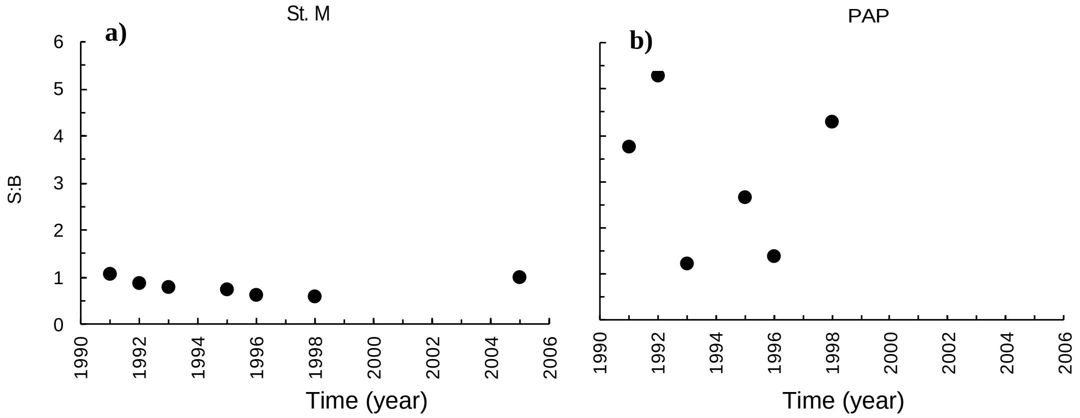

Figure 3.7 Functional group rank abundance yearly dynamics represented by the ratio of surface to sub-surface deposit-feeder densities (SB ratio) over year at (a) Sta. M (b) PAP. Note that the ratio is one or less at Sta. M and superior to one at PAP.

3.3.5 Polychaete assemblage relationships with megafauna and environmental factors

In terms of statistical relationships between polychaetes and megafauna, several Sta. M polychaete assemblage descriptors were correlated with *S. globosa* but not with any other species or megafauna indicators (Table 3.3). At PAP, many polychaete assemblage descriptors were correlated with *A .rosea*, total echinoderm density, total holothurian surface deposit-feeder density, and total holothurian sub-surface deposit-feeder biomass (Table 3.3). No correlations with compatible statistical and mechanistic rationale were found with POC flux or climate indices at either locality.

Table 3.3 Spearman correlation of *Scotoplanes globosa* with Sta. M polychaete assemblage descriptors, n = 6 and of *Amperima rosea*, *Oneirophanta mutabilis*, Total Echinoderm Density (TED), Total Holothurian Surface deposit-feeder Density (THS D), Total Holothurian Sub-surface deposit-feeder Biomass (THB B) with PAP polychaete assemblage descriptors, n = 6. R is the coefficient of correlation with its associate p-value (SigmaPlot v.11). Ord. stands for ordinate. MPD stands for mean polychaete density.

Station	Megafauna descriptor	Polychaete descriptor	R	p	Polychaete descriptor	R	p
Sta. M	*S. globosa*	RAD$_F$ MDS x-ord.	1.000	0.028	Cirratulidae	1.000	0.028
		RAD$_G$ MDS x-ord.	0.943	0.017	Spionidae	0.943	0.017
		Ampharetidae	0.943	0.017	SDT	1.000	0.028
		Capitellidae	0.886	0.033	SMT	0.943	0.017
PAP	*A. rosea*	MPD	0.943	0.017	Spionidae	0.886	0.033
		RAD$_G$ MDS x-ord.	0.943	0.017	Syllidae	0.886	0.033
		MDS x-ord.	0.926	0.017	PMJ	0.810	0.010
		Ampharetidae	0.943	0.017	SDT	0.943	0.017
		Cirratulidae	0.886	0.017	SMT	0.943	0.017
		Sabellidae	0.886	0.033			
	O. mutabilis	SB ratio	0.943	0.017			
	TED	MPD	0.886	0.033	RAD$_G$ MDS x-ord.	0.886	0.033
		Lumbrineridae	0.899	0.017	SBMx	0.886	0.033
		Sabellidae	0.943	0.017	SDT	0.943	0.017
		Spionidae	0.943	0.017	SMT	0.943	0.017
		SB ratio	0.943	0.017			
	THS D	MPD	0.943	0.017	Spionidae	0.886	0.033
		MDS x-ord.	0.926	0.017	Syllidae	0.943	0.017
		RAD$_G$ MDS x-ord.	0.943	0.017	PMJ	0.943	0.017
		Ampharetidae	0.899	0.017	SMT	0.886	0.033
		Cirratulidae	0.886	0.033	SDT	0.886	0.033
		Sabellidae	0.886	0.033			
	THB B	Lumbrineridae	0.928	0.017	OMJ	0.943	0.017
		Sabellidae	0.886	0.033	SDT	0.886	0.033
		Spionidae	0.886	0.033			

3.4 Discussion

3.4.1 Inter-annual variations in abyssal polychaete assemblage structure

Sta. M and PAP polychaetes showed significant changes in family composition, family evenness, RAD_F and RAD_G in addition to the density variations reported by Ruhl et al. (2008) and Soto et al. (2010). At both stations, structural changes occurred, the strongest being in 1998 when polychaete densities peaked at both localities, and switches in the densities of most abundant families and functional groups took place. The changes in dominance were initiated in 1996 when switches started to occur in RAD_F and RAD_G composition and evenness. At PAP, changes observed during the '*Amperima* Event' lasted through 1999. However, the persistence of these changes could not be assessed at a later date than 1999 owing to low replication and gear change issues from 2002 to 2010. A study to assess gear change impact on macrofauna when sampling abyssal systems is underway as done by Bett et al. (1994) on meiofauna.

The main difference in inter-annual variations of the polychaete communities at Sta. M and PAP was the constancy at Sta. M of the rarefied family richness over the years. Although it may be due to a sampling artefact of the FVGR, consistently missing some polychaete families, it may also be linked to differences in the regional family pool in the vicinity of both stations. Thibault et al. (2004) also observed changes in RAD and not in species richness in a long-term study of a desert rodent community, suggesting that RAD and species richness may not be as closely connected as previously thought (*e.g.* MacArthur, 1957).

Despite inter-annual variations, the polychaete assemblage compositions at Sta. M and PAP showed some consistent features. These were more evident in assemblage structure than in the specific composition of the families. Both localities shared 34 families. This is not surprising because few polychaete families are endemic to the deep sea and many have broad geographic and bathymetric distributions (Paterson et al., 2009). The Paraonidae was the only family present during each sampling time at both stations. Most species belonging to this family are thought to be opportunistic and may be more suited to environments with seasonal and limited food supply (Smith and Hessler, 1987, Levin et al., 1999, Hilbig and Blake, 2000). Paraonidae was the dominant family at Sta. M, representing 25 to 30% of the assemblage, except in 1998 when oligochaetes became dominant. The presence of oligochaetes in benthic macro-infaunal communities has been scarcely reported at abyssal depths. Blake (1997) described oligochaetes from Santa Maria basin and Western Santa Barbara Channel seafloor off the California coast. Oligochaetes could be present in the regional species pool associated with Sta. M and not in the one associated with PAP. Although Sta. M and PAP were sampled with different gear, recent sampling at PAP using a megacorer did not sample macrofaunal oligochaetes. Another difference between the stations was that the Paraonidae was never the dominant family at PAP; Cirratulidae was. This difference is unlikely to be an artefact of the different sampling methodologies because Sweetman and Witte (2008) also noticed this difference between Sta. M and PAP during enrichment experiments conducted with the same design of incubation chambers at the two localities. At PAP, Cirratulidae represented 25 to 30% of the polychaete assemblage except in 1998 when Opheliidae became dominant. Differences in regional family and species pools and/or environmental settings may explain Sta. M and PAP dissimilarities in composition.

Ecological and environmental factors could also be forcing variables. Switches in polychaete RAD_F and RAD_G observed in 1998 at both localities may indicate competitive interactions in an environment where resources were variable in supply, and/or niche-based difference environmental tolerances. The main changes in 1998 were not accompanied by negative correlations between polychaete families or functional group suggesting no compensatory effect as defined by Houlahan et al. (2007). However, oligochaetes became more dominant than Paraonidae at St. M and Opheliidae were more dominant than Cirratulidae at PAP in 1998. The change in dominance could be due to a greater numbers of individuals collected following a particularly good recruitment due to factors unrelated to competition, although biomass data may be better at unravelling competition processes (Ernest and Brown, 2001). However, in fragile deep-sea samples there are many fragmented polychaete specimens precluding a biomass analysis at the family level. Vanreusel et al. (2001) suggested that a synchronised recruitment event occurred in Ophelidae at PAP in fall 1996 as only small juveniles were present in meiofauna at a single period of time over the time-series. Episodic growth and/or reproduction events could also influence the population structure (Smith, 1994). The lack of obvious compensatory effects could also be related to some taxon pairs belonging to mis-matched trophic levels (Houlahan et al., 2007). Houlahan et al. (2007) suggest in such cases that, if there were compensatory effects, they may have been weaker than other forcing variables such as megafaunal abundance and sediment reworking rates, food supply or environmental factors. The inter-annual variations in polychaete family assemblage structure and composition were not isolated in time from the other faunal changes noted in both time series, but were part of broad-scale changes observed across all abyssal faunal-size groups (Ruhl et al., 2008, Gooday et al., 2010, Kalogeropoulou et al., 2010). Such comprehensive variations suggest forcing variables rather than ecological drift as drivers of changes (Ruhl, 2008, Smith et al., 2009, Billett et al., 2010).

3.4.2 Inter-annual variations in polychaete assemblage, megafauna and environmental factors

At both stations, changes in the megafauna and polychaete communities were synchronous even though the polychaete density shifts were not as great in magnitude as for the megafauna (Ruhl and Smith, 2004, Ruhl et al., 2008, Billett et al., 2010). Several polychaete assemblage features were positively and significantly correlated with *Scotoplanes globosa* (not a dominant species) at Sta. M and *Amperima rosea* and other megafauna descriptors at PAP. Positive correlations between megafauna and polychaete assemblage features indicate a lack of substantial compensatory effect. However, it does not preclude ecological interactions because several processes may be interrelated between megafauna and macrofauna over time. Holothurians have been shown to ingest the bulk of phytodetritus pulses, at least at PAP during the '*Amperima* Event', and may have more direct access to the more liable food fraction (Bett et al., 2001) changing the amount and/or nature of food available for polychaetes. There is also some evidence that benthic megafauna may facilitate macrofauna density *via* bioturbation leading to oxygenation of sediments and mixing of organic matter to deeper depths (Thistle et al., 2008). At PAP, the positive correlation in polychaete assemblage variations with total echinoderm density and total surface deposit-feeder holothurian density provides limited evidence that facilitation processes could be important for polychaetes, particularly for polychaete surface feeders (Table 3.3).

In addition to ecological interactions, megafauna and macrofauna may have been influenced by the same environmental forcing variables. At Sta. M, *Scotoplanes globosa* was positively and significantly correlated with a 14-month lagged NOI and an 8-month lagged POC flux (Ruhl and Smith, 2004). At PAP, POC flux quantity/quality has been proposed as a likely driver of inter-annual variations in *Amperima rosea* density (Billett et al., 2001, Iken et al., 2001, Billett et al., 2010, FitzGeorge-Balfour et al., 2010). Even if a satisfactory mechanistic understanding of pelagic-benthic coupling has not been reached yet (Lampitt et al., 2010b, Smythe-Wright et al., 2010), climate is likely to influence POC flux. Positive NAO have been associated with increased primary production and POC flux (Ruhl and Smith, 2004, Smith et al., 2009) and therefore will have effects on benthic communities. However, polychaete assemblage descriptors did not show correlations with POC flux or climate indexes at the family level at either Sta. M or PAP.

The lack of correlation between polychaete assemblage descriptors and POC flux, NOI or NAO does not rule out environmental factors as drivers of inter-annual variations. Synchronous variations between megafauna and polychaete density variation give some support to this hypothesis. Several reasons may account for the lack of direct correlation between environmental factors and polychaete assemblage features: 1) small-scale spatial heterogeneity may introduce unexplained variation in time-series. Heterogeneity in space is likely to be as small as centimetre scale for polychaetes (Jumars, 1975). However, any spatial patterns in the analysed samples were less important than time in explaining variation; 2) some important forcing variables may have not been accounted for; 3) the temporal extent of sampling may be critical to infer mechanisms underlying patterns in time. Chalcraft et al. (2004) highlighted that extending the temporal extent of time series observations increases the likelihood of including extreme and episodic data that often drive ecological patterns. With a larger data set including 1989 and 1990 polychaete density data, Ruhl et al. (2008) found a positive significant correlation between Annelida density, mostly dominated by polychaetes, and 9-month lagged NOI. Herein, in the current study, we did not have family level data for 1989 and 1990, perhaps leading to the 9-month correlation between polychaete density and NOI not being significant; (4) gaps in the time-series may prevent identification of correlations with the present method. While there is tantalising evidence to suggest non-random processes as drivers of inter-annual variations of polychaete communities, the factors behind these processes remain evasive likely because of numerous interactions between all potential forcing variables.

3.4.3 Inter-annual variations in polychaete assemblage in terms of abyssal system functioning

Although POC flux did not directly correlate with density, evenness, RAD_F, RAD_G at both Sta. M and PAP, several lines of evidence suggest that POC flux played a role in polychaete assemblage temporal variations for the following reasons: 1) higher density and major changes in RAD composition occurred during higher POC flux as seen for megafauna (Ruhl and Smith, 2004, Ruhl et al., 2008, Billett et al., 2010); 2) POC flux seems to influence at least mean polychaete density at each station. Station M had a higher mean annual POC flux and polychaete density compared to PAP: 1.9 g C m^{-2} y^{-1} at Sta. M in 1990-1996 and 1.3 g C m^{-2} y^{-1} at PAP in 1989-1999 (Baldwin et al., 1998, Smith et al., 2001, Lampitt et al., 2001). At an inter-annual scale, POC flux may drive less family structure and composition variations than density variations, because there was no statistical difference in family accumulation rate at the two localities despite the difference in organic matter input. One critical difference that may occur is the connection to and size of regional family and species pools. The mechanisms of family turnover may be different in the two areas and may be linked to factors other than POC flux (Shurin, 2007); 3) while POC flux may be an important factor for abyssal systems, it may not be the best surrogate of polychaete energy supply (Drazen et al., 2008). For example, there may be a threshold in POC flux quality/quantity to impact polychaete assemblage structure that may be different for surface and sub-surface deposit feeders (Iken et al., 2001); 4) little is known about food web flows in deep-sea systems (Witte et al., 2003, Brandt, 2008, Soetaert and Van Oevelen, 2009). Because stable isotope analysis remains difficult to perform on abyssal polychaetes (Witte, pers. comm.), the food compounds polychaetes rely on, in particular for their reproductive biochemistry, are unknown in contrast to megafauna, such as holothurians (*e.g.* Wigham et al., 2003, FitzGeorge-Balfour et al., 2010). Stable isotopes and fatty acid studies conducted in deep-sea systems have confirmed that polychaetes responded to a fresh input of food (Levin et al., 1999, Witte et al., 2003, Sweetman and Witte, 2008). However, these experiments often exclude a portion of the food web such as megafauna (Witte et al., 2003) or give ambiguous results with stable isotope signatures suggesting that deposit feeders may switch mode in completely unexpected or unseen/unobserved way (e.g., Ophelidae, Sweetman and Witte, 2008). Overall, the lack of knowledge in abyssal infaunal polychaete natural history, particularly regarding reproduction, dispersal and recruitment restricts our understanding of the mechanisms that shape polychaete communities in time.

Whatever processes underpin polychaete assemblage inter-annual variations, changes in density and functional group dominance has consequences on abyssal system functioning. Infaunal polychaetes influence not only sediment biogeochemistry (Cosson et al., 1997, Olsgard et al., 2003), but also interact with infaunal meiofauna, protists and bacteria *via* competition, predation and facilitation mechanisms (Smith, 1994, Levin and Edesa, 1997, Witte et al., 2003, Van Nugteren et al., 2009). In this context, a shift from surface deposit-feeder to sub-surface deposit-feeder dominance or *vice-versa,* as seen at both localities between 1991 and 1999, may have important consequences, in particular for carbon processes. For example, Sweetman and Witte (2008) have suggested that the dominance of Cirratulidae at PAP and Paraonidae at Sta. M could explain the difference in carbon processing rates measured at the stations. Surface deposit feeders such as Cirratulidae may have access to fresher food increasing carbon degradation rates. In fact, this study suggests that not only Cirratulidae, but also surface deposit feeders in general were relatively more abundant at PAP than Sta. M. This observation points to faster bioturbation rates at Sta. M than PAP, taking nutrients away from the surface down to the subsurface more quickly. Sta. M may be more suitable for sub-surface rather than surface deposit-feeder polychaetes. Overall a clearer characterisation of the relationship between POC flux, megafauna, macrofauna and carbon process rates would help understanding of carbon cycle processes, particularly over longer time scales (Ruhl, 2007).

3.5 Conclusions

Abyssal infaunal polychaetes showed inter-annual variation in density, family number, family composition, and functional group rank abundance distribution at Sta. M and PAP and in family richness at PAP. In particular, in 1998, both stations had increases in polychaete density with a shift in the dominance of the most abundant family and functional group ranks. Changes occurred in synchronicity with other taxa, in particular to some holothurian species during periods of greater POC flux. These results suggest a common driver for change. There is, at present, no reason to believe that observed intra- and inter- annual change in polychaetes would not extend to longer period changes that are expected with climate change related to global warming. However, factors behind these processes remain elusive likely due to numerous biological and environmental interactions. Future work to better constrain factors driving changes and carbon processing by polychaetes at abyssal seafloor will include: 1) the addition of new time points at each station; 2) analysis of small-spatial scale heterogeneity at each station; 3) analyses of body size distribution of the same samples over time to investigate possible reproduction and/or recruitment events and biomass variation; 4) species-level analysis of the same samples as family level results are the combination of numerous species responses, which can obscure patterns; and (5) the development of experimental approaches *in situ* on the seafloor.

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Chapter 4

Demographics of abyssal North East Pacific density-dominant polychaete species

This chapter is a modified version of paper in preparation: Laguionie-Marchais, C., Ruhl, H.A., Smith, K.L.Jr., Paterson, G.L.J. Descriptions and demographics of North East Pacific density-dominant abyssal polychaete species. Marine Ecology.

Abstract

Life histories of deep-sea organisms are scarcely known. Understanding connections between species life history and environmental spatio-temporal variation is key to adequately assess deep-sea fauna responses to anthropogenic impacts. Here the variability of the five density-dominant polychaetes (Annelida), for which enough individuals were available for statistical analyses, was examined over a 20-year period (1991-2011) at an abyssal station in the North East Pacific (Station M, ~4000 m): *Aphelochaeta* sp. *A* (Cirratulidae), *Cossura* cf. *rostrata* (Cossuridae), *Levinsenia* cf. *oligobranchiata, Paradoneis* cf. *lyra* (Paraonidae) *and Sphaerosyllis* sp. A (Syllidae). All species had significant inter-annual variability in density and/or median body size that differed from one species to another. Assuming that sampling site re-location did not drive variation, density and body size dynamics could be related to life-history events for two species. *Paradoneis* cf. *lyra* dynamics may have been related to enhanced survivorship or migration of adult individuals during periods of low food supply. By contrast, *Cossura* cf. *rostrata* dynamics may have been related to individuals shifting between growth and reproduction leading to have more numerous smaller individuals during low food supply periods. Processes behind inter-annual variations of *Aphelochaeta* sp. A, *Levinsenia* cf. *oligobranchiata* and *Sphaerosyllis* sp. A densities were less clear. Observation of reproductive specimens suggested that reproduction was opportunistic and/or year-round for *Cossura* cf. *rostrata* and *Sphaerosyllis* sp. A and maybe periodic for *Levinsenia* cf. *oligobranchiata*. Further studies are required to directly measure population parameters such as generation times, reproduction and growth rates and more fully understand the influence of spatial sampling artefacts *versus* possible shifts in demographics.

4.1 Introduction

Information on life histories of deep-sea organisms remains scarce. A better understanding of deep-sea faunal life histories is necessary to interpret biodiversity patterns (Ruhl, 2007) and predict impacts of environmental changes such as climate change or resource exploitation on their populations (Glover and Smith, 2003, Thiel, 2003). Most knowledge on deep-sea species life history has come from fortuitous observations. However, long-term studies of deep-sea systems can give important insights into the life histories of their fauna. As deep-sea population parameters such as reproduction or growth rate can not be directly measured for numerous species, the detailed temporal abundance and size frequency distribution data provide the best information available to help elucidate population dynamics (Ruhl, 2007).

Long-term studies have been conducted in abyssal sedimentary areas (> 3000 m) at Station M (Sta. M, Ruhl and Smith, 2004) in the North East Pacific and at the Porcupine Abyssal Plain (PAP, Billett et al., 2010) in the North East Atlantic since 1989. The temporal data sets have given information on the life histories of several megafauna species dominated by mobile holothurians and echinoids. At Sta. M, several species responded to food supply by increasing their densities while decreasing their body size, suggesting reproduction followed by juvenile recruitment (Ruhl, 2007, Booth et al., 2008, Smith et al., 2009). At PAP, holothurian reproduction requiring specific phytopigments has been shown to be an important mechanism to explain holothurian species dynamics. The species *Amperima rosea* may have an advantage in using carotenoids leading to successful reproduction and recruitment when these pigments are abundant (Wigham et al., 2003). So far, these long-term studies have not been analysed to uncover macrofauna life histories.

In the deep sea, the polychaetes often dominate the infaunal macrofauna from chemosynthetic to abyssal plain systems (Gage and Tyler, 1991, Van Dover, 2000, Young, 2003, Ruhl et al., 2008, Soto et al., 2010, Laguionie-Marchais et al., 2013). Despite their importance, only about 3% of polychaete species had their life histories described, most of them in shallow water (Giangrande, 1997). Knowledge of infaunal polychaete species life histories in abyssal sedimentary areas is particularly scant (Gage and Tyler, 1991). In his review, Young (2003) reported 16 deep-sea, non-chemosynthetic species of polychaetes for which there was some knowledge on their life histories. Of these 16 species, only four inhabit at depths greater than 3000 m and only one species came from the North East

Pacific. Young (2003) found that: most of the studied deep-sea polychaete species had separate sexes (but see Thornhill et al., 2012), continuously reproduced (but see Blake, 1993, Mercier et al., 2014 for example of seasonal reproduction), and were brooders (Levin and Bridges, 1994, Paxton and Arias, 2014). Since the review of Young (2003), only a few more species had their life histories described (Eckelbarger et al., 2005, Mincks et al., 2009, Paxton and Arias, 2014, Mercier et al., 2014).

Sta. M macrofauna has also been dominated by polychaetes (Ruhl et al., 2008, Laguionie-Marchais et al., 2013). Overall, 167 species were collected between 1991 and 2011 representing almost 4 000 individuals (Appendix C, Laguionie-Marchais et al., submitted). Most species occurred unfrequently and/or in low density which precluded using their time-series data to elucidate their life history and population dynamics. Only five species belonging to four families had enough individuals: the Cirratulidae *Aphelochaeta* sp. A., the Cossuridae *Cossura* cf. *rostrata,* the Paraonidae *Levinsenia* cf. *oligobranchiata* and *Paradoneis* cf. *lyra* and the Syllidae *Sphaerosyllis* sp. A (see taxonomic descriptions in Appendix D). Except the Syllidae, Cirratulidae, Cossuridae, and Paraonidae are conspicuous inhabitants of sedimentary abyssal areas (Blake, 1996a,b, Hilbig, 1996, Glover et al., 2001, Paterson et al. 2009, Soto et al., 2010). In deep waters, the Syllidae is only represented by a few genera mostly of the Exogoninae sub-family (Kudenov and Harris, 1995).

Virtually nothing is known about the life histories of deep-sea species of Cirratulidae, Cossuridae, Paraonidae and Syllidae. In shallower systems, cirratulids are free living surface deposit feeders that burrow or crawl through the sediment (Blake, 1996a). Cirratulids usually have separate sexes although hermaphroditism exists (Petersen, 1994) with lecithotrophic, direct or viviparous development. Cossurids are free motile burrowers (Fauchald and Jumars, 1979), surface to sub-surface deposit feeders (Hilbig, 1996), for which eggs and sperms as well as facultative hermaphroditism have been reported (Fournier and Petersen, 1991, Blake, 1993). Paraonids live in mud or sand (Pettibone, 1982) in vertical burrows (Blake, 1996b) and are mainly sub-surface feeders although other methods of feeding have been frequently reported (Fauchald and Jumars, 1979, Penry and Jumars, 1990, Gaston et al., 1992). Eggs have been observed in some species and direct development has been proposed as a larval development mode (Strezlov, 1973, Lȯpez-Jamar et al., 1987). Syllids of the subfamily Exogoninae are found living in crevices on corals and rocks, interstitially in the sediment (San Martin, 2005). Syllids are highly mobile and are considered to be carnivorous (Kudenov and Harris, 1995 but see Day, 1967, Fauchald and Jumars, 1979, Pettibone, 1982, Kudenov and Harris, 1995). In Exogoninae, dorsal or ventral egg incubation as well as viviparity have been reported (Pocklington and Hutchenson, 1983, San Martín, 1991, San Martin, 2005).

This study used a long-term data set of deep-sea polychaetes collected at Sta. M to gain insight into their life histories. To overcome the lack of direct measurement of population parameters such as reproduction rate, information was obtained from the conjoint analysis of abundance and size frequency distribution dynamics. Only five polychaete species had enough individuals over the 20-year period to conduct such an analysis (the study of the whole Sta. M polychaete assemblage is presented in chapter 5, Laguionie-Marchais et al., submitted). For each of the five species, three hypotheses were tested: 1) each species had inter-annual significant variation in density and body size. 2) The density and body size dynamics of each species co-varied, being indicative of life-history events. 3) The density and body size dynamics of each species were related to megafauna and food supply dynamics.

4.2 Materials and Methods

4.2.1 Sampling location

From 1991 to 2011, macrofauna was sampled in twenty-eight research cruises at Sta. M in the North East Pacific (see details in Chapter 5). Location of St. M sampling shifted from 34^{o} 50’ N, 123˚00’ W, 4100 m depth in 1991-2005 to 35^{o} 10´ N, 122^{o} 59´ W, 4000 m depth in 2006-2011 (see details in Smith and Druffel, 1998, Kuhnz et al., 2014). No macrofauna sampling took place during 2006-2008. A Free-Vehicle Grab Respirometer (FVGR, described in Smith et al., 2001) was used to collect macrofauna. The FVGR had four 413-cm^{2} grabs, 25 cm apart (square design) keeping the top 15 cm of sediment. After recovery, the material was sieved on board through a 300 µm mesh and preserved in 10% borate-buffered formalin solution (Drazen et al., 1998).

4.2.2 Polychaete sorting and identification

Class sorting was undertaken at the Scripps Institution of Oceanography prior to 2006 and thereafter at the Natural History Museum of London. Samples were washed in distilled water and transferred into 70% alcohol. Rose Bengal was added to the sample for 24 h to stain the organisms and ease the sorting. Organisms were then picked under a dissecting microscope and sorted into taxonomic classes. Identification of deep-sea polychaete species was then performed at the Natural History Museum of London by me ensuring uniformity in species identification. Specimens were first sorted to family level under a dissecting microscope. Then morphotypes in each family were defined using stereo (Zeiss Discovery v20 Stereo) and compound microscopes (Leica DM 5000 B). Two issues arise when identifying deep-sea polychaetes. First, despite all precautions, deep-sea polychaetes are easily damaged by the sampling processes, in particular sieving. Many specimens lose important characters such as branchiae, antennae, palps, therefore making identification harder. Second, few deep-sea polychaete species have been described and there are few taxonomic papers to compare specimens to (Paterson et al., 2009). In numerous ecological quantitative studies, taxonomic work has been carried out to morphotype (sp. A, B, C, etc., Paterson et al., 2009). Named species identification (where possible) was carried out using published identification keys. Only individuals with a head were kept for further analyses, to give a conservative assessment of density and diversity with respect to individual counts (Paterson et al., 2009). The number of specimens for each species was computed and the species with more than 100 individuals over the whole time-series were kept for further analyses.

The body sizes of the specimens were measured under a compound microscope. A proxy of polychaete size was used as only 100 complete individuals were found over the 3800 specimens collected at Sta. M over the study period (all species included). The first chaetiger width (W_1) has proven to be a reliable indicator of polychaete total length (L_{tot}, Paterson et al., 2006). A significant relationship between W_1 and L_{tot} was found with the present specimens: $L_{tot} = 22.72 \times W_1$ ($R = 0.63$, $F = 168.13$, $p < 0.001$, regression analysis, Sokal and Rohlf, 2012, Minitab v.17, Fig. 4.1).

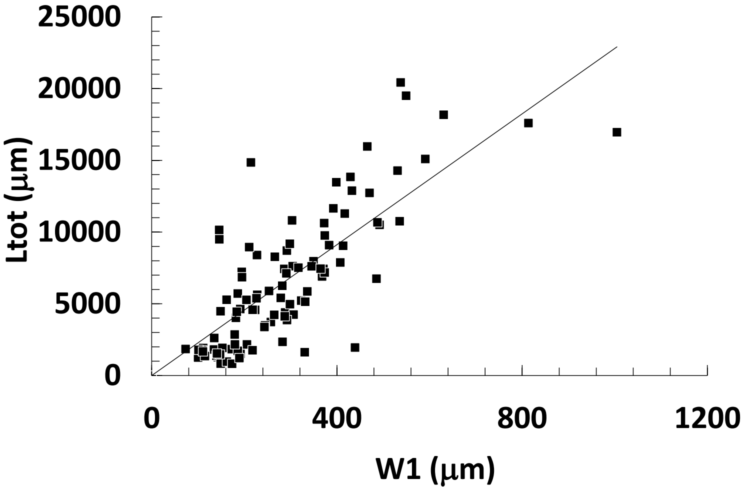

Figure 4.1 Statistically significant linear relationship between polychaete specimen total length (L_{tot} in μm) and the first chaetiger width (W_1 in μm).

4.2.3 Statistical analyses

Two caveats must be pointed out regarding the data set. Firstly, the number of deployments per year was variable. Although most analyses were conducted at yearly time scale, I acknowledged that the sampling months were not controlled over year. Secondly, the change of sampling location between 1991-2005 and 2009-2011 may confuse the temporal analysis. To acknowledge the potential significance of the corresponding shift in the sampling area in the time-series, I conducted tests on 1991-2005 and on1991-2011 periods.

4.2.3.1 Density and body size dynamics

For the statistical analyses, the primary sampling unit was FVGR deployment. Data from individual grabs were pooled within deployment to yield deployment-level data (i.e. grabs regarded as subsamples, not independent replicates). The deployment-level data were then averaged within cruise to provide ‘month-level’ data (n = 22), and the month-level data were then averaged within year to yield give ‘year-level’ data (n = 10) (i.e. sampled months are given equal weight within year). Polychaete species densities were computed for each sampling date and year. Monthly and yearly differences in time were tested using log(x+1) transformed density data and applying an Analysis of Variance (ANOVA) with a Tukey pairwise comparison to examine which dates/years were leading the differences (Minitab v.17, Sokal and Rohlf, 2012). Relationships between species densities were investigated with Spearman Rank correlation (r_s, Minitab v17, Sokal and Rohlf, 2012).

In the same way, the median body sizes of each species were computed for each sampling date and year. An ANOVA with Tukey pairwise comparison was performed on log(x+1) transformed median body sizes to test for differences between sampling dates and years. Spearman-rank correlations were used to test for relationships between: 1) the median body size dynamics of the different species (inter-species correlation); 2) the median body size and density dynamics of each species (intra-species correlation).

4.2.3.2 Body size spectra

For each species, the occurrence of specimens with reproductive tissues and of juveniles was recorded. In addition, the density body-size spectra (DBS) were computed (number of individuals in doubling size class with class 1 = 50-75 µm) at monthly and yearly time scales to identify potential recruitment events to adult size classes and to examine distribution variations. DBS were analysed using multivariate techniques (Primer v.6, Clarke and Gorley, 2006). The DBSs were compared over time by creating a size distribution similarity matrix (DOMDIS routine, Primer v6, Clarke, 1990) and applying an Analysis Of SIMilarity (ANOSIM, R, Primer v.6, Clarke, 1993, 999 permutations employed, year as factor). An ANOSIM test was also conducted to test if a positive or negative deviation in overall median body size (factor) was significantly linked to the variations in the size distribution similarity (see details in Ruhl, 2007).

Non-parametric Multi-Dimensional Scaling (MDS, Kruskal and Wish, 1978) was also applied to the size distribution similarity matrix of each species. The multidimensional scaling (MDS) x-ordinate of each species DBS (DBS-MDSx) was used as an univariate index of similarity to compare species DBS and their temporal variations. Spearman rank correlations (r_s) were computed between DBS-MDSx and: 1) the median body size of each species to test if DBS-MDSx was a reliable descriptor of the size distribution; 2) time, to assess if DBS changes were continuous and monotonic over the time-series.

4.2.3.3 Relationship with megafauna and environmental factors

To test if polychaete species density and body size dynamics were linked to external factors, the correlations between each species density and body size dynamics and the dominant holothurian density dynamics (detailed in Kuhnz et al., 2014) as well as the estimated POC flux dynamics were tested (Spearman's rank correlation, Minitab v17.1; see e.g. Sokal and Rohlf, 2012). The available POC flux data represented a near-continuous monthly data set obtained as a composite measure from sediment trap data at 50 and 600 mab (Smith et al., 2013). Spearman rank cross correlations (r_s) were made between monthly polychaete species and monthly POC flux for the period s1991-2011 and 1991-2005, where polychaete variables were allowed to lag changes in POC flux by monthly time steps of up to 11 months. The correlations for the time of the peak in correlation were reported without p-value adjustment for multiple comparisons. Such multiple comparison adjustments can reduce type I errors, but increase type II errors in small sample sizes like those here (Feise, 2002).

4.3 Results

4.3.1 Polychaete species density dynamics

All species had statistically significant variations in density at monthly and/or yearly time scales. No clear seasonality pattern was observed among the species although no spectral analysis could be conducted on data with uneven temporal distributions. Monthly figures are presented in Appendix E.1, E.2.

Aphelochaeta sp. A density was highest in 1998 with 72.80 ind.m^{-2} and lowest in 2005 with 4.04 ± 4.04 ind.m^{-2} (Fig. 4.2a). The density differences in time were significant at monthly and yearly time scales over 1991-2011 and only yearly time scale over 1991-2005 (Table 4.1). This appeared to be driven solely by the low value in 2005, with no significant differences detected between any other comparisons of years. A*phelochaeta* sp. A density represented between 3 to 11% of the total polychaete density at monthly time scale and 2 to 8% at yearly time scales.

In terms of the species *Cossura* cf. *rostrata*, the highest density occurred in 1998 with 127.40 ± 54.59 ind.m^{-2} and the lowest in 2010 with 9.10 ± 3.03 ind.m^{-2} (Fig. 4.2b). Differences in *Cossura* cf. *rostrata* densities were significant yearly over 1991-2011 and over 1991-2005 (ANOVA, Table 4.1). The difference appeared to be driven by the high value in 1998 and the low values in 2009-2010. *Cossura* cf. *rostrata* represented 1 to 17% of the total polychaete density in monthly estimates and 1 to 13% in yearly estimates.

Levinsenia cf. *oligobranchiata* density was at a maximum in 2009 with 63.70 ± 15.17 ind.m^{-2} and minimal in 2005 with 4.04 ± 4.04 ind.m^{-2} (Fig. 4.2c). Significant differences in *Levinsenia* cf. *oligobranchiata* densities were found in both monthly and yearly observations over 1991-2011 and 1991-2005 (ANOVA, Table 4.1). This appeared to be driven by low values in 1993 and 2005 and by high value in 2009. *Levinsenia* cf.

oligobranchiata represented 1-14% of the total polychaete density monthly and 1 to 11% yearly.

Paradoneis cf. *lyra* highest density was found in 1991 with 96.05 ± 17.19 ind.m^{-2} and no *Paradoneis* cf. *lyra* was sampled in 2010 and 2011 (Fig. 4.2d). The absence of *Paradoneis* cf. *lyra* over 2010-2011 led to significant differences in density over 1991-2011 (ANOVA, Table 4.1). This appeared to be driven solely by the low value in 2009. Over 1991-2005 when *Paradoneis* cf. *lyra* was often the dominant species, its density was stable in time (Table 4.1). *Paradoneis* cf. *lyra* represented 1 to 17% of the monthly total polychaete densities and 1 to 11% of the yearly data.

Sphaerosyllis sp. A had a maximum density in 1996 with 130.10 ± 58. 98 ind.m^{-2} and a minimum in 2005 with 8.09 ± 8.09 ind.m^{-2} (Fig. 4.2e). Difference in *Sphaerosyllis* sp. A densities were significant monthly over 1991-2011 (ANOVA, Table 4.1) driven by a low value in February 2005. *Sphaerosyllis* sp. A accounted for 1 to 26% of the total polychaete density monthly and 1 to 14% yearly.

Overall, between 1991 and 2011, the inter-annual variations of *Cossura* cf. *rostrata* was similar to that of *Paradoneis* cf. *lyra* (r_s = 0.662, p = 0.0332, n = 10) and *Sphaerosyllis* sp. A (r_s = 0.747, p = 0.0108, n = 10). *Paradoneis* cf. *lyra* and *Sphaerosyllis* sp. A also had similar temporal variation (r_s = 0.631, p = 0.042, n = 10). Similar results were found at monthly time scale. But over 1991-2005, none of the species had similar yearly dynamics. The two species of the Paraonidae did not co-vary and exhibited different temporal responses in 1991-2011 and 1991-2005.

Table 4.1 One-way analysis of variance (ANOVA, F, p) of the density and of the median body size of Sta. M polychaete density-dominant species over time: *Aphelochaeta* sp. A, *Cossura* cf. *rostrata*, *Levinsenia* cf. *oligobranchiata*, *Paradoneis* cf. *lyra*, *Sphaerosyllis* sp. A. Two periods were tested 1991-2011 and 1991-2005 with monthly and yearly estimates. Significant ANOVA are in bold ($p < 0.05$).

Period/Location	Species	Density				Median body size			
		month		year		month		year	
		F	p	F	p	F	p	F	p
1991-2011	*Aphelochaeta* sp. A	**3.150**	**0.040**	**3.100**	**0.016**	2.210	0.111	**3.500**	**0.009**
	Cossura cf. *rostrata*	2.580	0.078	**5.540**	**0.001**	1.370	0.323	**4.080**	**0.004**
	Levinsenia cf. *oligobranchiata*	**8.000**	**0.001**	**7.640**	**< 0.001**	1.87	0.168	1.630	0.448
	Paradoneis cf. *lyra*	1.440	0.293	**3.610**	**0.012**	**4.630**	**0.017**	**6.880**	**0.010**
	Sphaerosyllis sp. A	**3.170**	**0.039**	2.200	0.065	0.860	0.632	1.340	0.279
1991-2005	*Aphelochaeta* sp. A	1.660	0.255	**2.780**	**0.045**	2.680	0.070	**3.720**	**0.015**
	Cossura cf. *rostrata*	1.680	0.383	**2.810**	**0.041**	0.240	0.383	**3.500**	**0.018**
	Levinsenia cf. *oligobranchiata*	**9.710**	**0.001**	**9.240**	**< 0.001**	2.450	0.090	1.370	0.283
	Paradoneis cf. *lyra*	0.660	0.771	1.400	0.266	**4.170**	**0.024**	**6.50**	**0.001**
	Sphaerosyllis sp. A	**3.520**	**0.031**	1.910	0.134	0.980	0.529	1.220	0.343

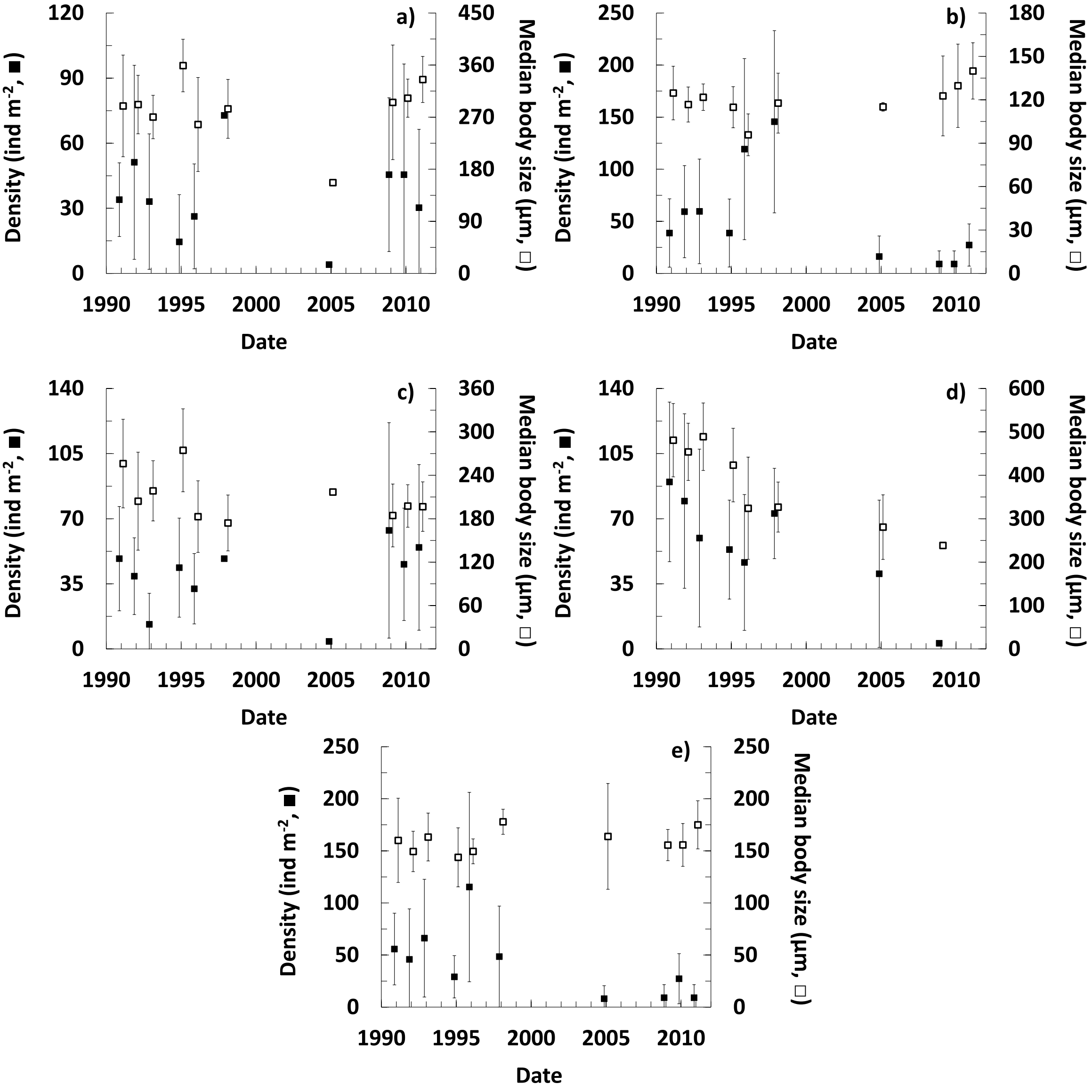

Figure 4.2 Mean densities (■, ind.m^{-2}) and median body sizes (□, µm) over year with associated standard deviation for (a) *Aphelochaeta* sp. A, whose density and body size were significantly different over years owing to 2005 values, (b) *Cossura* cf. *rostrata,* whose density and body size were significantly different over years, (c) *Levinsenia* cf. *oligobranchiata* whose density only was significantly different over years, (d) *Paradoneis* cf. *lyra*, whose density and body size were significantly different over years with no individual found after 2009, (e) *Sphaerosyllis* sp. A, whose density only was significantly different over months, not years.

4.3.2 Polychaete species body size dynamics

Three species significantly varied at intra- and inter-annual scales in terms of body size: *Aphelochaeta* sp. A, *Cossura* cf. *rostrata, Paradoneis* cf. *lyra*. Monthly figures are given in Appendix E.1, E.2.

Aphelochaeta sp. A median body size significantly varied yearly over 1991-2011 and 1991-2005 (Table 4.1). The difference was driven by the low values in 2005. Overall

Aphelochaeta sp. A median body size was the smallest in 2005 with a157 µm and was the biggest in 1995 with 376.96 µm (Fig. 4.2a).

Cossura cf. *rostrata* median body size was the smallest in 1996 with 94 µm and was the biggest in 2011 with 149.62 µm (Fig. 4.2b). *Cossura* cf. *rostrata* median body sizes were significantly different between yearly data only in the 1991-2011 and 1991-2005 periods (ANOVA, Table 4.1). The differences were driven by low value in 1996 and high values in 1992 and 2010.

Levinsenia cf. *oligobranchiata* had the smallest median body size in 1998 with 178.66 µm and the biggest in 1995 with 299.85 µm (Fig. 4.2c). *Levinsenia* cf. *oligobranchiata* median body sizes were not significantly different over time in the 1991-2011 or 1991-2005 period (ANOVA, Table 4.1).

Paradoneis cf. *lyra* median body size was the smallest in 2010 with 238.41 µm and was the biggest in 1993 with 533.71 µm (Fig. 4.2d). *Paradoneis* cf. *lyra* median body sizes were significantly different at monthly and yearly time scale over 1991-2011 and 1991-2005 periods (ANOVA, Table 4.1). Yearly differences were driven by low values in 1996 and 2009 and high values in 1993.

Sphaerosyllis sp. A median body size was the smallest in 1992 with 139.54 µm and was the biggest in 2011 with 187.29 µm (Fig. 4.2e). *Sphaerosyllis* sp. A median body sizes were not significantly different over time in the 1991-2011 or 1991-2005 period (ANOVA, Table 4.1).

At monthly time scale over 1991-2011, *Aphelochaeta* sp. A and *Cossura* cf. *rostrata* median body sizes were significantly correlated to each other ($r_s = 0.464$, $p = 0.034$, $n = 22$) as well as *Paradoneis* cf. *lyra* and *Sphaerosyllis* sp. A ($r_s = -0.497$, $p = 0.050$, $n = 22$). No inter-species correlation in median body size occurred over 1991-2005 at monthly or yearly time scales. No intra-species correlations between density and median body size of each was found over 1991-2005 (Table 4.2). Significant yearly correlations were however found in the case of *Cossura* cf. *rostrata* and *Paradoneis* cf. *lyra* over 1991-2011 (Table 4.2). The former decreased in size when its density was higher and the latter decreased in size when its density was lower.

4.3.3 Polychaete species body size spectra

The body size spectra (DBSs) of several species were significantly different over years between 1991 and 2011: *Cossura* cf. *rostrata* (ANOSIM, R = 0.252, p = 0.026) and *Paradoneis* cf. *lyra* (ANOSIM, R = 0.555, p = 0.002). Over 1991-2005, only *Paradoneis* cf. *lyra* DBS was significantly different at inter-annual scale (ANOSIM, R = 0.426, p = 0.004). DBS-MDSx were significantly correlated to median body sizes: 1) at monthly time scale for all species except *Levinsenia* cf. *oligobranchiata* over 1991-2011 and 1991-2005 (Table 4.2); 2) at yearly time scale, only for *Aphelochaeta* sp. A and *Paradoneis* cf. *lyra* over 1991-2011 and only for *Paradoneis* cf. *lyra* over 1991-2005 (Table 4.3). In addition, DBS-MDSx were significantly different when the monthly body size was either higher or lower than the overall median: 1) for all species except for *Cossura* cf. *rostrata* over 1991-2011; 2) for *Paradoneis* cf. *lyra* and *Sphaerosyllis* sp. A over 1991-2005 (Table 4.3). Overall, results indicated that the median was a reasonable descriptor of the overall DBS at monthly time scale (Table 4.3). At yearly time scale, change in DBS-MDSx over time were continuous and monotonic for *Cossura* cf. *rostrata*, *Paradoneis* cf. *lyra* and *Sphaerosyllis* sp. A over 1991-2011 and for *Aphelochaeta* sp. A and *Paradoneis* cf. *lyra* over 1991-2005 (Table 4.3).

There was no clear indication of potential recruitment events in the monthly or yearly species DBS except for *Cossura* cf. *rostrata* in 1996 (see Appendix E.3-E.7). For this species, the monthly and yearly body size medians were lower than the overall median in 1996 and only in 1996. Occurrences of specimens with reproductive tissues and of juveniles were observed almost year round for *Sphaerosyllis* sp. A. By contrast, reproductive/juvenile specimens were mostly observed in November and February for *Levinsenia* cf. *oligobranchiata* and between May-October for *Aphelochaeta* sp. A (Table 4.4, see also Appendix E.8, E.9).

Table 4.2 Spearman rank correlations (r_s) between median body size and density and between median body size and body size spectra multidimensional scaling (DBS-MDSx) x-ordinates for Sta. M polychaete density-dominant species: *Aphelochaeta* sp. A, *Cossura* cf. *rostrata, Levinsenia* cf. *oligobranchiata*, *Paradoneis* cf. *lyra*, *Sphaerosyllis* sp. A. Two periods were tested 1991-2011 and 1991-2005 with monthly and yearly estimates. Correlations are given with p-value and n, the number of data used for computation. Significant correlations are in bold ($p < 0.05$).

Period/Location	Species	Density *vs.* median body size						Median body size *vs.* DBS-MDSx					
		Month			Year			Month			Year		
		r_s	p	n	r_s	p	n	r_s	p	n	r_s	p	n
1991-2011	*Aphelochaeta* sp. A	0.295	0.194	21	0.254	0.479	10	**0.499**	**0.021**	**21**	**0.806**	**0.003**	**10**
	Cossura cf. *rostrata*	**-0.438**	**0.041**	**22**	**-0.657**	**0.039**	**10**	**0.616**	**0.002**	**22**	0.497	0.126	10
	Levinsenia cf. *oligobranchiata*	-0.016	0.945	21	-0.005	0.988	10	0.350	0.127	20	0.370	0.275	10
	Paradoneis cf. *lyra*	0.271	0.292	17	**0.662**	**0.044**	**8**	**0.785**	**< 0.001**	**16**	**0.929**	**< 0.001**	**7**
	Sphaerosyllis sp. A	-0.153	0.508	21	-0.347	0.326	10	**0.787**	**< 0.001**	**21**	0.552	0.089	10
1991-2005	*Aphelochaeta sp. A*	0.337	0.219	15	0.284	0.537	7	**0.725**	**0.002**	**15**	0.214	0.602	7
	Cossura cf. rostrata	-0.285	0.285	16	-0.547	0.204	7	0.150	0.571	**16**	0.393	0.341	7
	Levinsenia cf. oligobranchiata	0.257	0.356	15	0.256	0.579	7	0.209	0.441	**15**	0.429	0.297	7
	Paradoneis cf. lyra	0.106	0.695	16	0.438	0.325	7	**0.826**	**< 0.001**	**16**	**0.786**	**0.025**	7
	Sphaerosyllis sp. A	0.024	0.934	15	-0.256	0.657	7	**0.607**	**0.016**	**15**	0.107	0.781	7

Table 4.3 Correlations (r_s) between body size spectra multidimensional scaling (DBS-MDSx) x-ordinates and time and ANOSIM comparisons (R, 999 permutations) between DBS-MDSx and deviation (positive or negative) from the overall median body size for Sta. M polychaete density-dominant species *Aphelochaeta* sp. A, *Cossura* cf. *rostrata*, *Levinsenia* cf. *oligobranchiata*, *Paradoneis* cf. *lyra*, *Sphaerosyllis* sp. A. Two periods were tested 1991-2011 and 1991-2005 with monthly and yearly estimates. Correlations are given with p-value and n, the number of data used for computation. Significant correlations/ANOSIM are in bold ($p < 0.05$).

Period/Location	Species	DBS-MDSx *vs.* time						DBS-MDSx *vs.* deviation			
		month			year			month		year	
		r_s	p	n	r_s	p	n	R	p	R	p
1991-2011	*Aphelochaeta* sp. A	0.167	0.456	21	0.134	0.713	10	**0.331**	**0.001**	0.020	0.397
	Cossura cf. *rostrata*	**0.566**	**0.006**	**22**	**0.699**	**0.025**	**10**	0.154	0.147	0.296	0.400
	Levinsenia cf. *oligobranchiata*	0.158	0.982	20	0.214	0.552	10	**0.145**	**0.027**	0.175	0.103
	Paradoneis cf. *lyra*	**0.785**	**< 0.001**	**16**	**0.671**	**0.034**	**7**	**0.501**	**0.002**	**0.796**	**0.029**
	Sphaerosyllis sp. A	0.156	0.488	21	**0.649**	**0.042**	**10**	0.171	0.068	0.067	0.281
1991-2005	*Aphelochaeta sp. A*	**0.612**	**0.012**	15	**0.923**	**0.023**	**7**	0.143	0.076	-0.111	0.771
	Cossura cf. rostrata	0.052	0.848	16	0.334	0.464	**7**	0.276	0.059	0.400	0.286
	Levinsenia cf. oligobranchiata	**0.592**	**0.016**	15	0.686	0.089	**7**	0.049	0.226	0.352	0.086
	Paradoneis cf. lyra	**0.683**	**0.004**	16	**0.848**	**0.016**	**7**	**0.519**	**0.003**	**0.741**	**0.029**
	Sphaerosyllis sp. A	**0.592**	**0.016**	15	0.569	0.183	**7**	**0.213**	**0.018**	-0.111	0.743

Table 4.4 Occurrences of specimens with reproductive tissues and of juveniles of Sta. M density-dominant species over 1991-2011: *Aphelochaeta* sp. A, *Cossura* cf. *rostrata*, *Levinsenia* cf. *oligobranchiata*, *Paradoneis* cf. *lyra*, *Sphaerosyllis* sp. A according to a Julian year. Occurrences of specimens with reproductive tissues are in plain text. Occurrences of juveniles are in bold italic.

Species	Jan-Feb	Mar-Apr	May-Jun	Jul-Aug	Sept-Oct	Nov-Dec
Aphelochaeta sp. A		1998	***2010***	1991	1996	
Cossura cf. *rostrata*				***1998***		***1998***
Levinsenia cf. *oligobranchiata*	1995, 2009 ***1995, 2009***		2011			2010, 2011
Paradoneis cf. *lyra*			***1992***			
Sphaerosyllis sp. A	1991, 1993, 1995, 1996 ***1996***	1998	1996	1998	***1991***	1993

4.3.4 Polychaete species relationships with megafauna and environmental factors

Over 1991-2011, two polychaete species were related to megafauna dynamics. *Aphelochaeta sp. A* density (r_s = 0.553, p =0.022) and body size (r_s = 0.510, p = 0.037) dynamics were correlated with *Abyssocucumis abyssorum* dynamics. *Cossura* cf. *rostrata* was correlated with *Oneirophanta mutabilis* in terms of density (r_s = -0.619, p = 0.008) and body size (r_s = -0.556, p = 0.020). Correlations with megafauna over 1991-2005 are reported in Appendix E.10.

All polychaete species except *Aphelochaeta sp. A* had significant correlations with POC flux over 1991-2011 with species specific time lag between 4 and 9 months (Table 4.5) *Levinsenia* cf. *oligobranchiata* was the only species having a positive relationship with POC flux. Considering only the period 1991-2005, only *Cossura* cf. *rostrata* was significantly related to POC flux.

Table 4.5 Significant ($p < 0.05$) Spearman rank cross correlations (r_s) made between monthly polychaete species and monthly POC flux for the periods1991-2011 and 1991-2005, where polychaete variables were allowed to lag changes in POC flux by monthly time steps of up to 11 months. The type of polychaete data used: D for density, B for body size.

Period/Location	Species	Data type	r_s	p	Time lag
1991-2011	*Cossura* cf. *rostrata*	D	-0.651	0.003	4
		B	-0.610	0.004	5
	Levinsenia cf. *oligobranchiata*	D	0.519	0.029	7
		B	0.529	0.025	7
	Paradoneis cf. *lyra*	D	-0.518	0.021	9
		B	-0.447	0.050	9
	Sphaerosyllis sp. A	D	-0.641	0.002	6
		B	-0.555	0.010	6
1991-2005	*Cossura* cf. *rostrata*	D	-0.642	0.012	4
		B	-0.636	0.013	4

4.4 Discussion

4.4.1 Dynamics of density and body size of the density-dominant polychaete species at Sta. M

Variations in the densities and body sizes of the five density-dominant polychaete species were linked to temporal changes rather than spatial heterogeneity. These inter-annual variations were observed when considering one or both Sta. M sampling location(s).

Therefore, these temporal changes were unlikely to be an artefact due to spatial variability. The variations were significant for all species except for *Sphaerosyllis* sp. A and each species had different dynamics. The years accounting for the difference in density and body size dynamics were also different depending on the species. So despite several species having a correlation between time and density and/or body size (e.g. *Cossura* cf. *rostrata* and *Paradoneis* cf. *lyra*), the differences in their dynamics were likely linked to different mechanisms and/or response times. For all the species, the density/body size dynamics appeared irregular (i.e. not periodic). In the case of *Aphelochaeta* sp. A, the differences in density and body size was even due to low values in a single year, 2005, suggesting a unique event. Such irregularity and species differentially preclude prediction of polychaete species and assemblage dynamics at Sta. M.

Distinguishing cohorts in the polychaete species body size spectra was challenging. Several factors may account for it: 1) despite being the five density-dominant species over the 20 year time series, the actual number of specimens for each species was potentially low to detect cohorts with confidence. 2) The larvae mortality rate for which no *in situ* study exists may have been high and/or variable. Tyler (1988) suggested that high post-larval mortality after successful recruitment might frequently occur. In the deep sea, the post-larval bottleneck theory suggests that body-size related constraints on nutrition of post-larvae, competition with microphage deposit feeders, and vulnerability to non-selective grazing by larger deposit feeders create a restrictive transition between the post-larval and sub-adult/adult groups (Jumars et al., 1990, Gage, 1994). 3) The growth rate to adult sizes may be faster than can be observed with current samples. Fast and slow growth rates of deep-sea species have been observed (Gage and Tyler, 1991, Gage, 1994, Vanreusel et al., 2001, Gage et al., 2004). However, the fastest growth rates reported were of about one year (*Capitella* sp., *Laonice* sp., recolonization tray experiments, Snelgrove et al., 1996) suggesting that observation of several cohorts in density body size spectra taken less than a year apart should have been possible. 4) With a variable number and time of deployments per studied year, unquantified intra-annual variation may have further obfuscated cohort detection.

Overall, few juveniles were recorded and few could be related to an adult species (Appendix E.9 and E.11). In the case of *Sphaerosyllis* sp. A, specimens with reproductive tissues and juveniles were observed all year round (Table 4.4) between 1991 and 2005 suggesting that the species may have opportunistic reproduction/recruitment. Young

(2003) suggested that continuous reproduction may be frequent in deep-sea polychaetes. By contrast, reproductive specimens of *Levinsenia* cf. *oligobranchiata* mainly occurred between November and February after 2009. *Levinsenia* cf. *oligobranchiata* may have a more seasonal reproduction pattern but care must be taken to not over-interpret these data as the latter are only based on three years of sampling (encompassing three different months). Not enough juveniles were observed for the three other species. Incorporating meiofauna data as suggested by Vanreusel et al. (2001) may increase the record of juveniles because adult deep-sea polychaetes are close in size to the meiofauna (32-250 µm). Their juveniles may likely appear first in the meiofaunal fraction as observed for an Opheliidae species at the Porcupine Abyssal Plain in the North East Atlantic in 1996-1998 (Vanreusel et al., 2001). Vanreusel et al. (2001) concluded that a holistic approach, rather than the examination of segregated size categories, was necessary to address the life cycle of deep-sea polychaetes. Overall, deep-sea macrofauna sampling needs to be improved to collect a larger number of specimens with greater precision.

4.4.2 Polychaete species life-history events related to density and body size dynamics

The five polychaete species appeared to have different mechanisms involved in their population dynamics. The interpretation of these mechanisms was complicated by the change of sampling location after 2005. Two scenarios can be proposed: 1) different polychaete assemblages were sampled before and after 2005. Under the later assumption, none of the species had a significant relationship between their density and body size. The lack of correlation between density and body size may be real or due to uneven temporal sampling, small-scale spatial heterogeneity (sampler size), low statistical power preventing detection of such relationships. 2) The same polychaete assemblage was sampled from 1991 to 2011 .Even under this scenario, processes behind inter-annual variations of *Aphelochaeta* sp. A, *Levinsenia* cf. *oligobranchiata* and *Sphaerosyllis* sp. A densities remained unclear as none of these species had a significant relationship between their density and body size. In the case of *Paradoneis* cf. *lyra* and *Cossura* cf. *rostrata* different life-history events appeared to be linked to their population dynamics.

Under the assumption of a single sampled polychaete assemblage, *Paradoneis* cf. *lyra* shifted in density over the time-series without obvious indication of reproductive events. *Paradoneis* cf. *lyra* density positively co-varied with the median body size at inter-annual scale. Such a relationship may indicate: 1) an increased survivorship of *Paradoneis* cf. *lyra* at a larger size; 2) a migration of adults from the neighbouring continental shelf and canyon. This hypothesis could be supported by the fact that only one juvenile specimen and none with reproductive tissues were sampled over the whole time series. However, in the case of a migration of similarly sized individuals, the body size would be far less likely to shift in synchrony with density (Ruhl, 2007); 3) a lower survivorship of smaller specimens due to predation, disease, or size specific competitive interactions (Ruhl, 2007). No information exists on predation rate and disease of macrofauna at the abyssal seafloor while the role of competition remains unclear (Wilson, 1990, Gage, 2004) and is further discussed below.

Still under the assumption of a single sampled polychaete assemblage, *Cossura* cf. *rostrata* density and body size inter-annual dynamics suggested that individuals shift between growth and reproduction over time. In contrast to *Paradoneis* cf. *lyra*, *Cossura* cf. *rostrata* density negatively co-varied with the median body size at yearly time scale. The negative correlation between density and body size was not significant when only considering 1991-2005. However the highest density of the species occurred during this period, in 1996-1998, when the median body size was the smallest suggesting a reproduction/recruitment event might have occurred. The event may have been: 1) real and was not picked up by the statistics due to high variability linked for example to a patchy recruitment; 2) due to stochastic variations. No specimens with reproductive tissues were observed except in 1998 but there was hiatus in sampling between February 1995 and the first density peak in 1996 and a gap of two years between the peaks in 1996 and 1998 when reproductive specimens may have occurred. However, juveniles were observed in 1998 suggesting recruitment did occur. When including 2009-2011, the correlation between the density and body size became significant. During this period, *Cossura* c.f. *rostrata* density decreased and body size increased. The individuals may have shifted from reproduction to growth or reproduced at a later stage (Paterson et al., 2006).

4.4.3 Links between polychaete species, megafauna and food supply dynamics

Environmental factors may partly control the dynamics of the polychaete species as suggested by the correlations between the megafauna and polychaete species dynamics. The correlations were negative between *Cossura* cf. *rostrata* and *Oneirophanta mutabilis* and positive between *Aphelochaeta sp. A* and *Abyssocucumis abyssorum.* None of the latter holothurian species were dominant at Sta. M (Ruhl, 2007, Kuhnz et al., 2014). Negative correlations may be indicative of competition, predation or opposite response to an environmental factor whereas positive correlations may be indicative of facilitation or similar responses to a common environmental factor. Deciphering polychaete-holothurian ecological interactions remains difficult due to a lack of data/direct observations in the deep sea and the fact that several processes may be interrelated over time. The megafauna may positively interact with polychaetes *via* bioturbation leading to oxygenation of sediments and mixing of organic matter to deeper depths (Thistle et al., 2008). In the same time, ingesting the bulk of phytodetritus pulses and having a more direct access to more liable food (Bett et al., 2001), holothurians may change the quantity and/or quality of the food available to polychaetes.

The POC flux dynamics appeared to be a potential factor influencing the polychaete species dynamics as observed for megafauna (Ruhl and Smith, 2004, Smith et al., 2009). Four of the five studied polychaete species were correlated to POC flux with specific lag between 4 and 9 months. Inter-annual variation in food supply may influence polychaete dynamics via impact on reproduction/recruitment, migration, recruitment, and survivorship. For both *Cossura* cf. *rostrata* and *Paradoneis* cf. *lyra,* a negative correlation was found with POC flux. After 2009, *Paradoneis* cf. *lyra* was not present in the sample anymore at a time when the food pulses reaching the seafloor at Sta. M increased in magnitude (Smith et al., 2013). The greater proportion of opportunistic species of spionids, cirratulids and paraonids may have out-competed *Paradoneis* cf. *lyra*. In particular, *Levinsenia* cf. *oligobranchiata* became the most dominant Paraonidae species and had a significant positive correlation to POC flux. Differential responses of species, some favoured under low food supply and other under high food supply are indicative of competitive interactions for a common resource. The increase in POC flux quantity and quality that occurred in 2007 (Smith et al., 2013) may have favoured the opportunistic *Levinsenia* cf. *oligobranchiata.* In the case of *Cossura* cf. *rostrata,* the change in POC flux may have shifted the way individual shared resource between growth and reproduction (Paterson et al., 2006). Variations in food quality and quantity have been shown to influence size of females and other fecundity features in polychaetes (Levin, 1986, Levin and Creed, 1986, Grémare et al., 1988, Marsh et al., 1989, Qian and Chia, 1991, Grémare, 1994). *Cossura* reproduction could have been favoured in 1996-1998 whereas growth was favoured in 2009-2011.

4.5 Conclusions

The cirratulid *Aphelochaeta* sp. A, the cossurid *Cossura* cf. *rostrata*, the paraonids, *Levinsenia* cf. *oligobranchiata* and *Paradoneis* cf. *lyra*, and the syllid, *Sphaerosyllis* sp. A had significant variability in density and/or median body size at an inter-annual scale. Each species displayed different temporal dynamics. The processes behind these dynamics remain unclear as polychaete population parameters such as larval mortality rate, growth rate to adult size may be faster than can be observed with the current sampling frequency. Under the assumption that only one polychaete population was sampled over the time series, *Paradoneis* cf. *lyra* dynamics may be related processes such as enhanced survivorship during period of low food supply. By contrast, *Cossura* cf. *rostrata* increased density was linked to decreased body size suggesting shifts between growth and reproduction over time with a higher proportion of larger individuals under higher food supply. Observation of reproductive specimens suggested that reproduction was opportunistic and/or year-round for *Cossura* cf. *rostrata* and *Sphaerosyllis* sp. A and maybe periodic for *Levinsenia* cf. *oligobranchiata*. Understanding natural variations in deep-sea polychaete assemblages is critical to assess anthropogenic impacts on abyssal ecosystems. Such understanding need to be improved by further studying abyssal population parameters: life-span, growth rate, reproduction, and biological interactions. Future work to better constrain processes driving temporal changes in polychaete species and carbon cycling at abyssal seafloor might include: 1) longer data sets to assess the predictability of dynamics detected for each species; 2) jointly study of meiofaunal and macrofaunal polychaetes to detect juveniles; 3) an increased intra-annual sampling to investigate shorter term variations.

References of chapter 4

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Chapter 5

Inter-annual species-level variations in an abyssal polychaete assemblage (Sta. M, NE Pacific, 4000 m)

This chapter is a modified version of two papers:

- Laguionie-Marchais, C., Bett, B.J., Smith, K.L.Jr., Paterson, G.L.D. Ruhl, H.A. Inter-annual species-level variations in an abyssal polychaete assemblage (Sta. M, NE Pacific, 4000 m). Progress in Oceanography Accepted.

- Laguionie-Marchais, C., Bett, B.J., Smith, K.L.Jr., Paterson, G.L.D. Ruhl, H.A. Abyssal polychaete size spectra, metabolic theory and macroecology. Marine Ecological Progress Series (in preparation)

Abstract

Understanding the dynamics of abyssal community structure and function has become increasingly important as deep-sea resource exploitation and climate change pressures are expected to ramp up. This time-series study investigates macrofaunal polychaete dynamics at a station in the North East Pacific (Sta. M; 35˚ N 123˚ W, 4000 m, 1991-2011). Infaunal polychaete species were identified and their proxy biomass and proxy energy use rate estimated. The assemblage comprised 167 species, having a composition consistent with other abyssal areas globally. Significant changes in univariate and multivariate parameters (rank abundance distribution, Simpson's diversity index, and species and functional group composition) were detected across 1991-2011. However, no change in biomass or energy use rate was apparent through the time-series. The largest changes in the polychaete assemblage coincided with both an increase in sinking particulate organic carbon flux to the seafloor in 2007, and a 40 km relocation of the sampling location to a site 100 m shallower, preventing a conclusive assessment of which might drive the observed variation. Analyses prior to the change of sampling location showed that the polychaete assemblage composition dynamics were primary driven by food supply variation. Changes in several species were also lagged to changes in POC flux by 4 to 10 months. The polychaete fauna exhibited a significant positive relationship between total density and total energy use rate, suggesting population-level tracking of a common resource (e.g. POC flux food supply). Neither compensatory nor energetic zero-sum dynamics were detected among the polychaete assemblage, but the results suggest that the latter occur in the macrofaunal community as a whole. The polychaete assemblage followed the predictions of the metabolic theory indicating some stability in the body size structure. Overall, the results do indicate: 1) potential control of species composition, and the density of

individual key species, by food supply, when the time-series prior to the sampling location was analysed separately; 2) generally sensitive detection of environmental change by species-level analysis of the abyssal polychaete assemblage.

5.1 Introduction

Temporal changes in food supply, quantified as particulate organic carbon (POC) flux, have been shown to influence abyssal benthic communities (e.g. Ruhl and Smith, 2004, Smith et al., 2009, Billett et al., 2010). However, the mechanisms by which environmentally-driven resource variations impact the structure and function of abyssal faunas are challenging to disentangle. A better understanding of the ecological and biogeochemical processes behind these dynamics is necessary to assess: 1) how deep-sea systems will respond to climate change (Mora et al., 2013, Jones et al., 2014); 2) increasing seabed resource exploitation (Ramirez-Llodra et al., 2011); 3) how long-term carbon cycles such as remineralisation, bioturbation, and burial (Smith et al., 2009), are influenced by benthic community dynamics. Significant inter-annual changes have been observed in abyssal macrofaunal communities (North East Pacific, Ruhl et al., 2008; North East Atlantic, Soto et al., 2010, Laguionie-Marchais et al., 2013) as exemplified by polychaetes, typically the dominant macrofaunal taxon (Paterson et al., 2009).

One of the longest time-series studies of abyssal system dynamics has been conducted at Station M (Sta. M) in the North-East Pacific. Over 25 years of study, the POC flux reaching the benthos underwent significant variations both in quantity and quality (Smith et al., 2006, 2013). In turn, POC flux variations have driven changes in the structure and function of the benthic community, in particular the mobile epibenthic megafauna (Ruhl and Smith, 2004, Kuhnz et al., 2014, Ruhl et al., 2014).

The extent to which mechanisms of megafaunal change can be generalised to other abyssal faunal groups is not known. At the Porcupine Abyssal Plain in the North East Atlantic, changes in megafaunal composition and density were also observed at macro- and meio-faunal levels (Billett et al., 2010). At Sta. M, the macrofauna is dominated by polychaetes that varied between 1991-2005 in terms of total density, family and functional group compositions, and in family rank abundance distributions (RADs; Laguionie-Marchais et al., 2013). The latter authors showed that potential relationships between POC flux and polychaete assemblage attributes were complex. Polychaete and megafauna density changes occurred in apparent positive correlation suggesting that common external factors may be driving dynamics across the different faunal groups. Sta. M polychaetes have been shown to respond within days to the input of fresh phytodetritus during feeding experiments (Witte et al., 2003, Sweetman and Witte, 2008, Jeffreys et al., 2013). Variations in the Sta. M polychaete fauna might then be expected to depend directly on food supply, with the deep sea generally regarded as a food limited environment (Rex and Etter, 2010).

Resource limitation is a central concept in many ecological theories, whether niche-based or neutral (Tilman, 1982, Hubbell, 2001). It gives an ultimate limit to total community-level carrying capacity (e.g. Ernest and Brown, 2001). Under compensatory dynamics, density compensation should occur where any increase in the density of one species is compensated by a decrease in others, **Hypothesis A:** species covariance will be significantly negative (see 2.4 below). Note that species level compensatory dynamics may occur with or without community level compensation (Gonzalez and Loreau, 2009). Ernest et al. (2008) suggested that energetic demand may be a more suitable currency than density to address the occurrence of compensatory dynamics. Further they suggest that under a metabolism-based zero-sum framework there could be a direct trade-off between population density and mean individual energy use rate (see also Ernest et al., 2009), **Hypothesis B:** under zero-sum dynamics, there will be a significant negative relationship between density and mean individual energy use.

Body size is a key predictor of individual energy use rate (e.g. Peters and Wassenberg, 1983), and the importance of size-related mechanisms in structuring communities is another important field of research in ecology (White et al., 2007, Isaac et al., 2013). Smaller organisms tend to have a higher mass-specific consumption rate than larger organisms (Brown et al., 2004). So for a constant limiting resource, a lower total biomass of small organisms can be supported relative to larger organisms (Gerlach et al., 1985, Ernest, 2005, Ernest et al., 2009). Benthic size spectra may be a useful tool in assessing the trade-offs between body size, density and energetic requirements (Bett, 2013, Kelly-Gerryn et al., 2014). Two main hypotheses have been proposed: the energetic equivalence rule (EER) with an equal division of resource among geometric size classes (e.g. Savage et al., 2004), **hypothesis C,** or an unequal division as some body sizes preferentially access the resource**:** non-uniform resource use size spectra (Ernest, 2005). Under the hypothesis of equitable resource use across geometric body mass classes (e.g. "energetic equivalence rule" Damuth, 1987), metabolic theory predicts that faunal density should fall with mass to a -3/4 power with increasing geometric class, that biomass should increase predicts with 1/4 power while total metabolism should remain approximately constant. In addition, size class richness should decrease with -3/8 power of the mass (Siemann et al., 1996, 1999, Bett, 2013, 2014).

In this study, a range of polychaete assemblage descriptors (density, biomass, rate of energy use, diversity, species composition, functional group composition, and rank abundance distributions) were examined to test: 1) if inter-annual variations in assemblage structure and dynamics are detectable; 2) if assemblage variation is linked to food supply; 3) if there is evidence for compensatory dynamics (**Hypothesis A**) and/or zero-sum dynamics (**Hypothesis B**); 4) if polychaete assemblage follows EER body size spectra predictions (**hypothesis C**).

5.2 Materials and Methods

5.2.1 Study areas, macrofauna sampling and species identification

Data from twenty-two research cruises (Table 5.1) from 1991 to 2011, were used conducted at Sta. M in the North East Pacific (Smith and Druffel, 1998). To accommodate the water depth limitations of the remotely operated vehicles *Tiburon* and *Doc Ricketts* used during later collections, the sampling area was relocated some 40 km between the 1991-2005 period (34^{o} 50´ N, 123˚00´ W, c. 4100 m water depth) and the present (35^{o} 10´ N, 122^{o} 59´ W, c. 4000 m water depth; Fig. 5.1). Macrofauna were sampled with a free-vehicle grab respirometer (FVGR; Smith et al., 2001), a system comprised of four 413-cm^{2} grabs that collected the top 15 cm of the sediment column (Table 5.1). After recovery, sediment from each grab was sieved through a 300 µm mesh and preserved in 10% borax-buffered formalin solution.

Table 5.1 Station M macrofauna samples assessed, date and location (Lat. for latitude and Long. for longitude), number of grabs (and deployments) available per month.

Year	Month	Grab (deployments)	Lat. ˚N	Long. ˚W
1991	Jun	7 (2)	34.90	123.05
	Oct	3 (1)	34.88	123.11
1992	Feb	5 (2)	34.88	123.12
	Jun	5 (2)	34.91	123.11
	Jul	3 (1)	34.78	122.95
	Oct	6 (2)	34.85	123.15
1993	Feb	3 (1)	34.79	122.92
	Jul	3 (1)	34.82	123.07
	Nov	5 (2)	34.80	122.93
1995	Feb	5 (2)	34.93	123.12
1996	Feb	4 (2)	34.72	122.98
	Jun	3 (1)	34.68	122.94
	Oct	5 (2)	34.69	122.90
1998	Aug	3 (2)	34.78	123.03
2005	Feb	3 (1)	34.85	123.20
	Jun	3 (1)	34.93	123.25
2009	Feb	4 (1)	35.12	122.92
	Nov	4 (1)	35.14	122.92
2010	May	4 (1)	35.15	122.90
	Nov	4 (1)	35.16	122.92
2011	May	4 (1)	35.15	122.93
	Nov	4 (1)	35.14	122.93

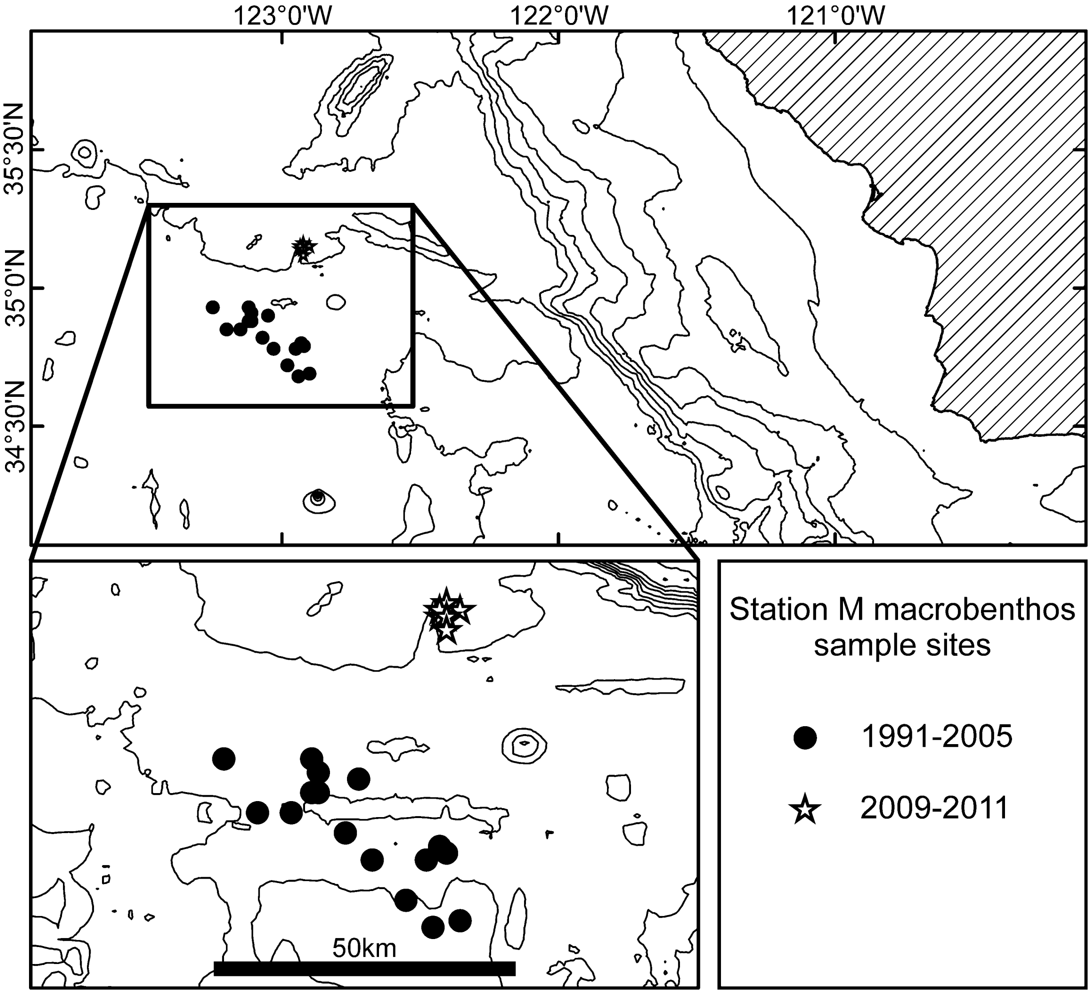

Figure 5.1 Chart showing location of Station M area, North East Pacific, 220 km off the California coast. Inset: sampling sites occupied during the two periods of study, 1991-2005 (solid symbols), 2009-2012 (open symbols).

All polychaete specimens recovered from the grab samples were identified to species level using high-power microscopes (Zeiss Discovery v20 Stereo and high power Leica DM 5000 B), published identification keys, and original taxonomic descriptions (e.g. Fauchald, 1972, 1977, 1981). I identified all the specimens of the time-series to species level. Only individuals with a head were considered in the subsequent analyses, to give an objective assessment of density and diversity with respect to individual counts (Paterson et al., 2009). Of the 3800 headed-individuals, 3646 could be classified to family level and 3077 to species level. Many species appeared to be undescribed, and were designated as sp. A, sp. B, and so forth. Each family was assigned to a single functional group among those defined by Fauchald and Jumars (1979), as detailed in Laguionie-Marchais et al. (2013) and in Table 5.2.

Table 5.2 Three-letter code key of polychaete functional groups as defined by Fauchald and Jumars (1979).

First Letter Feeding Mode	Second Letter Mobility	Third Letter Feeding Apparatus
B – Subsurface deposit feeder	D – Discretely motile	J – Jaw
F – Filter feeder	M – Motile	T – Tentacle
P - Predator	S - Sessile	X – non-armed structure
S –Surface deposit feeder		

5.2.2 Proxies of polychaete biomass and energy use rate

Of the 3077 identified specimens, only 100 were complete individuals, consequently a proxy of polychaete body volume was employed. The width of the first chaetiger (W_1) was measured for all specimens (see Paterson et al., 2006) and cubed as a proxy for individual body mass ($=W_1^3$). Proxy rates of energy use (respiration, R) were then estimated for each specimen using standard mass scaling (e.g. $\text{mass}^{3/4}$, Brown et al., 2004), such that proxy energy use rate $R = (W1^3)^{3/4} = W_1^{2.25}$. Neither a proportionality coefficient, nor a temperature coefficient was applied as *in situ* temperature was near-constant at Sta. M (Ruhl et al., 2014). Hereafter, the terms proxy biomass and proxy energy use rate are simply referred to as biomass and energy use rate.

5.2.3 Analyses of polychaete assemblage temporal variations

For the statistical analyses, the primary sampling unit was FVGR deployment. Data from individual grabs were pooled within deployment to yield deployment-level data (i.e. grabs regarded as subsamples, not independent replicates). The deployment-level data were then averaged within cruise to provide ‘month-level’ data (n = 22), and the month-level data were then averaged within year to yield give ‘year-level’ data (n = 10) (i.e. sampled months are given equal weight within year). It should be noted that time of sampling was not fixed within year. A change of primary sampling area occurred during the time-series. In terms of POC flux, the expected difference between the two sampled depths (4000 and 4100m) would be of order 2% (Martin et al., 1987), a quantity greatly out-scaled by recorded temporal variability in POC flux at Sta. M (Smith et al., 2013, Fig. 5.2). Nevertheless, to acknowledge the potential significance of the shift in sampling area during the time-series, where possible, separate tests were conducted on the 1991-2011 and 1991-2005 data (i.e. with and without the influence of the change in location).

Analysis of Variance (ANOVA, Minitab v17.1; see e.g. Sokal and Rohlf, 2012) of log(x+1) transformed month data was used to test temporal and sampling location differences for total density (D_{tot}), total biomass (B_{tot}), and total rate of energy use (R_{tot}). Diversity was assessed with estimated species richness (S_{est}), an asymptotic richness estimator (Chao1), the Shannon index, and Simpson’s index (Magurran, 2004). In each case, diversity was estimated for: 1) an individual-based rarefied sample of 91 individuals; 2) a sample-based rarefaction to the two grab level, encompassing a range of 90-113 individuals (EstimateS, v.9.1.0, Colwell et al., 2012). Comparisons of diversity were made by visual inspection of the confidence intervals produced by the EstimateS package (see e.g. Colwell, 2013, Chao et al., 2014).

Multivariate analyses of the polychaete assemblage were conducted at both species- and functional group-levels. Similarity in composition was calculated as the Bray-Curtis index, based on log(x+1) transformations of density, biomass and energy use rate at monthly and yearly time scales. 2d non-metric multi-dimensional scaling ordinations (MDS; Kruskal and Wish, 1978; Primer v.6; Clarke and Gorley, 2006) were then applied to examine the resultant similarity matrices (S_D, species density composition; S_B, species biomass composition; S_R, species energy use rate composition; S_{FD}, for functional group [FG] density composition; S_{FB}, for FG biomass composition; S_{FR}, for FG energy use rate composition). Where possible, inter-annual and sampling site changes were assessed using analysis of similarities (ANOSIM; Primer v.6; Clarke, 1993; 999 permutations employed). A nested ANOSIM, with years nested in site, was also run to investigate temporal variation without the influence of site.

MDS x- and y-ordinates were used as summary variables of species composition (MDS-x_D, species density; -x_B, species biomass; -x_R, species energy use rate; -x_{FD}, functional group [FG] density; -x_{FB}, FG biomass; -x_{FR}, FG energy use rate). These parameters were tested for potential correlations with spatial variables (latitude, longitude, water depth), and temporal variables (date, measures of food supply), using the Spearman's rank method (r_s, Minitab v17.1; see e.g. Sokal and Rohlf, 2012). For these assessments of potential temporal and spatial variations, several transformations (no transformation, square-root, fourth-root, log[x+1], presence-absence) were applied to the data in order to assess both: 1) the robustness of the results; 2) the relative importance of abundance- and identity-related changes. The measures of potential food supply tested were: 1) total POC flux in the 6-month preceding period; 2) in the 12-month preceding period; 3) total polychaete density, as a proxy of food consumption. The POC flux data (Fig. 5.2) represented a near-continuous monthly data set obtained as a composite measure from sediment trap data at 50 and 600 mab, as provided by Smith et al. (2013).

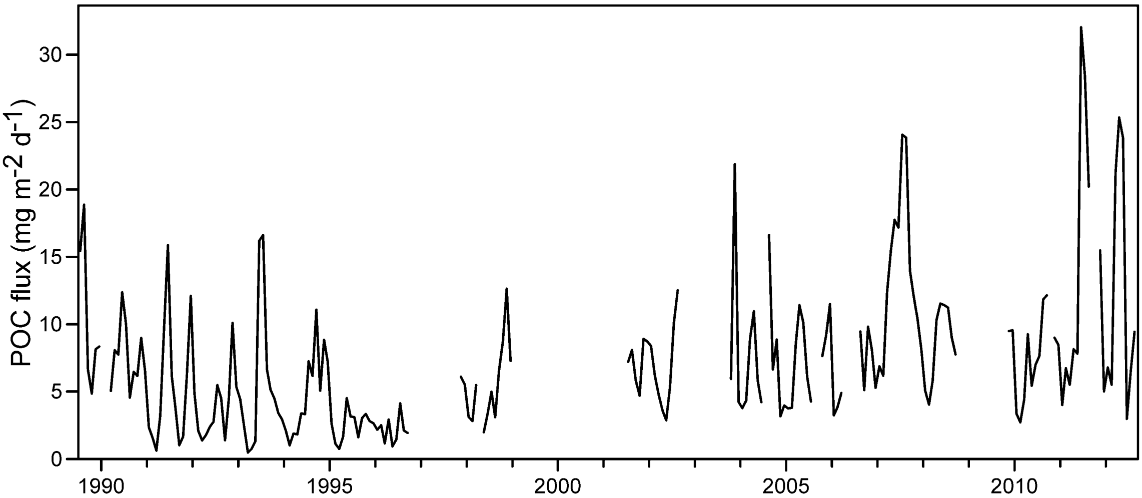

Figure 5.2 Temporal variation in particulate organic carbon (POC) flux to the seabed at Station M (data from Smith et al., 2013) displaying both intra- and inter-annual variations.

Variations in polychaete assemblage composition (density, biomass, energy use rate) were also assessed by examining rank abundance distributions. Changes in species rank switching were visualised using a method based on top-down correlation (see e.g. Zar, 1999). For each parameter separately, only the top 50 species, determined across all deployments, were included in these analyses. These top 50 species were then ranked within deployment and the rank values (1 high; 50 low) converted to Savage scores (Savage, 1956; i.e. in the 50 species case, rank 1 becomes 4.50, and rank 50 becomes 0.02), giving greater weight to higher ranks. The resultant species by deployment matrices of Savage scores were then plotted using principal component analysis (using a correlation approach; Primer v.6).

5.2.4 Analyses of potential mechanisms of change

To further assess the potential importance of food supply, correlations of polychaete assemblage parameters with 1-11 month lags in particulate organic carbon flux (for 1991-2011 and 1991-2005 periods separately) were examined. To reduce the multiplicity of correlations, species-level testing was limited to density and biomass parameters only, and included only the most abundant species. In an attempt to reduce the reporting of ‘false positive' results, the method of Benjamini and Hochberg (1995) in controlling the false discovery rate was followed.

Compensatory dynamics as defined by Houlahan et al. (2007), (**hypothesis A**) were tested using the variance ratio (VR) method (Schluter, 1984, Klug et al., 2000, Ernest and Brown, 2001, Hallett et al., 2014). Both species and functional group density, biomass and energy use rate were assessed in this manner (Eq. 5.1), with var(X) the variance across sampling units of a given parameter at the assemblage level, and var(Y_i) the variance of the same parameter at species level, for species i = 1 to n

$$VR = \frac{Var(X)}{\sum_{i=1}^{n} Var(Y_i)} \qquad \text{Eq. 5.1}$$

VR was then tested for difference from unity with a χ^2-test (VR*n distributed as χ^2; Schluter, 1984). VR values significantly less than unity suggest negative covariance among species, potentially indicative of compensatory dynamics. These tests were conducted at year, month and deployment level to assess potential compensatory dynamics at different levels of data organisation.

The energetic zero-sum dynamics hypothesis, (Ernest et al., 2008, 2009), was tested by correlation (Spearman's rank method, r_s) of geometric mean individual polychaete energy use rate with polychaete total density, D_{tot} (**hypothesis B**). Similarly, the correlation between the total energy use rate and total density was also computed.

Body size spectra were constructed using geometric size classes (doubling size classes). Spectra were constructed for assemblage density, biomass, energy use rate, number of species, and number of functional groups by pooling all data together (**hypothesis C**). The species and FG body size spectrum were constructed using the maximum biomass for each species/FG as it was not possible to use the adult female body size as no sexual decimation was conducted on the specimens. The logarithmic size spectra distributions were compared with predictions of metabolic theory and macroecology: density scales mass$^{-3/4}$, biomass scales mass$^{1/4}$, respiration scales mass^{0}, species richness scales mass$^{-3/8}$ using linear regression (F, R^2, p, Minitab v17.1, Sokal and Rohlf, 2012).

5.3 Results

5.3.1 Taxonomic results

A total of 3077 specimens were identified belonging to 167 species. Only 14 species were recorded every year: two Cirratulidae, *Aphelochaeta* sp. A and *Chaetozone* sp. A, one Cossuridae, *Cossura* cf. *rostrata*, one Fauveliopsidae, *Laubieriopsis* cf. *brevis,* one Lumbrineridae, *Abyssoninoe* sp. B, one Nephtyidae, *Aglaophamus* sp. A, one Opheliidae, *Ophelina* cf. *farallonensis,* five Paraonidae species, *Aricidea abranchiata*, *Aricidea* sp. A, B, and D, *Levinsenia* sp. A, one Pilargidae, *Ancistrosyllis* sp. A, one Syllidae, *Sphaerosyllis* sp. A. Overall, 33 species were recorded through at least 80 % of the time-series, 65 species in at least 50 % of the time-series and 50 species were recorded only in a single year. Across all samples, five species represented 30% of the total density: *Cossura cf. rostrata, Sphaerosyllis* sp. A, *Paradoneis* sp. A, *Levinsenia* sp. A and *Aphelochaeta* sp. A. One species represented 30% of the total biomass (*Notomastus* cf. *latericeus*) with four species comprising 50% of the total biomass*: N.* cf. *latericeus, N.* sp. A, *N.* sp. B and *Paradoneis* sp. A.

5.3.2 Polychaete density, biomass, energy use rate and diversity

Polychaete assemblage total density, D_{tot}, varied between years, Fig. 5.3a. The highest D_{tot} was recorded in 1998 (1232 ± 134 SE ind.m^{-2}) and the lowest in 2005 (377 ± 170 SE ind.m^{-2}) c. 3.5 fold range over the study period. Total biomass (Fig. 5.3c), B_{tot}, ranged 4.4 fold and total energy use rate (Fig. 5.3e), R_{tot}, 3.4 fold over 1991-2011. ANOVA indicated significant differences between years only in the case of D_{tot} in 1991-2011 and 1991-2005 (Table 5.3). No significant variation in D_{tot}, B_{tot}, or R_{tot} was detected between sampling locations. There was no evidence of significant variation in species diversity (Fig. 5.3b,d).

Table 5.3 ANOVA results (F statistic with degrees of freedom, dof) for variation in polychaete total density (D_{tot}), total biomass (B_{tot}), and total energy use rate (R_{tot}) by year and location. Significant ($p < 0.05$) results highlighted in bold.

Period	Polychaete	Factor	F (dof)	p-value
1991-2011	D_{tot}	Year	**5.04 (9, 21)**	**0.001**
		Location	0.33 (1. 29)	0.568
	B_{tot}	Year	1.52 (9, 21)	0.205
		Location	0.75 (1. 29)	0.394
	R_{tot}	Year	1,92 (9, 21)	0.105
		Location	0.57 (1. 29)	0.457
1991-2005	D_{tot}	Year	**5.36 (6, 18)**	**0.002**
	B_{tot}	Year	1.28 (6, 18)	0.315
	R_{tot}	Year	1.93 (6, 18)	0.131

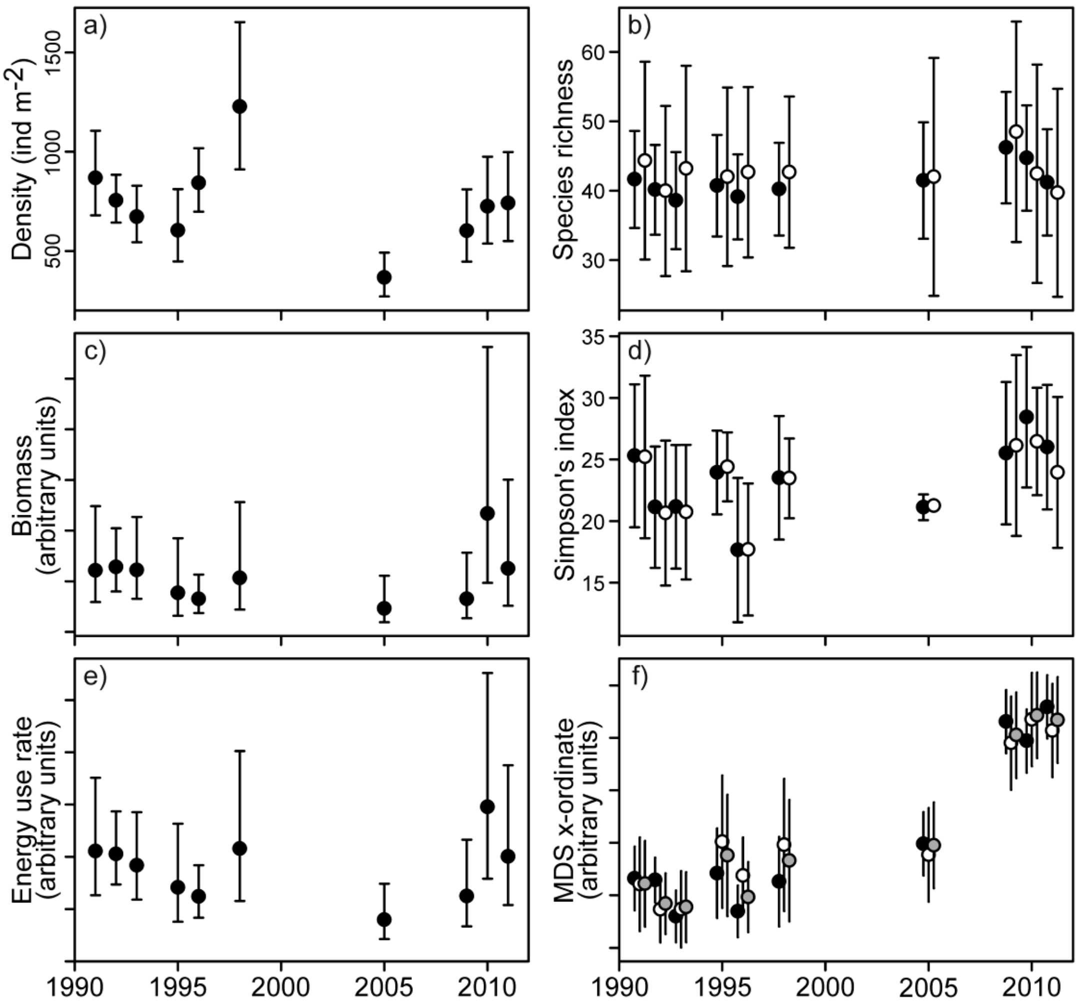

Figure 5.3 Temporal variation in annual mean polychaete assemblage parameters, shown with estimated 95% confidence intervals: a) total density, D_{tot}; b) rarefied species richness (solid symbol, 91 individuals; open symbol, two grabs); c) total biomass, B_{tot}; d) rarefied Simpson's index (inverse form; solid symbol, 91 individuals; open symbol, two grabs); e) energy use rate, R_{tot}; f) species composition represented by yearly x-ordinate of 2d non-metric multi-dimensional scaling ordination (solid symbol, density, MDS-x_D; open symbol, biomass, MDS-x_B; shaded symbol, energy use rate, MDS-x_R). Note that only D_{tot} and MDS-x ordinates are significantly different over years.

5.3.3 Species and functional group composition

Species and functional group composition varied significantly by density, biomass, and energy use rate across years and between 1991-2005 and 2009-2011 (Fig. 5.3f, Fig. 5.4 and Table 5.4). Assessed over 1991-2005 only, species composition by density, and functional group composition by density also exhibited significant differences between years ($p < 0.05$, Table 5.4). When assessed via two-way nested ANOSIM, S_D, S_B, and S_R showed highly significant ($p = 0.008$) differences between periods (locations), but no significant ($p > 0.05$) differences between years.

Table 5.4 ANOSIM results of one- and two-way nested comparisons of year and/or location for polychaete species composition (by density, S_D; biomass, S_B; energy use rate, S_R) and functional group composition (by density, S_{FD}; biomass, S_{FB}; energy use rate, S_{FR}). Significant ($p < 0.05$) results highlighted in bold.

Period	ANOSIM	Variable	Factor	R	p-value
1991-2011	1-Way	S_D	Year	**0.409**	**0.001**
			Location	**0.768**	**0.001**
		S_B	Year	**0.299**	**0.007**
			Location	**0.696**	**0.001**
		S_R	Year	**0.300**	**0.005**
			Location	**0.700**	**0.001**
		S_{FD}	Year	**0.303**	**0.005**
			Location	0.215	0.068
		S_{FB}	Year	0.100	0.152
			Location	0.169	0.083
		S_{FR}	Year	0.099	0.164
			Location	0.107	0.082
	2-Way nested	S_D	Year	0.171	0.051
			Location	**0.859**	**0.008**
		S_B	Year	0.050	0.317
			Location	**0.897**	**0.008**
		S_R	Year	0.050	0.306
			Location	**0.897**	**0.008**
		S_{FD}	Year	**0.236**	**0.012**
			Location	0.183	0.192
		S_{FB}	Year	0.030	0.366
			Location	0.250	0.108
		S_{FR}	Year	0.027	0.354
			Location	0.272	0.100
1991-2005	1-Way	S_D	Year	**0.185**	**0.047**
		S_B	Year	0.066	0.271
		S_R	Year	0.066	0.269
		S_{FD}	Year	**0.232**	**0.015**
		S_{FB}	Year	0.026	0.386
		S_{FR}	Year	0.026	0.382

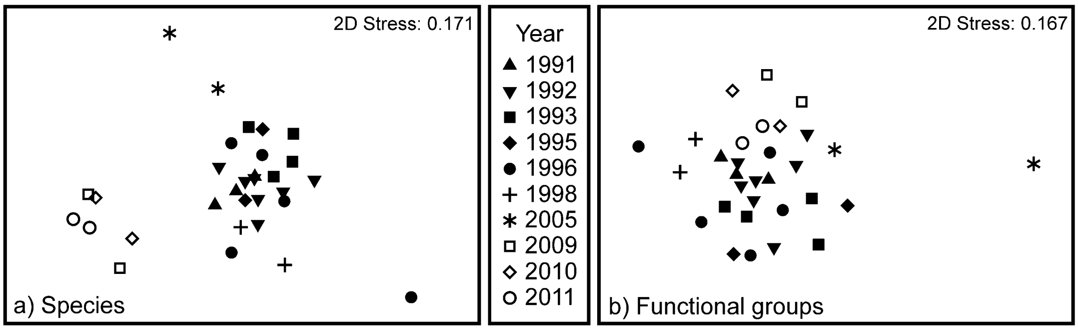

Figure 5.4 2d non-metric multi-dimensional scaling ordination, (a) polychaete species density composition, S_D, with period 1991-2005 and 2009-2011 separated and (b) polychaete functional group density composition, S_{FD}.

Correlations with selected spatial and temporal variables showed that regardless of data transformation, the strongest correlations with primary faunal variation (MDS-x) during 1991-2011 were with latitude and depth (Table 5.5). Secondary variation (MDS-y) appeared to be linked with potential resource supply (POC, density). When assessed over 1991-2005 alone (i.e. the influence of location removed), the primary variation appeared to be linked with potential food supply.

Table 5.5 Spearman's rank correlations of selected environmental variables with descriptors of polychaete species composition by density (2d MDS ordinates), for the full data set (period 1991-2011) and the period 1991-2005 alone. Note that the absolute value of the correlation is shown. For each polychaete descriptor, the two strongest, significant ($p < 0.05$), correlations are highlighted. (Long., longitude; Lat., latitude; POC6M, particulate organic carbon flux in preceding 6-months; 12M, preceding 12-months; Den., total polychaete density; ord., ordinate; Transformations: None, no transformation; Sqrt, square-root; Fort, forth-root; Log, log(x+1); P/A, presence-absence).

		Period 1991-2011							Period 1991-2005						
		Long.	Lat.	Depth	Date	POC6M	POC12M	Den.	Long.	Lat.	Depth	Date	POC6M	POC12M	Den.
	Lat.	0.144							0.792						
	Depth	0.087	0.802						0.377	0.624					
	Date	0.444	0.264	0.404					0.132	0.398	0.125				
	POC6M	0.167	0.628	0.550	0.251				0.474	0.519	0.404	0.090			
	POC12M	0.138	0.746	0.600	0.281	0.875			0.580	0.589	0.343	0.236	0.839		
	Den.	0.164	0.328	0.271	0.250	0.404	0.308		0.304	0.334	0.232	0.194	0.415	0.301	
MDS x-ord.	None	0.165	**0.668**	0.545	0.508	0.235	0.483	0.190	0.272	0.214	0.166	0.096	0.537	0.417	**0.676**
	Sqrt	0.094	**0.748**	0.615	0.455	0.293	0.516	0.150	0.288	0.244	0.148	0.143	0.593	0.398	**0.667**
	Fort	0.090	**0.782**	0.674	0.463	0.414	0.584	0.225	0.158	0.078	0.220	0.014	0.470	**0.477**	0.068
	Log	0.216	**0.632**	0.516	0.493	0.201	0.465	0.125	0.323	0.317	0.279	0.033	**0.563**	0.491	0.471
	P/A	0.148	**0.658**	0.597	0.552	0.473	0.576	0.157	0.175	0.037	0.321	0.198	0.229	0.220	0.148
MDS y-ord.	None	0.174	0.373	0.292	0.210	0.606	0.444	**0.732**	0.355	0.526	0.254	0.030	0.147	0.150	**0.629**
	Sqrt	0.217	0.263	0.160	0.165	0.515	0.297	**0.643**	0.104	0.214	0.017	0.137	0.243	0.258	0.286
	Fort	0.280	0.205	0.285	0.061	**0.521**	0.404	0.154	0.182	0.146	0.351	0.390	0.058	0.130	0.099
	Log	0.193	0.266	0.155	0.149	0.519	0.318	**0.645**	0.316	0.397	0.083	0.151	0.099	0.010	**0.641**
	P/A	0.032	0.100	0.096	0.291	0.168	0.274	0.208	0.153	0.078	0.171	0.448	0.213	0.307	0.003

As visualised by the principal component analysis of the Savage scores, species rank distributions by density (RAD_D), and energy use rate (RAD_R) varied substantially between periods (1991-2005 and 2009-2011, i.e. locations), with only modest, if any, variation between years within locations (Fig. 5.5a,d). The underlying drivers of this distinction between locations were examined by reference to rank switching among selected key species, e.g. note opposing patterns in the Savage scores of: 1) *Paradoneis* sp. A (Fig. 5.5b) and *Chaetozone* sp. A (Fig. 5.5c) density; 2) *Notomastus cf. latericeus* (Fig. 5.5e) and *Notomastus* sp. C (Fig. 5.5f) energy use rate.

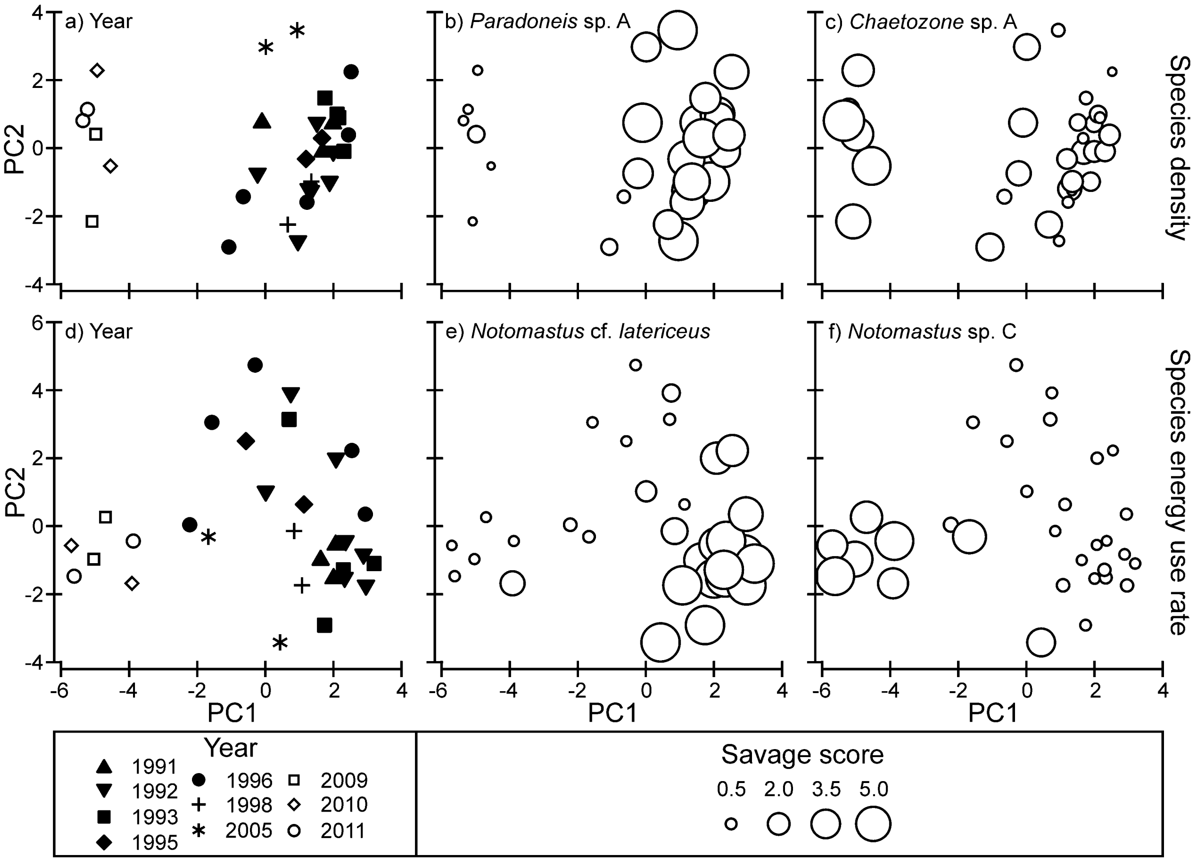

Figure 5.5 Principal component analysis of species rank Savage scores by density (a-c) and energy use rate (d-e), with year coding (a,d), and bubble plots of selected species' Savage scores. Note the separation of period 1991-2005 and 2009-2011 in all figures and opposing patterns in the Savage scores of *Paradoneis* sp. A and *Chaetozone* sp. A density and *Notomastus* cf. *latericeus* and *Notomastus* sp. C energy use rate.

5.3.4 Analyses of potential mechanisms of change

No significant cross-correlation was detected between POC flux and D_{tot}, B_{tot} or R_{tot} at the monthly time scale, over 1991-2011, or 1991-2005. There was, however, significant correlation of POC flux with species composition (MDS-x) by density, biomass, and energy use rate (Table 5.6) over 1991-2011. Significant correlations were also detected between POC flux and some species and functional groups (Table 5.6). In particular, *Cossura* cf. *rostrata*, *Aricidea* sp. B and BMx exhibited significant correlations with similar lags during both 1991-2011 and 1991-2005 (i.e. with and without the location change).

Table 5.6 Spearman's rank correlations of biological variables with 1-11 month lags of particulate organic carbon flux, for the full data set (period 1991-2011) and the period 1991-2005 alone. Correlations are highlighted by significance level (for period 1991-2011 p≤0.019, FDR=0.02, p≤0.011, FDR=0.01; for period 1991-2005 p≤0.021, FDR=0.02, p≤0.011, FDR=0.01; FDR, false discovery rate). (Variables: B, biomass; D, density; E, energy use rate. Parameters: MDS-x, x-ordinate of 2d non-metric multidimensional scaling ordination; BMx and PMJ, feeding groups as detailed in Table 5.2).

	Biological parameter	Variable	Particulate organic carbon flux, months of lag									
			2	3	4	5	6	7	8	9	10	11
Period 1991-2011	*Abyssoninoe* sp. B	B	0.167	0.180	0.395	**0.629**	0.314	0.329	0.141	0.217	0.226	0.414
	Aricidea sp. A	D	0.007	0.052	0.319	0.206	-0.061	-0.117	-0.068	-0.081	0.010	**0.592**
	Aricidea sp. B	D	0.205	-0.139	-0.167	-0.276	0.204	0.108	0.546	**0.578**	0.163	0.046
	Chaetozone sp. A	B	0.332	0.165	0.188	0.220	0.350	0.299	0.288	0.525	0.326	0.386
	Cossura cf. *rostrata*	D	-0.536	-0.524	**-0.651**	**-0.565**	-0.519	-0.347	-0.155	-0.391	**-0.619**	-0.577
	Cossura cf. *rostrata*	B	-0.402	-0.489	**-0.591**	-0.529	-0.388	-0.115	0.096	-0.168	-0.544	-0.358
	Notomastus sp. B	D	-0.013	-0.199	-0.280	-0.473	-0.539	-0.356	-0.282	-0.203	-0.202	-0.425
	Notomastus sp. B	B	-0.054	-0.241	-0.350	-0.532	-0.528	-0.164	-0.166	-0.182	-0.321	-0.512
	Orbiniidae sp. A	B	-0.466	**-0.590**	-0.313	-0.135	-0.164	-0.018	-0.303	-0.409	-0.339	-0.187
	Paradoneis sp. A	D	-0.250	-0.341	-0.247	-0.405	-0.310	-0.150	-0.340	-0.518	-0.241	-0.166
	Paradoneis abranchiata	D	-0.214	-0.272	-0.177	-0.469	**-0.560**	**-0.667**	-0.279	-0.243	-0.243	-0.351
	Paradoneis abranchiata	B	-0.149	-0.230	-0.248	-0.393	**-0.546**	-0.369	-0.279	-0.232	-0.341	-0.431
	Sphaerosyllis sp. A	D	-0.142	-0.243	-0.220	-0.402	**-0.641**	-0.461	-0.263	-0.219	-0.473	-0.405
	Sphaerosyllis sp. A	B	-0.093	-0.244	-0.182	-0.323	**-0.555**	-0.276	-0.185	-0.105	-0.421	-0.333
	BMx	D	-0.211	-0.282	-0.453	-0.545	-0.487	-0.243	-0.121	-0.211	-0.439	-0.518
	PMJ	D	-0.052	-0.244	-0.102	-0.277	-0.537	-0.370	-0.284	-0.195	-0.406	-0.263
	MDS-x	D	-0.496	-0.382	-0.365	-0.482	**-0.662**	-0.501	-0.329	-0.552	**-0.684**	**-0.643**
	MDS-x	B	0.518	0.465	0.458	**0.606**	**0.636**	0.461	0.277	0.481	**0.649**	0.562
	MDS-x	E	-0.532	-0.477	-0.484	**-0.626**	**-0.620**	-0.421	-0.265	-0.494	**-0.672**	-0.581
Period 1991-2005	*Ancistrosyllis* sp. A	B	0.141	0.029	0.179	0.218	**0.656**	0.550	0.121	-0.003	0.146	0.244
	Aricidea sp. B	D	0.138	-0.212	-0.158	-0.364	0.095	0.090	0.531	**0.637**	0.068	-0.133
	Cossura cf. *rostrata*	D	-0.416	-0.393	**-0.642**	-0.440	-0.283	-0.025	0.128	-0.228	-0.611	-0.367
	Cossura cf. *rostrata*	B	-0.279	-0.462	**-0.636**	-0.474	-0.144	0.182	0.335	-0.050	-0.571	-0.165
	BMx	D	-0.049	-0.137	-0.388	-0.570	-0.336	0.029	0.046	-0.063	-0.404	-0.433

The variance ratios of species and functional group density, biomass, and energy use rate were either not significantly different from unity (p > 0.05), or were significantly greater than unity ($p < 0.05$) over 1991-2011, 1991-2005 and 2009-2011 (Table 5.7). Consequently, no evidence of compensatory dynamics (**hypotheses A**) was detected.

Table 5.7 Variance ratio of species (S) and functional group (FG) density (D), biomass (B), and energy use (R) over 1991-2011, 1991-2005 and 2009-2011 at deployment-, month-, and year-level with associated number of data points (n). Values significantly different ($p < 0.05$) from unity are highlighted in bold. .

Period/Location	Level	n	S-D	S-B	S-R	FG-D	FG-B	FG-R
1991-2011	Deployment	31	**3.043**	1.375	**1.650**	**1.824**	1.085	1.193
	Month	22	**3.566**	1.302	**1.676**	**2.069**	0.966	1.125
	Year	10	**5.157**	1.493	1.672	**2.277**	1.155	1.556
1991-2005	Deployment	25	**3.737**	1.465	**1.882**	**2.119**	1.285	1.513
	Month	16	**5.248**	1.404	**2.157**	**2.678**	1.242	1.688
	Year	7	**8.460**	1.238	1.200	**2.960**	1.199	1.595
2009-2011	Deployment	6	1.016	1.580	1.824	0.905	0.915	0.972
	Month	6	1.016	1.580	1.824	0.905	0.915	0.972
	Year	3	2.116	2.424	2.729	1.850	1.484	1.539

No significant relationship was detected between yearly total density and (geometric) mean individual energy use rate over 1991-2011 ($r_s = -0.285$, $p = 0.425$, $n = 10$) or 1991-2005 ($r_s = -0.424$, $p = 0.294$, $n = 7$). Consequently, no direct evidence of “zero-sum dynamics” (**hypothesis B)** was detected**.** In contrast, total density and total energy use rate were significantly correlated over 1991-2011 ($r_s = -0.782$, $p = 0.008$, $n = 10$) and 1991-2005 ($r_s = 0.821$, $p = 0.023$, $n = 7$).

The total polychaete density, biomass, energy use rate as well as species size spectra matched the EER prediction of the metabolic theory and macroecology (**hypothesis C**, Fig. 5.6, Table 5.8). Results were significant over 1991-2011, 1991-2005 and 2009-2011.

Table 5.8 Linear regression (R^2, F, p) of the upper classes of polychaete size spectra for density, biomass, energy use rate and species over 1991-2011, 1991-2005 and 2009-2011 for data pooled across all samples. The mass scaling coefficient compares with the prediction of the metabolic theory.

Period/Location		Scaling coefficient	R^2	F	p
1991-2011	Density	-0.744	96.9	253.13	< 0.001
	Biomass	0.233	74.4	24.23	0.002
	Energy use rate	-0.015	0.0	0.10	0.761
	Species	-0.382	83.3	25.97	0.007
1991-2005	Density	-0.770	95.8	183.96	< 0.001
	Biomass	0.210	57.8	11.78	0.011
	Energy use rate	-0.048	0.0	0.68	0.438
	Species	-0.385	80.8	30.44	0.001
2009-2011	Density	-0.689	97.4	262.94	< 0.001
	Biomass	0.254	89.1	58.04	< 0.001
	Energy use rate	0.008	0.0	0.06	0.822
	Species	-0.351	71.6	18.64	0.005

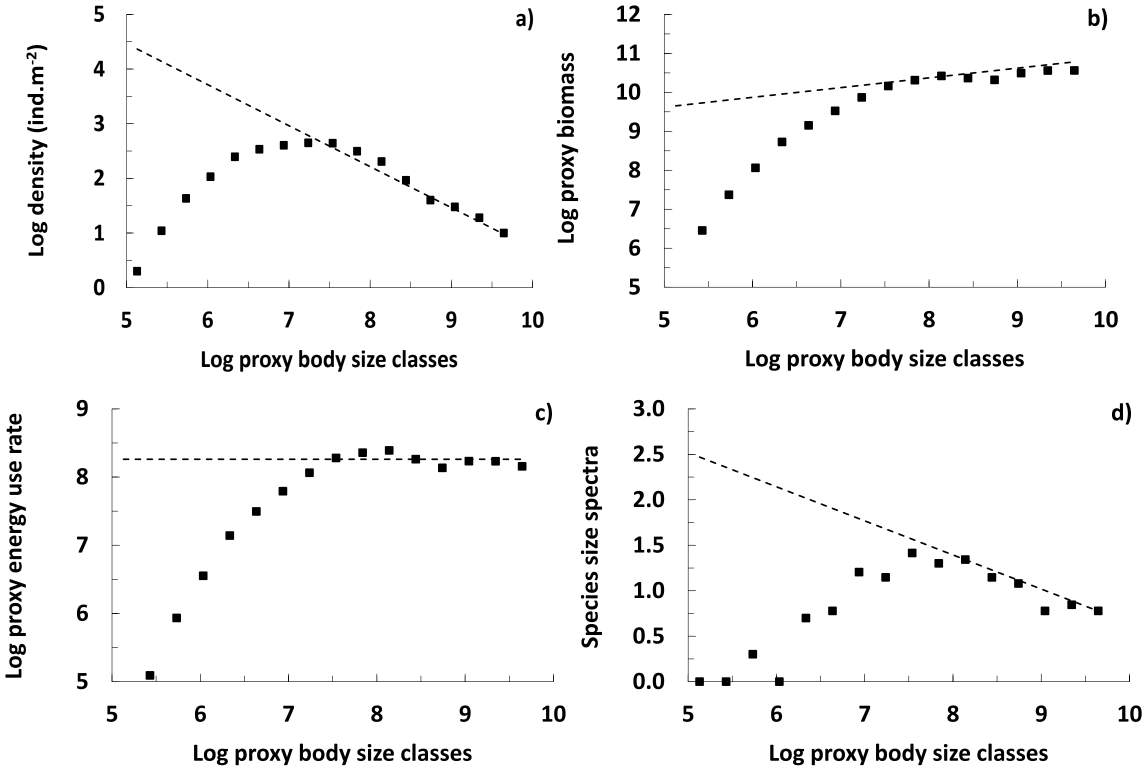

Figure 5.6 Total polychaete (a) density with prediction (dashed line) of the metabolic theory as density scales $\text{mass}^{-3/4}$, (b) biomass with prediction (dashed line) of the metabolic theory as biomass scales $\text{mass}^{1/4}$, (c) energy use rate with prediction (dashed line) of the metabolic theory as respiration scales mass^{0}, (d) species size spectra with predictions (dashed line) of macroecology as species richness scales $\text{mass}^{-3/8}$.

5.4 Discussion

5.4.1 Sta. M polychaete assemblage

The Sta. M polychaete assemblage was composed of families and genera often reported in abyssal sediments (Paterson et al., 2009). Cossuridae, Paraonidae, Syllidae, Cirratulidae, Lumbrineridae and Capitellidae dominated polychaete density and biomass over 1991-2011. The main difference in polychaete composition between Sta. M and other well studied abyssal areas (NE North Atlantic: Porcupine, Madeira, Tagus, and Cape Verde Abyssal Plains; Equatorial Pacific: DOMES, ECHO1, and PRA sites) was the low relative abundance of Spionidae (Glover, 2000; Glover et al., 2001, 2002). When comparing Sta. M and the Porcupine Abyssal Plain (NE Atlantic), Laguionie-Marchais et al. (2013) suggested that the difference in Spionidae relative abundance might be at least partly explained by differences in surface productivity and consequently POC flux to the seafloor. Members of the family Spionidae have previously been noted for their occurrence in organically enriched sediments (Grassle and Morse-Porteous, 1987). They are considered to be potential opportunists (Grassle and Grassle, 1974; Smith and Hessler, 1987), capable of rapid population growth and switching from suspension to deposit feeding when food is in abundance (Blake, 1996). Detailed comparison of abyssal sites is hampered by the difficulty in assigning specimens to formally (or informally) described species, a continuing problem in deep-sea polychaete taxonomy and ecology (Paterson et al., 2009).

5.4.2 Inter-annual variation in the polychaete assemblage and its energetics

Our examination of polychaete species-level variation provides the most detailed view of temporal changes in the Sta. M macrofaunal assemblage undertaken to date. Significant, and substantive, change was observed in a number of descriptors, including total density and multivariate measures (rank distributions, species and functional group composition), between the periods 1991-2005 and 2009-2011. Thus, it was not possible to conclusively isolate sampling location or temporal change per se. In contrast, no significant change was detected in yearly measures of biomass, energy use rate, or species richness (though note that some variation in species dominance between locations was suggested, Fig. 5.3d). Across the time-series (1991-2011), polychaete energy use rate (respiration) ranged by a factor of 3 among annual means. These variations were of similar magnitude to that recorded for the Sta. M megafauna (factor of 4, Ruhl et al., 2014). In addition to respiration, polychaetes perform other important carbon cycle functions such as bioturbation and sediment reworking (Rouse and Pleijel, 2001, Olsgaard et al., 2003), that may all vary with a similar magnitude.

5.4.3 Assemblage variation links to environmental variables

In a number of attributes, the polychaete assemblage appeared to vary with food supply, as indicated by several significant correlations with POC flux. Interpretation is, however, complicated by the coincidence of the change in sampling location with an apparent increase in organic matter supply to the seabed in the latter years of the time-series. For the macrofauna sampling years between 1991 and 2005, mean annual POC flux was estimated as 1.7 $gCm^{-2}yr^{-1}$, for the period 2009-2011 the corresponding value was 3.7 $gC\ m^{-2}yr^{-1}$ (data from Smith et al., 2013). No simultaneous sampling of the polychaete fauna at both locations was undertaken, such that it was not possible to directly assess that change. Consequently, two non-mutually exclusive options were considered in assessing the nature of the changes detected in the polychaete assemblage: 1) that it may be consistent with continuous change in species composition over a 100 m bathymetric interval (i.e. between locations), likely driven by a suite of co-varying environmental factors; and/or 2) that it may have been driven by a change in POC flux to the seabed.

Evidence of the former option (1) seems to be suggested by the substantive change in faunal composition (Fig. 5.3f, 5.4a, 5.5), despite no corresponding change in faunal abundance or diversity (Fig. 5.3a-e). There has been change in community structure, but no change in headline community function (e.g. resource use). Such change is potentially consistent with change in the background environment (location), not change in food supply (POC flux). Nonetheless, evidence of the latter option (2) also seems to be apparent in our analyses. Secondary variation in polychaete assemblage composition (MDS-y) appeared to be correlated with food supply over 1991-2011, a potential relationship that was maintained as primary variation (MDS-x) when analysed over 1991-2005 alone (Table 5.5). Similarly, two important species, *Cossura* cf. *rostrata* (rank 1 across the time-series) and *Aricidea* sp. B (rank 8) exhibited significant lagged-correlations with POC flux at consistent lags in analyses of both periods (1991-2011, and 1991-2005; Table 5.6). Some species were consistently positively correlated with potential food supply (e.g. *Aricidea* sp. B), while others were consistently negatively correlated (e.g. *C.* cf. *rostrata*), suggesting differential responses to food supply, as previously noted among holothurians at Sta. M (Ruhl, 2007).

Significant changes have occurred more generally among Sta. M megafauna during both periods, (i.e. at both locations, 1991-2005 [1989-2004; Ruhl et al., 2014] and 2009-2011 [2006-2012; Kuhnz et al., 2014]). It is conceivable that small active surface deposit feeding megafauna may have intercepted much of the incoming organic matter flux, reducing the magnitude of temporal variation experienced by the infaunal benthos (Bett et al., 2001). It should also be noted that the FVGR sampler may also suffer from a bow-wave effect that impacts the quantitative recovery of smaller polychaetes (e.g. Bett, 1994). The latter may be the most reactive to organic enrichment as noted in the case of an opheliid in the Porcupine Abyssal Plain time-series. Vanreusel et al. (2001) reported that 95% of the opheliids were restricted to the unconsolidated superficial sediment layer, i.e. the most subject to sampler bow-wave effect. The only sampling of polychaetes conducted in 2007 at Sta. M was done during a feeding experiment (Jeffreys et al., 2013). The latter authors reported that Spionidae was one of the three most dominant families at that time. As Jeffreys et al. (2013) used a different sampler, it is not possible to ascribe the presence of Spionidae to either a reduced bow-wave effect or an increase of opportunistic surface deposit feeders under enrichment conditions as observed in other deep-sea systems (Smith and Hessler, 1987, Levin et al., 1999). On abyssal plains, greater numbers of surface deposit feeders have previously been linked to higher POC flux (Laguionie-Marchais et al., 2013).

Resolving the influence of above average POC flux deposition events on abyssal benthic polychaetes may become important under various climate change scenarios. Smith et al. (2013) noted that the frequency and magnitude of such events had increased at Sta. M since 2007, with a particularly marked salp deposition event in 2012. Continued time-series research will be needed to evaluate if and how the polychaete assemblage responds to such large POC flux events and which aspects of these events (quality, quantity) might trigger assemblage change. It is conceivable, for example, that salp-derived POC flux may have sufficiently different characteristics to drive assemblage responses despite minimal change in total organic carbon supply.

5.4.4 Mechanisms of polychaete assemblage structure dynamics

Compensatory dynamics *sensu* Houlahan et al. (2007) were not detected in Sta. M polychaete assemblage density, biomass, or energy use rate (**Hypothesis A,** not supported). Overall, a similar lack of compensatory dynamics was also reported for Sta. M megafauna by Ruhl et al. (2014), as has been noted in other ecosystems (Houlahan et al., 2007). Hubbell (2001) suggested that compensatory mechanisms could be hidden when studying species that are not at the same trophic level. Although the Sta. M polychaete fauna belong to several different feeding groups that are all ultimately dependant on POC flux (Jeffreys et al., 2013), little is known about their species-specific feeding characteristics. Recent experiments conducted at Sta. M have shown that the polychaetes have a $\delta^{15}N$ value indicating omnivory (Jeffreys et al., 2013). Given their relatively low densities and small body sizes, performing gut content analyses remains a challenge, and the life histories of deep-sea polychaetes remain speculative (Jumars et al., 2015). Finally, compensatory dynamics may be most detectable in assemblages with limited species richness; the Sta. M polychaete fauna is rich, with 167 species recorded to date, many as singletons.

Energetic zero-sum dynamics were not observed among the Sta. M polychaete assemblage (**Hypothesis B,** not supported). Total polychaete density, although not correlated with mean individual energy use, was significantly and positively correlated with total energy use rate. This may indicate synchronous change, as might be expected if density was tracking a common resource. Energetic zero-sum dynamics may, nevertheless, operate among the wider Sta. M macrofaunal assemblage. Using total measured density and biomass to estimate mean individual mass (data from Drazen et al., 1998) over the period 1991-2005, macrofaunal density was negatively correlated with mean individual mass (r_s = -0.564, p = 0.006, n = 7). Although calculating mean individual mass by this method is not ideal, the significant relationship might suggest that energetic zero-sum dynamics operate among the macrofauna in total, if not among the polychaetes alone.

It is worth considering a number of other issues in connection with the detection of zero-sum dynamics among the Sta. M polychaete assemblage: 1) In common with the concept of ‘constant final yield’ (Weiner and Freckleton, 2010), the detection of zero-sum dynamics may be limited to particular circumstances; both most readily detected where the resource in question is constant and limiting. At Sta. M there is substantial intra- and inter-annual variation in organic matter supply to the seafloor (Smith et al., 2013). 2) Continuing change in assemblage body size distribution once resource limitation/carrying capacity has been reached (e.g. successional change introducing biomass dominants, Warwick, 1986) also improves the likelihood of detecting zero-sum dynamics. 3) Using a body mass proxy rather than direct measurements may have impacted our detection of zero-sum dynamics. However, as less than 3% of the specimens were complete, the use of a proxy was inevitable in this case. Nevertheless, the proxies were based on direct body size measurements of each specimen, and consequently the best possible predictors of population biomass and respiration.

Alternatively, the absence of zero-sum dynamics may be real at the polychaete assemblage level suggesting temporal stability in the body size structure of the assemblage. The present data, though limited, did not show obvious departure from the predictions of EER (hypothesis C), a results that appeared to hold-up in space and time. These observations add to a small body of deep-sea benthic community data on density and biomass size spectra, that all appear to exhibit similar trends (Schwinghamer 1985, see caveats in Bett 2013, 2014, Kelly-Gerryen et al. 2014) and is new example supporting a general relationship between abundance, diversity and body size (grassland insect community, Siemann et al., 1996, arthropod community, Siemann et al., 1999, rocky shore mollusca, Fa and Fa, 2002, shallow marine epibenthic community, Labra et al., 2015, deep-sea gastropods, McClain, 2004). The ‘energetic equivalence rule’ is not universally accepted (Isaac et al., 2013), with the latter authors stressing it should be seen as a null hypothesis, and urging the search for, and testing of, mechanisms that might underpin the density-energy relationship. Some of Isacc et al.’s (loc cit) concerns are largely specific to ‘global size-density relationships’ where density and body size are averaged at the species level, rather than the ‘individual size distributions (size spectra)’ that have been employed here (see terminology in White et al 2007). This distinction may be particularly important in considering temporal variations and the applicability of the concept of zero-sum dynamics (Ernest et al., 2008). The interpretation of size spectra via the MTE assumes the single trophic level case (Brown et al., 2004, Bett, 2013), or at least equal proportions of multiple trophic levels in each size class. This seems to be a reasonable simplification as stable isotope analyses conducted at Sta. M have suggested that polychaetes were all effectively feeding at the third trophic level (Jeffreys et al., 2013) with common consumption of fresh detrital material (Sweetman and White, 2008).

5.5 Conclusions

The polychaete assemblage at Sta. M appeared to exhibit temporal stability in some attributes (biomass, energy use rate, diversity) while displaying significant changes in density, composition and rank abundance distribution between 1991-2005 and 2009-2011. Across the same time period there has been substantial intra- and inter-annual variation in the supply of organic matter to the seabed. The changes detected in species and functional group composition appear to be associated with both (a) change in food supply, and (b) change in the location of the Sta. M study area. Although the relative influence of these factors can not definitively be weighted, it seems likely that both were responsible for substantive change. Analyses prior to the change of sampling location showed that the polychaete assemblage composition dynamics were primary driven by food supply variation. Changes in several species were also lagged to changes in POC flux by 4 to 10 months. Compensatory or zero-sum dynamics, in the Sta. M polychaete assemblage were not detected; however, zero-sum dynamics operated at the macrofaunal community level. The synchronous change in polychaete density and energy use rate suggested the tracking of a common resource, presumed to be particulate organic carbon flux. The polychaete assemblage followed the prediction of the metabolic theory indicating stability in the body size structure. Overall, the results do suggest the sensitive detection of environmental change (food supply and/or bathymetry) through the species-level study of deep-sea polychaete assemblages. Future work to better constrain changes in abyssal polychaetes at Sta. M should now include: 1) a characterisation of the polychaete assemblages at the two sampling location at the same time; 2) an assessment of FGVR bow-wave effect by comparing FVGR and megacorer at Sta. M; 3) a joint-study of meiofaunal and macrofaunal polychaetes.

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Chapter 6

Conclusions

6.1 Main findings and future work at Sta. M and PAP

This thesis work investigated the intermediate-scale (landscape spatial scale and inter-annual temporal scale) variation of macrofauna in two abyssal soft-sedimentary areas using annelid polychaetes as model organisms.

In terms of landscape spatial-scale variations (Chapter 2), the initial hypotheses were only partially supported:

- **Hc21** was only supported for the between and among hill (BH) analysis where macrofauna and polychaete assemblage compositions were related to the sediment particle size distribution. But no similar relationship was found within and surrounding a single abyssal hill (WH) between the faunal composition and sediment features.
- **Hc22** was also only partially supported. The WH analyses showed that only the macrofauna density and polychaete diversity changed along the hill.
- **Hc23** could not be proven as no significant difference was observed in faunal features (density, diversity, structure) between abyssal hill and plain sites.

However, these results were obtained with minimal sample size at best despite an intensive megacoring programme, highlighting the difficulty associated with abyssal macrofauna sampling. The data were sparse, the number of specimens low and the physical sample size was only 0.008-0.06 m^2, covering in total just about one meter square. Nonetheless, with the present data, the study showed that: 1) the macrofauna patterns differed from the megafauna patterns at the same station (Durden et al., 2015) and from macrofauna patterns observed on seamounts (Bongiorni et al., 2013, Chivers et al., 2013). 2) The macrofauna composition was likely affected by the same processes influencing the sediment particle size distribution, namely difference in near-bed current flows as observed in other systems (Snelgrove and Butman, 1994, Levin et al., 2001, Bongiorni et al., 2013). 3) Abyssal hills are not more diverse than surrounding areas but contribute to an enhanced regional biodiversity (as seen with seamounts, e.g. Chivers et al., 2013).

In terms of inter-annual time-scale variations, three studies were conducted using different taxonomic resolution and faunal organisation level. For the family-level study conducted at both Sta. M and PAP (Chapter 3), most of the initial hypotheses were supported:

- **Hc31** was supported: the polychaete assemblage density and composition were statistically different over the time-series both at PAP and Sta. M.
- **Hc32** was also supported: the polychaete rank abundance distributions were statistically different at inter-annual scales both at PAP and Sta. M. At each station, structural changes occurred with the strongest one taking place in 1998 with switches in the densities of most abundant families and functional groups.
- **Hc33** was only partly supported as polychaete feature dynamics were directly correlated to some megafauna species dynamics but not to climate indexes.

Overall, this study showed that: 1) the total polychaete density varied by fourfold over the time-series with changes in family and functional group dominance and composition at both stations in accordance with previous observations (Ruhl et al., 2008, Soto et al., 2010). These changes were more obvious over periods of time rather than from year to year. 2) Niche-partitioning mechanisms occurred at both stations and were dynamic over the time-series as seen in other ecosystems (Thibault et al., 2004). 3) Despite a lack of direct correlation with POC flux at the family level, maybe related to the differential response of individual specimens to food supply observed during feeding experiments (Witte et al., 2003, Sweetman and Witte, 2008, Jeffreys et al., 2013), polychaete changes occurred in synchronicity with other taxa, in particular with holothurian species (Ruhl and Smith, 2004, Billett et al., 2010) suggesting the influence of a common environmental factor.

For the temporal study of the density-dominant polychaete species at Sta. M (Chapter 4), the initial hypotheses were only partially supported:

- **Hc41** was only partly supported as not all of the five density-dominant species had their the density and body size statistically different at the yearly time scale (only four out of five in terms of density and three out of five in terms of body size).
- **Hc42** was also only partly supported as only two species had their density and body size dynamics correlated, giving indication that particular life-history events took place (e.g. reproduction, recruitment).
- **Hc43** was also only partly supported as not all of the five species had their density and body size dynamics correlated to megafauna and/or POC flux dynamics.

Again this study suffered from the low number of specimens collected during each cruise. Only five species had enough individuals over the whole time-series (more than 100) to be included in the analyses. And even the most dominant one had only 220 individuals in total. These data provide nonetheless the most detailed view of temporal dynamics in abyssal polychaete species. Overall, the study showed that: 1) for some polychaete species, life-history events may be inferred from density and body size dynamics as seen for holothurians (Ruhl, 2007, Billett et al., 2010). 2) Differences in polychaetes species dynamics may be explained by different life-history events (reproduction *versus* enhanced survivorship) in relation to variable food supply. 3) Life-history events were more easily/clearly inferred from megafauna density and body size inter-annual dynamics (Ruhl, 2007) compared to polychaetes. The latter taxon is smaller and therefore likely operates on shorter time scales whose detection would have required a higher temporal resolution.

For the temporal study of the whole polychaete species assemblage at Sta. M (Chapter 5), not all the initial hypotheses were supported:

- **Hc51** was only partially supported as only polychaete assemblage density and composition statistically change at inter-annual scale. Biomass and energy use rate were not statistically different over time.
- **Hc52** was also partially supported as only the assemblage composition was directly correlated to food supply, not the total density or biomass. But there was indication that the whole polychaete assemblage was tracking a common resource.
- **Hc53** was supported as no compensatory dynamics were observed in polychaete assemblage over the time-series.
- **Hc54** was partially supported as zero-sum dynamics were not detected among the polychaete assemblage, but occurred in the macrofaunal community as a whole.
- **Hc55** was supported as the polychaete body size structure was stable in time and show no obvious departure from the predictions of the energetic equivalence rule (EER).

Overall, this study showed that: 1) the polychaete assemblage at Sta. M appeared to exhibit temporal stability in some attributes (biomass, energy use rate, diversity) while displaying significant changes in density, composition and rank abundance distribution. Species-level analysis nuanced the results previously found with family-level study (Laguionie-Marchais et al., 2013). 2) The polychaete assemblage composition dynamics were primary driven by food supply variation as seen for megafauna but with shorter time lags (Ruhl and Smith, 2004). 3) Zero-sum dynamics were detected at macrofauna and not polychaete assemblage level suggesting that such mechanisms may only be relevant at larger scales. This is consistent with the observation of zero-sum dynamics for megafauna at the same station (Ruhl et al., 2014). 4) The polychaete assemblage body size structure followed the EER predictions and appeared to hold-up in space and time despite significant changes in species composition/dominance. This result is consistent with the notion that the total carrying capacity scales with body size regardless of whether that capacity is occupied by one or more species (density compensation among the individuals of different species within a size class, Savage et al., 2004).

The future work conducted at Sta. M and PAP would benefit from:

- sampling more macrofaunal organisms, for example by focusing on collecting a targeted number of specimens (about 100, Dr. Bett, pers. com.) rather than gear deployments per sampled site;
- including material for molecular analyses not only to barcode species but also to better assess endemism and dispersal. Some of these new species may help resolve uncertainties in phylogeny studies as likely found with Sta. M oligochaete species (Dr. Erseus, personal communication);
- pursuing the comparison of PAP and Sta. M time series over longer time scale at species level to assess the nature of variations (cyclic, episodic, long-term) and better unravel mechanisms behind abyssal polychaete dynamics;
- jointly studying meiofaunal and macrofaunal polychaete taxa to detect any juvenile recruitment that may not be translated into adult populations or be too ephemeral to be detected with the data present temporal resolution;
- comparing the polychaete species dynamics to other macrofaunal taxa such as crustaceans which are the second most-dominant taxa at both stations;
- characterising the polychaete assemblages at the two Sta. M sampling locations at the same time;
- better charactering environmental factors at both stations, in particular the sediment property (grain size, porosity) and its scales of variation as well as the POC flux quality (e.g. nutrients, lipids, pigments) and its dynamics.

6.2 Further implications of the thesis findings

Several conclusions of this work are relevant for deep-sea research beyond Sta. M and PAP and for community ecology research in general. Firstly, the variability in abyssal polychaete assemblages uncovered here at intermediate spatio-temporal scale is currently underappreciated. This may be a particularly timely consideration as the fast development of deep-sea resource exploitation is accompanied by environmental impact assessment studies that need to take this variability into account. For example, substantial effort is now being directed to characterise biodiversity and impact of prospective polymetallic nodule mining in the Central Pacific (Smith et al., 2008a, Clark et al., 2013, Wedding et al., 2013). The present study highlights that one-off or short-term/small-scale investigations may not be adequate to unravel the natural ecosystem variations and correctly assess impacts resulting from industrial activities in the deep sea.

Secondly, the results have implications for biodiversity estimation in abyssal systems. As abyssal hills are one of the most common topographic features on Earth, abyssal benthic macrofauna (and megafauna, Durden et al., 2015) may be higher than previously thought. Estimation of deep-sea diversity is a major question in deep-sea research (Hessler and Sanders, 1967, Sanders, 1968, Grassle and Macioleck, 1992, May 1992, Gray, 1994, Mora et al., 2011). In addition, biodiversity estimation is important to assess ecosystem functioning. An increasing number of studies have given evidences that biodiversity regulates functioning in all ecosystems (Cardinale et al., 2002, Worm et al., 2006). In the deep sea, an exponential relationship between biodiversity and ecosystem functioning and efficiency have been found consistent in a wide range of habitats (Danovaro et al., 2008, Danovaro, 2012).

Thirdly, in systems where food supply is limited to a short period of time, the choice of the study organisms is determinant. Overall, the polychaete variations were not as high as the megafauna ones both in time and space. Benthic density/biomass remains the best indicator of food supply spatio-temporal variations (Rex and Etter, 2010). However, when analysing different faunal size classes, which have different metabolic rates and response times, their density/biomass variations in relation to food supply can not be interpreted in the same way. The megafauna appeared to more efficiently access resource and showed marked changes in density and composition at inter-annual scales. These changes closely paralleled the POC flux variations at Sta. M and PAP (Ruhl and Smith, 2004, Kuhnz et al., 2014). The macro-infauna appeared more stable than epifauna. The macrofauna may be a more integrated measure of annual POC flux, smoothing out the variations in surface and making a living at a yearly-averaged POC flux. It is, however, worth highlighting that despite these differences, both megafauna and polychaetes had similar magnitude of variation in respiration rate at Sta. M over 1991-2011 (Chapter 5, Ruhl et al., 2014). Therefore a mechanistic understanding of all the faunal size categories (from bacteria to megafauna) is required to understand the carbon proces (burial, remineralisation) dynamics at the deep seafloor.

Fourthly, Sta. M and PAP studies contribute to the still limited but growing number of long-term time series data sets. The latter are not only important for assessing impact of climate change (requiring decades of observations, see section 6.4) but also for fundamental ecological theories. Marine, freshwater and terrestrial ecologists are increasingly aware of the limited knowledge of temporal changes in ecological communities, even in essential information such as background rates and direction of change (Magurran et al., 2010). Many species abundance models are essentially statics and therefore unrealistic: redefining these models by taking into account temporal variation is necessary (Magurran, 2011). New developments in statistical methods are promising (e.g. Mac Nally, 2007, Collins et al., 2008, see review in Magurran, 2011) but are irrelevant without long-term series observations of communities to help formulate, constrain and test the models. At PAP and Sta. M, the rank abundance distributions (RAD), indicative of resource partitioning (MacArthur, 1957, Sugihara et al., 2003) appeared as a dynamic property as observed in terrestrial studies (Thibault et al., 2004, Collins et al., 2008). The results presented above showed that even communities with relatively constant species richness may mask considerable temporal dynamics in relative species abundances. Using Sta. M, PAP, and deep-sea long time-series data sets in general may be potentially important for understanding what drive rates and direction of change in communities as deep sea is a unique ecosystem both physically and biologically where only a sub-set of factors operate compare to terrestrial systems (Rex and Etter, 2010).

Lastly, the conclusions on Sta. M polychaete species assemblage are relevant to generic community ecology theories. Sta. M results give another example that natural communities tend to positively, rather than negatively, covary suggesting that abiotic factors are more important than competitive interactions in driving inter-annual fluctuations in species abundance within communities (Houlahan et al., 2007). Sta. M results also suggest that zero-sum dynamics, present at macrofauna but not polychaete level, may operate at larger scales than previously thought and may be linked to the carrying capacity of wider areas. There may be limit of assemblage specificity to which zero-sum dynamics might be applicable. It would be interesting to determine this limit in other communities (e.g. desert rodent community, tropical forests, Ernest et al., 2008, 2009). In addition the Sta. M data appeared to be well summarised by the predictions of the metabolic theory of ecology (Brown et al., 2004). Consequently, the results are also consistent with the concept of energetic equivalence rule (EER, Damuth, 1987, Allen et al., 2002). These observation add a new example supporting a general relationship between abundance, diversity and body size so far observed in grassland insect community (Siemann et al., 1996), arthropod community (Siemann et al., 1999), shallow aquatic systems (rocky shore mollusca, Fa and Fa, 2002, shallow marine epibenthic community, Labra et al., 2015) and the deep sea (gastropods, McClain 2004). The apparent temporal stability of polychaete assemblage size structure, during a period of variable food supply and use, may suggest that effective mathematical modelling of benthic ecology and biogeochemistry may be achieved by relatively simple body size-based methods. This work also highlights the primary role of body size in structuring faunal communities. More studies should now be directed to adapt the metabolic theory of ecology to changing temporal framework (scaling rate of processes in time).

6.3 Suggestions for future lines of research in the deep-sea

In relation to this work, several lines of deep-sea research should be pursued in the future. The first line of research is at the heart of biodiversity assessment: describing species. Many undescribed species were found at Sta. M and PAP and among them were numerous potential new species. Important taxonomic work remains to be done in the deep sea in general. The current knowledge of basic taxonomy and distribution patterns of most deep-sea taxa is woefully inadequate. Too many deep-sea species lack quality morphological information, let alone DNA sequence data, leading to either apparent multi-ocean distribution or unique occurrence. The rate of species discovery and taxonomic/molecular description is strongly unbalanced (Paterson et al., 2009). Describing species is a priority to correctly assess biodiversity, allow baseline comparison between stations and oceans and understand species evolutionary history. Several online databases on marine biodiversity such as World Register of Marine Species (Appeltans et al., 2012), the Deep Sea ID App. (Glover et al., 2014) and the Ocean Biogeographic Information System 8 (OBIS 2013) have been developed. Although these databases are in their infancies, they offer promising tools with molecular barcoding to help standardised deep-sea fauna taxonomy in the future. In general, a greater interaction between taxonomists is needed to standardise species identification. More importantly, taxonomy is suffering from a serious lack of funding and need to be rehabilitated in research programmes and funding (e.g. Tahseen, 2014).

The second line of research should focus on tackling the technical constraints associated with deep-sea infauna sampling. More detailed estimates of abundance are needed, in particular for macrofauna whose size is: 1) too small to be readily visible on videos or photographs and therefore cannot be surveyed with time-lapse cameras or AUVs during and in-between research cruises; 2) too large to occur in enough number in the corers by opposition to meiofauna. So far, corers are the only systems to quantitatively collect macrofauna, although the low number of specimens they give leads to higher variation in abundance often reducing the power of statistical analyses performed on the data. In addition, the low number of specimens generates many singleton species (as seen in this work) so that many species appear rare. It is still unclear as to whether species rarity is a sampling artefact or a feature of abyssal communities. Such knowledge is, however, critical in the context of climate change as there are evidences that rare species may sustainably buffer effect of climate change on system functioning (Yachi and Loreau, 1999, but see Mora et al., 2013, Danovaro et al., 2014). Ideally, scientists should invest time and money to increase replication level during sampling. Another (non-mutually exclusive) alternative is to create new sampling methods to collect large samples of macrofauna with precision, not only in how deep into the seabed the sampling occurs but also in relation to the local bathymetry. There are few data on the variability of macrofauna on a small scale obtained from precision sampling (Dr. Billett, personal communication). The development of new, standardised, larger corers deployed by Remote Operated Vehicles (ROVs) should be actively pursued. In addition, a greater communication with statisticians could be beneficial to develop new statistical tools adapted to smaller data sets.

In addition to getting more individuals with a greater spatial accuracy, getting a better adequacy of the sampler area in relation to the spatial scales relevant to taxa is fundamental. The uncharacterised patch sizes at abyssal seafloor and potential mismatch of the sampler area in relation to these patches may be a real issue to unravel mechanisms driving macrofauna variations. For example, in this work, polychaetes appear to be randomly distributed at the scale of a 10 cm diameter corer (Appendix A) and their aggregation scale is still unknown. Such concerns have been discussed since the 1980s but still hold today because of the technological limitation to observe macrofauna *in situ*, to conduct *in situ* experiments or to bring back live specimens and study them in laboratory.

These limitations impede our knowledge on macrofauna basic life-history features such as reproduction, dispersal, swimming ability as well as on their response times. Macrofauna has been shown to respond more quickly to food inputs than megafauna (Ruhl et al., 2008, Chapter 5). The current annual or bi-annual ship-based sampling conducted at PAP and Sta. M likely miss seasonal/episodic events critical to the interpretation of changes in the abyssal macrofauna. Autonomous instrumentation such as cabled observatories and seafloor-moored arrays that allow adjusting sampling programmes to best evaluate a changing ecosystem (Smith et al., 2009) cannot currently assess changes in macrofauna. If future autonomous vehicles such as the Benthic Rover (McGill et al., 2009, Sherman and Smith, 2009) could sample and preserve sediment cores on a monthly basis, a better resolution of macrofauna dynamics could be obtained.

Another promising line of research is linked to the increasing recognition of the role of background chemosynthetic production (sometimes called dark energy) in non-chemosynthetic environments (e.g. in freshwater system, Santoro et al., 2014; in coastal system, Middelburg, 2011; in deep-sea systems, Molinari et al., 2013). Assessing dark energy production and its importance to the functioning of abyssal macrofauna (and meiofauna) is necessary when studying abyssal community dynamics, distributions, processes and functions. Most deep-sea studies are based on the assumption that benthic standing stock reflects the surface-derived POC flux. Rex and Etter (2010) stated that because there are so few long-term studies of pelagic-benthic coupling, benthic standing stock remains the best indication of spatial variation in the food supply that supports seafloor life. Although the information on dark energy production rates in deep-sea sediments is still very limited, recent estimates suggest that it could contribute for up to 20% to the total heterotrophic biomass production (Molinari et al., 2013). Consequently, the relationship between benthic standing stock and surface-derived POC flux may be less direct and more complex than previously thought and should be taken into consideration not only in long-term studies of abyssal infauna dynamics but also in the assessment of climate change impact on deep-sea ecosystems and potential feedback mechanisms of the latter.

6.4 Importance of deep-sea ecosystems for human kind

Advancing deep-sea research has a global relevance. Long considered out of sight, out of mind, the deep sea has now been shown to provide vital services supporting the current way of life of many humans (e.g. nutrient regeneration for surface productivity, detoxification of compounds through microbial activity, resources in fish, energy reserve, bioprospecting, Thurber et al., 2014). The entire global population benefits from the deep sea. In particular, the latter is an important component of the global carbon cycle that may play a role in centennial to millennial time scales in climate (Danovaro et al., 2008, Loreau, 2008, Larkin et al., 2010). The deep sea (defined here as depths greater than 200 m) has been estimated to currently store about 37 000 Gt of carbon and to have already absorbed a quarter of the carbon released from anthropogenic activities (Canadell et al., 2007, Sabine and Feely, 2007, Thurber et al., 2014). The carbon is indeed either respired in the water column or on the seafloor, being kept out of the atmosphere until the water rises to the surface again and releases the carbon back (1000-year time scales) or buried in sediments, removing CO_2 from the atmosphere for geological time scales (thousands to millions of years, Thurber at al., 2014). Current IPCC estimates indicate that the duration of climate change will begin to overlap with the deep-ocean ages of the Atlantic and Southern Ocean, so longer term carbon budgets may need to further consider deep-sea benthic ecosystem function.

Therefore a better understanding of the deep-sea systems and its biodiversity is of primary concern in a context of climate change and increased resource exploitation (e.g. Mengerink et al., 2014, Van Dover et al., 2014). With the occurrence of climate warming, human societies heavily rely on model predictions based on weather, water, ecosystems, and biodiversity data (Ruhl et al., 2011). To be better constrained and allow predictions, these models need long-term field observations. Although paleoceanographic records provide useful insight on climate impact (e.g. in the deep sea, Yasuhara et al., 2012), they can not just be extrapolated to the present communities, if at all (Glover et al., 2010). To help lessen human impact on the deep sea, being able to detect climate change signals from substantial natural variability is necessary and requires essential ecological baseline information obtained from long-term data sets. Only time-series on multi-decadal time scales can allow obtaining such information (Doney et al., 2012) and contribute to a comprehensive and integrated global ocean observation system (Ducklow et al., 2009, Larkin et al., 2010). But, with an average depth of 3 800 m, the seafloor remains one of the least accessible systems; one where it is still difficult and expensive to conduct surveys on appropriate spatio-temporal scales, which has limited deep-sea long-term studies (Gage and Tyler, 1991).

Overall, time-series are scarce even in shallow waters (see review in Ducklow et al., 2009). In the deep sea, time-series are even more scarce (see reviews in Glover et al., 2010, Larkin et al., 2010). The main stations and results of non-chemosynthetic time-series are summarised in Table 6.1 without including the new (and so shorter) time-series such as the Deep-Ocean Long-Term Environmental Research Station (DELOS, O'Brien et al., 2014) in the South Atlantic. At bathyal depth, shorter temporal (multi-year) studies were also conducted at the Bay of Biscay in the North East Atlantic (43°50'N, 2°23'W), at 550 m between 1997-2001 (Fontanier et al., 2003, 2005) in the Antarctic, FOODBANCS, (65°S, 65°W) at 500-600 m in 1999-2001 (Smith et al., 2008b). Overall, long-term studies have shown how quickly benthic systems may respond to intra- and inter-annual variations in upper ocean parameters, notably those linked to climate (Glover et al., 2010). So far, the results of PAP and Sta. M time-series have shown that in the largest realm on Earth's surface, communities can change on time scales comparable to that of terrestrial and shallower marine ecosystems (Lavaniegos and Ohman, 2003, Thibault et al., 2004), a consideration that should be appropriately formulated in global models including deep-sea ecosystems (Glover et al., 2010). Future advent in *in situ* infrastructures such as cabled networks and/or moorings and observatory programmes in globally organized frameworks should be developed to improve time-series studies and forecast models (Larkin et al., 2010).

Analyses conducted with the most recent models predict that more than 80% of potential deep-water biodiversity hotspots known around the world (e.g. canyons, seamounts, cold-water coral reefs) will experience negative changes in biomass under climate change conditions (Jones et al., 2014). The change will be linked to organisms having smaller sizes requiring less energy, a trend particularly affecting sediment-dwelling infauna such as macrofauna. The study of Sta. M polychaete assemblage has highlighted the primary role of body size in structuring abyssal macrofauna communities. A decrease in faunal size may therefore have important impacts on deep-sea biodiversity. In addition, smaller fauna may reduce energy transfer rates and modify the services provided by benthic ecosystems such as carbon mineralisation and burial with consequences on the global carbon cycle over centennial and longer scales (that will be modulated depending on location, Smith et al., 2008a, Jones et al., 2014).

Table 6.1 Time-series stations in deep-sea ecosystems with the zone of the study (bathyal or abyssal), the station name, coordinates, depth, date of the time-series, main observations and temporal signal detected with references.

Zone	Station	Coordinates	Depth	Date	Observations	Detected temporal signals	References
Bathyal	Eastern Mediterranean Cretan Sea	35°76'N, 25°10'E	1540	1989-1998	Changes in the thermohaline properties Changes in the phytoplankton composition and average phytoplankton cell size Change in deep-sea nematode density and diversity	Either natural variability, longer term trend or both	Danovaro et al., 2001, 2004
	Sagami Bay North West Pacific	35°N 39°22'E	1450	1996-	Decreases in foraminifera population size during 1996-1997 Anthropogenic disturbance as presence of fluorescent whitening agents and polychlorinated biphenyls in sediments and benthic faunal tissues.	El Niño long-term trend?	Kitazato et al., 2000, 2003
	Rockall Trough North East Atlantic	54°40'-57°18'N , 10°11'-12°16'W	2200-2900	1973-1984	Seasonal reproductive patterns of echinoderm and fish species	Inter-annual variability or stochastic variability?	Gage et al., 1980 Tyler, 1988
Bathyal and abyssal	Mediterranean Sea Ierapetra Basin	34°24'-34°26'N 26°04'E	2500-4500	1987-	Occasional periods of very high organic matter inputs with significant changes in abundance and composition of the meiofauna, macrofauna and planktonic assemblages Period of nematode decreased density but increased microbial component within the benthic food webs	?	Kröncke et al., 2003, Tselepides and Lampadariou, 2004, Lampadariou et al., 2009
	HAUSGARTEN	79°N 4°E	1200-5500	1999-	Increase temperature the Fram Strait in recent years Decrease and modification of flux of phytodetrital matter to the seafloor Variability in nematode community structure, sediment-bound phaeopigment and chlorophyll a concentrations Decrease in total megafauna and microbial biomass of sediments	Either natural variability, longer term trend or both	Soltwedel et al., 2005 Hoste et al., 2007 Bauerfeind et al., 2009 Bergmann et al., 2011

Table 6.1 continued

Zone	Station	Coordinates	Depth	Date	Observations	Detected temporal signals	References
Abyssal	Sigsbee Abyssal Plain Gulf of Mexico	22°–30°N latitude to 85°E–96°W	3800	1997-	Inter-annual variability in macrofauna	El Niño long-term trend?	Escobar-Briones and García-Villalobos, 2009
	Sta. M North East Pacific		4000-4100	1989-	See section 1.2	See section 1.2	See section 1.2
	Porcupine Abyssal Plain North East Atlantic	48˚ 50 N, 16˚ 30 W	4850	1989-	See section 1.2	See section 1.2	See section 1.2

References of chapter 6

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Appendix A

Spatial dispersion of polychaetes and macrofauna in abyssal sedimentary areas

Abstract

This study investigates the degree of aggregation of macro-infauna in abyssal sedimentary areas from scales of 0.1's of m to 10's of km with sampling in the North East Pacific (Station M, 4000 m) and in the North East Atlantic (Porcupine Abyssal Plain, 4850 m). The index of dispersion was computed. The hypothesis of random distribution could not be disproved for polychaete family. Aggregation was however detected at macrofauna level from 0.1- to 300-m scales. Overall, the multivariate analyses indicated that polychaete and macrofauna assemblage compositions were not related to the distance between the samples. In the context of the temporal studies conducted at both stations since 1989, such results do not suggest a significant influence of spatial processes in temporal variability.

A.1 Introduction

Spatial heterogeneity is a central concept both in sampling design and theoretical ecology. Identifying biotic and abiotic spatial distributions and their variability is a prerequisite to unravel the mechanisms generating patterns in an ecosystem (Levin, 1992). Spatial heterogeneity may bring variability in temporal studies such as the long-term monitoring of abyssal sedimentary areas conducted in the North East Pacific Station M (Sta. M) and the North East Atlantic Porcupine Abyssal Plain (PAP). In this context, we examined the degree of aggregation of macro-infauna in abyssal sedimentary plains.

Benthic macrofauna spatial heterogeneity has been studied in several deep-sea systems. Using index of dispersion, defined by a variance to mean ratio, Jumars and colleagues assessed Polychaeta (Annelida) spatial distribution at scales of 10's of cm (within sampler distances, using a 'vegematic' box-corer) and 100's of km' (between sampling location distances) at bathyal depths (Jumars, 1975a,b, 1976) and at scales of 10's of cm to 10's of km at abyssal depths (Hessler and Jumars, 1974) in the North East Pacific. Most polychaete species had a random distribution. Similar results were obtained using distributional techniques (Jumars, 1978). However, Jumars (1975b, 1976) suggested that processes at scales smaller than 0.01 m^2 may be important to structure deep-sea communities. In the North East Atlantic, macrofauna also showed a predominance of random patterns with a low degree of aggregation for species departing from random distribution (Gage, 1977, Lamont et al., 1995). Jumars and Eckman (1983) underlined that index of dispersion studies could not give evidence of spatial randomness but rather showed that the random dispersion hypothesis could not be rejected. The low abundance of deep-sea macrofauna and small sample size in most studies often lowered the power of statistical tests and may have limited the detection of aggregation leading Gage and Tyler (1991) to conclude that it would be unjustified to state that macrofauna had a random dispersion based on existing data at that time. When studying the more abundant meiofauna, more species had significant aggregation (Bernstein, 1978, Thistle et al., 1985, 1991, Rice and Lambshead, 1994). However, Rex and Etter (2010) suggested that as some macrofauna species were found to have a tendency to aggregation in Jumars' studies either at scales of cm's or km's, heterogeneity mechanisms could operate at all scales within this range.

We investigate if the polychaetes/macrofauna were randomly dispersed from 10's of cm to 10's of km scales in abyssal sedimentary areas.

A.2 Materials and methods

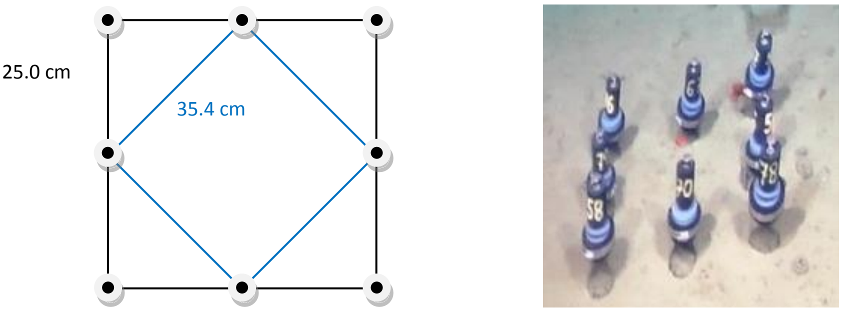
A.2.1 Sta. M sampling

In the North East Pacific, a research cruise was conducted at Sta. M (50˚00 N, 123˚00 W, ~4000 m depth - see details in Kuhnz et al., 2014) in November 2011. Overall, silty-clay particles dominated the sediments and little topographic relief was found over large areas (< 60 m relief over 770 km^2, Smith et al., 1993). Samples were acquired during three Remote Operated Vehicle ROV *Doc Ricketts* dives (Table A.1).

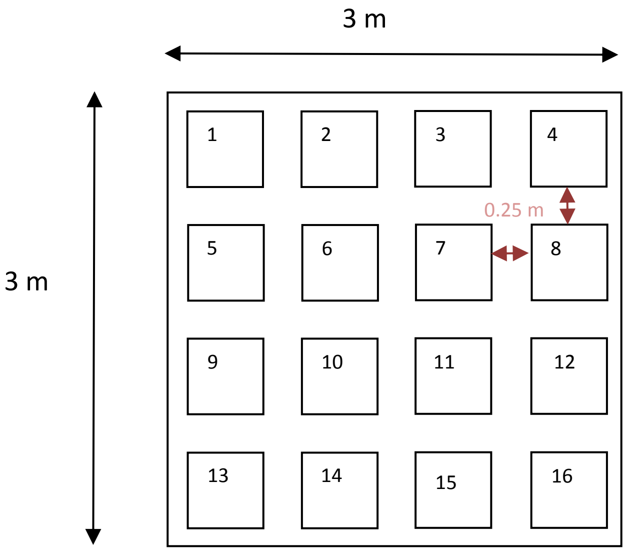
For each ROV dive, 32 core tubes (7 cm diameter) were used to sample the site. Four replicates of 8 core tubes were chosen to represent a site. Core tubes were spaced at a minimal distance of 25 cm to avoid sampling disturbances between core tubes and a square configuration was chosen (Fig. A.1). Push-core tubes were placed by eye using the Ikegama high definition cameras fitted with HA10Xt.2 Fujinon lenses and lasers (spaced 29 cm apart). The eight push-core tubes covered a 0.25 m^2 area called patch. Four patches separated by about 25 cm to 30 cm from each other were considered as a replicate in one site with a randomised sampling of the replicates at each site. Four patches were randomly selected from a sixteen patch grid of 9 m^2 (Fig. A.1). For each site and patch sampling, core tube sampling order was chosen according to the main current flow direction and ROV arm mobility capacity. The three dives were successful and a total of 96 core tube was taken.

Table A.1 Sta. M sampling details: date of sampling, Remote Operated Vehicle (ROV) *Doc Ricketts* dive number, station number, depth in m, site name, patch number, coordinates as well as the precision obtained with the level of sampling, D (%) for polychaete number.

Date	Dive ROV	Station number	Depth (m)	Site	Patch	N	W	D
17/11/2011	321	5903	3962	D0	14	35.16034	-122.936	9.753
				D0	9	35.16030	-122.936	6.453
				D0	7	35.16029	-122.936	7.443
				D0	2	35.16030	-122.936	8.534
19/11/2011	323	5903	3962	D40	13	35.16047	-122.936	6.577
				D40	9	35.16079	-122.936	7.856
				D40	3	35.16088	-122.936	7.252
				D40	4	35.16088	-122.936	7.644
21/11/2011	324	5909	3975	Dx	16	35.09108	-123.089	8.570
				Dx	12	35.09105	-123.089	9.753
				Dx	7	35.09108	-123.089	9.799
				Dx	1	35.09101	-123.089	5.892



(a)



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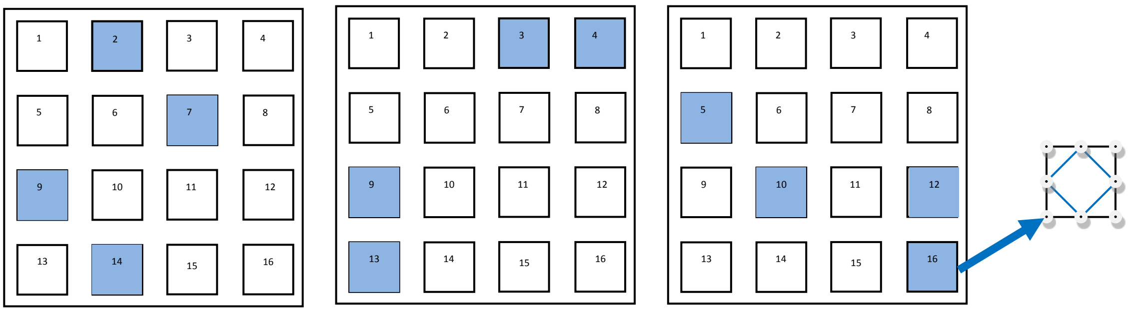


(c)

Figure A.1 Sampling design at Sta. M (a) patch sampling: 8 cores were taken in a square shape, (b) conceptual visualization of a sampling site as a grid of 16 patches, (c) sampling of each site as 4 random patch replicates within a site, from left to right: D0, D40 and Dx.

A.2.2 PAP sampling

See 2.1 in chapter 2.

A.2.3 Sample preservation and taxonomic identification

See 2.2 in chapter 2. Macrofauna specimens were identified to phylum and class level.

A.2.4 Spatial heterogeneity analysis

Since cruise constraints imposed the number of macrofauna cores taken, the resulting sampling intensity was assessed by computing the level of precision (D). The precision was defined as the ratio of the variance and the square mean multiplied by the number of replicates. The spatial heterogeneity analysis was therefore conducted as a preliminary study since the sampling intensity was limited.

Spatial heterogeneity was first assessed using the univariate index of dispersion as defined by Fisher (1970): density mean to variance ratio multiplied by the degree of freedom (n-1) and comparing the index with a Poisson distribution (Jumars, 1975a,b). For a population of individuals randomly arranged in space, the variance of a sample equals its mean. For a given degree of freedom, Fisher’s index higher than the upper confidence limit of a Poisson distribution ($p < 0.05$) indicated an aggregated distribution whereas a Fisher’s lower than the upper confidence limit of a Poisson distribution indicated a random distribution. The test was performed between the stations of Sta. M and PAP 2012 (core tubes samples for each megacorer deployment were pooled for PAP 2011) and between the sites for Sta. M, PAP 2011 (Table A.2) and PAP 2012 (Table A.3). This analysis was performed on polychaete families (P), polychaete functional groups (FG), macrofauna classes (MC) and macrofauna phyla (MP) densities.

Table A.2 Degree of freedom used in Chi^2 test for Sta. M and PAP 2011 cruise by sampling site (DFs) and number of core tubes within each sampling site (DFc) for Sta. M. The number of core tubes per one sampler as well as the number of drop of each sampler corresponding with a station was also indicated.

Cruise	Sampling site	Number of stations	D_{Fs}	Number of cores	D_{Fc}
Sta. M	D0	4	29	8, 7	7, 6
	D40	4	31	8	7
	Dx	4	30	8, 7	7, 6
PAP 2011	PAP	5	4	8 or 4 tubes (pooled)	
	F1	5	4	4 or 3 tubes (pooled)	
	F2	5	4	8 to 1 tubes (pooled)	
	H1	5	4	6 to 1 tubes (pooled)	
	H2	5	4	6 to 2 tubes (pooled)	
	H3	5	4	6 to 3 tubes (pooled)	
	H4	5	4	4 to 2 tubes (pooled)	

Table A.3 Degree of freedom used in Chi^2 test for PAP 2012 cruise by station (DFs) and number of core tubes within each station.

Station	Number of cores	D_{Fs}
A1	6	5
A2	5	4
A3	5	4
AA1	6	5
B1	4	3
B2	6	5
B3	6	5
BB1	4	3
C1	3	2
C2	4	3
C3	3	2
C4	4	3
CC1	5	4
D1	4	3
D2	4	3
D3	4	3
D4	4	3
D5	4	3
DD2	6	5
E2	4	3
E3	4	3

Each time a significant aggregation was detected, a heterogeneity Chi Squared (χ^2) test was performed as defined in Jumars (1975a,b) and Jumars and Eckman (1983). The total χ^2 corresponded with the Fisher's index and indicated if the total density departed on average from a Poisson distribution. The significant pooled χ^2 corresponded with the sum of the Fisher's index of each taxonomic level (P, FG, MC, MP) density. A significant pooled χ^2 indicated that the summed density of taxonomic levels were not independent of each other. The heterogeneity χ^2 defined as total χ^2- pooled χ^2 indicated whether specimens tended to be concordant (specimens tending to be homogeneous in the same unit) or discordant (specimens tending to be heterogeneous in the same unit) in their densities. All significances were assessed for $p < 0.05$.

Spatial heterogeneity was also assessed at between-site (Sta. M, PAP 2011) and station (PAP 2012) scales using a distributional technique. These distributional techniques compute an index of covariance for a series of lag distances from each point. The Moran's I autocorrelation index was used in this study (Moran, 1950) and computed with the Rookcase Excel add-in (Sawada, 1999). The Moran's index varies between -1 (perfect negative correlation between the data and itself lagged by various distances) and +1 (perfect positive correlation). The index significance was computed by converting I to its normal deviate and comparing it to tabled values of the normal curve. The distances tested were computed in relation to the sampling design: 5, 10, 50, 100, and 13930 m at Sta. M, 500, 1000, 5000, 10000, 36000 m at PAP 2011, and 500, 1000, 2500, 5000, 10000 m at PAP 2012.

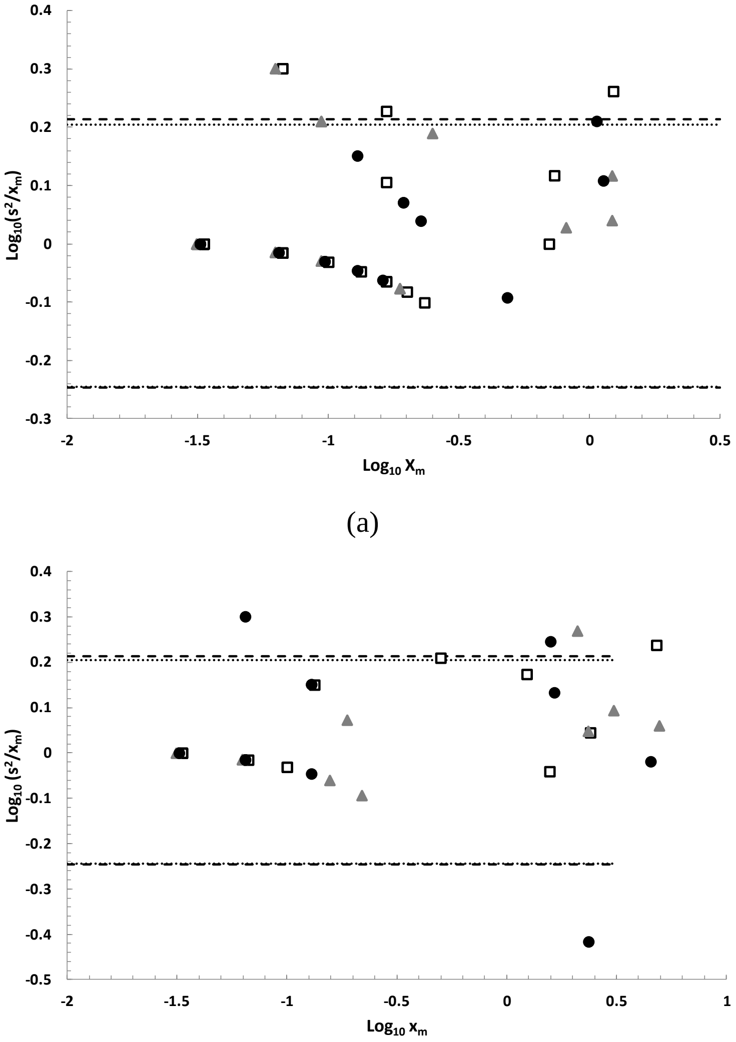
At last, spatial heterogeneity was assessed using multivariate ordination techniques (Primer v.6, Clarke and Gorley, 2006). The assemblage composition (S) as Bray-Curtis Similarity of the squared root-transformed density data was computed (S_P for P, S_{FG} for FG, S_{MC} for MC and S_{MP} for MP). Spatial Euclidian distance similarity matrices were also created (using core tube distances for Sta. M and PAP 2012 as well as station/patch distances for Sta. M, PAP 2011, PAP 2012). Relationships between faunal assemblage similarity matrices and spatial distance matrices were investigated using the RELATE routine (Mantel test, ρ, Primer v.6).

A.3 Results

At Sta. M, polychaete specimens were mostly randomly distributed between cores except in one patch of site D0 ($p < 0.05$, Table A.4), with reasonable precision (Table A.1). The Cirratulidae was the family displaying aggregation at D0. At the macrofauna level, specimens were significantly aggregated in one patch (0.1-0.05 m scale) at site D0 and 2 patches in site D40 (Table A.4). No particular class was found as aggregated. Between sites, the polychaete distribution was aggregated in D0 and random in D40, Dx (4-31 m scale, Fig. A.2). Several polychaete families were aggregated in D0: Sigalionidae, Sabellidae, Phyllodocidae, Cirratulidae and Ampharetidae. The macrofauna distribution was aggregated in both D0 and D40 but not Dx (Fig. A.2). At D0, Bivalvia and Polychaeta drove the aggregation whereas at D40, Maxillopoda did. In all cases, the heterogeneity χ^2 tests did not found the aggregation was discordant. Details of heterogeneity χ^2 tests are given in the annex on the data CD as well as the details of results for FG and macrofauna phyla. There were only a few significant autocorrelations for polychaetes or macrofauna for the tested distances (Table A.5). In terms of assemblage structure, there was no significant difference in S_P, S_{FG}, S_{MC}, S_{MF} with patch, site or patch nested within site as factor ($p > 0.05$). There was no correlation either between the distance matrices (core distances, patch distances, site distances) and fauna similarity matrix ($\rho < 0.08$, $p > 0.05$).

Table A.4 Site of sampling, patch within the sampling site, dispersion coefficient s^2/x_m (variance to mean ratio), degree of freedom D_F, distribution given for $p < 0.05$ level of confidence for total polychaete (both families and functional groups) and total macrofauna specimens of Sta. M.

Fauna	Site	Patch	s^2/x_m	D_F	Distribution
Polychaete	D0	14	3.860	7	aggregated
		9	1.220	6	random
		7	1.610	7	random
		2	0.520	6	random
	D40	13	1.000	7	random
		9	1.210	7	random
		3	0.850	7	random
		4	1.970	7	random
	Dx	16	1.900	7	random
		12	0.470	7	random
		7	0.300	6	random
		1	0.670	7	random
Macrofauna	D0	14	6.514	7	aggregated
		9	1.204	6	random
		7	1.428	7	random
		2	0.550	6	random
	D40	13	2.811	7	aggregated
		9	1.017	7	random
		3	2.457	7	aggregated
		4	1.613	7	random
	Dx	16	2.249	7	random
		12	0.285	7	random
		7	0.580	6	random
		1	0.857	7	random



(a)

(b)

Figure A.2 Log_{10} variance to mean ratio ($Log_{10}(s^2/x_m)$) *versus* Log10 mean number (log_{10} x_m) of individuals at all Sta. M site. Each site is distinguished by a different symbol: D0 (□), D40 (▲), Dx (●). Poisson expectation are given in line (n= 29 in dotted line, n = 31 in dashed line) with the upper confidence limit on top and the lower confidence limit on the bottom (a) for polychaete specimens, (b) for macrofauna specimens.

Table A.5 Significant ($I > 0.5$ and $p < 0.005$) autocorrelation as Moran's index (I) with its variance (Var I normal) and z value transform with associated p-value for fauna of each research cruise. The distance indicated the lag distance used for autocorrelation. N indicated the number of pairs used for the computation.

Cruise	Fauna	Distance in m	N	I	Var I normal	z-normal	p-value
Sta. M	Spionidae	0-10	13	0.533	0.053	2.699	< 0.001
	BMx	0-5	7	-0.571	0.112	-1.430	0.042
	Arthropoda	0-100	34	-0.631	0.011	0.011	< 0.001
PAP 2012	Annelida	0-500	10	0.599	0.085	2.221	< 0.001

At PAP 2011, polychaete specimens were randomly distributed between all sites whereas macrofauna classes were aggregated in F2, H1, H2 and H3 (100-300 m scales, Table A.6) with good precision (D < 1%). At F2, Anthozoa, Aplacophora, Maxillopoda, Scaphopoda and Turbellaria were all aggregated. At H1, Bivalvia, Malacostraca, Maxillopoda were aggregated, at H2 and H3, Malacostraca and Polychaeta were aggregated. The heterogeneity χ^2 test showed that macrofauna specimens tended to be discordantly aggregated at F2 (χ^2 = 184, 117, χ^2 pooled = 22.261, χ^2 heterogeneity = 161.856, p < 0.001), at H1 (χ^2 = 103.293, χ^2 pooled = 33,796, χ^2 heterogeneity = 69.497, p < 0.001) and H3 (χ^2 = 67.394, χ^2 pooled = 10.348, χ^2 heterogeneity = 57.046, p = 0.002). Details of heterogeneity χ^2 tests are given in the annex on the data CD as well as details of results for FG and macrofauna phyla. There was no significant correlation for the fauna at the investigated scale. In terms of assemblage structure, there was no correlation either between the site distance matrices (core distances, patch distances, site distances) and fauna similarity matrix ($\rho < 0.11$, $p > 0.05$) except between site distances and polychaete FG similarity matrix ($\rho = 0.602$, $p = 0.01$).It is worth noting that considering only the abyssal plain sites, polychaetes were randomly distributed.

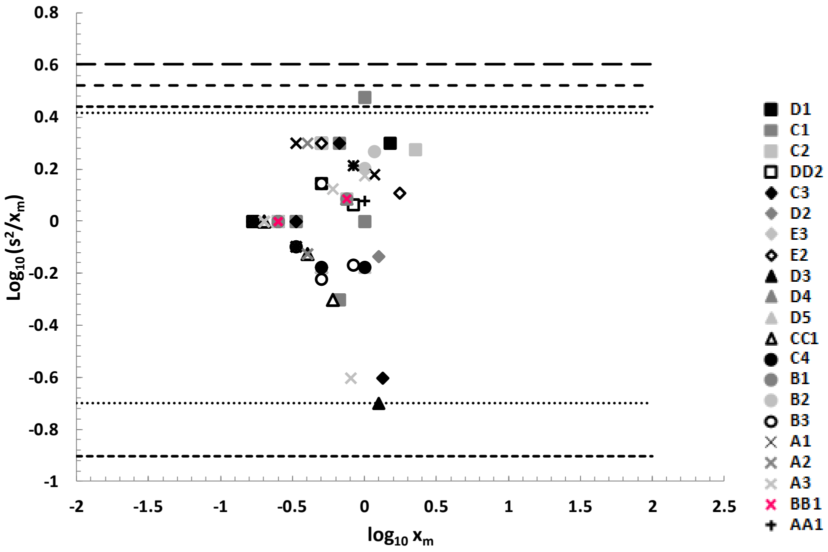
Table A.6 Dispersion coefficient s^2/x_m (variance to mean ratio), degree of freedom D_F, distribution given for p < 0.05 level of confidence for total polychaete (both families and functional groups) and total macrofauna specimens of PAP 2011 at each sampling site.

Fauna	Site	s^2/x_m	D_F	Distribution
Polychaetes	PAP	2.325	4	random
	F1	0.621	4	random
	F2	1.274	4	random
	H1	0.614	4	random
	H2	2.689	4	random
	H3	2.530	4	random
	H4	0.705	4	random
Macrofauna	PAP	2.298	4	random
	F1	4.277	4	random
	F2	5.848	4	aggregated
	H1	10.221	4	aggregated
	H2	11.877	4	aggregated
	H3	7.557	4	aggregated
	H4	2.019	4	random

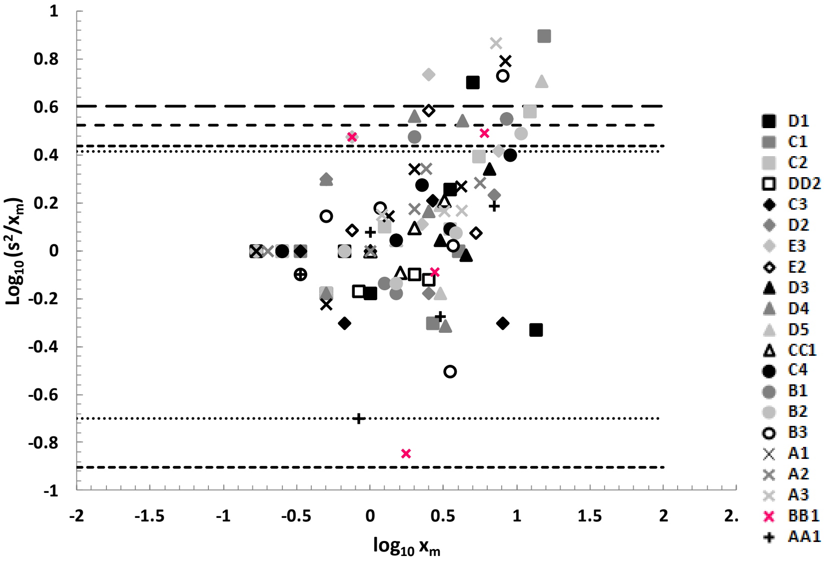
For PAP 2012, the precision in determining the mean and variance of data densities were below 25% for each station (only CC1 and PAP1 had a higher value, Table A.7, Fig. A.3). Polychaete specimens were randomly distributed between cores at all sites whereas macrofauna specimens were aggregated in C2, E2, E3, D5, B1, B2, B3 and A3 stations (0.1-m scale, Table A.8). No particular class was driven the aggregation except Maxillopoda at E3 and E2. The heterogeneity χ^2 test did not find the aggregation was discordant except in A3 (χ^2 = 47.002, χ^2 pooled = 19.2914, χ^2 heterogeneity = 27.711, p = 0.012). Details of heterogeneity χ^2 tests are given in the annex on the data CD as well as the details of results for FG and macrofauna phyla are given in S7. In terms of autocorrelation, only the Annelida was moderately auto-correlated on distance 0-500 m (Table A.5). In terms of assemblage structure, there was no significant difference in S_{P12}, S_{FG12}, S_{MC12}, S_{MF12} with megacorer core tube or station as factor (ANOSIM). There was no correlation either between the distance matrices (core tube distances, megacorer drop distances, site distances) and fauna similarity matrix ($\rho < 0.1$, $p > 0.05$). It is worth noting that considering only the abyssal plain stations, polychaetes were randomly distributed.

Table A.7 PAP 2012 sampling details: date of sampling, Megacorer drop number, station, depth in m, coordinates, depth band, large scale habitat category (LSH), and site type (abyssal plain areas, P or hill, H) as well as the precision obtained with the level of sampling, D (%) for polychaete number.

Date	D
13/07/2012	10.206
13/07/2012	24.845
14/07/2012	11.180
15/07/2012	13.608
12/07/2012	25.000
12/07/2012	11.664
13/07/2012	12.247
15/07/2012	25.000
10/07/2012	8.267
10/07/2012	10.000
11/07/2012	0.000
12/07/2012	16.666
16/07/2012	31.943
09/07/2012	14.285
09/07/2012	20.000
11/07/2012	11.764
11/07/2012	16.666
11/07/2012	20.000
17/07/2012	22.268
11/07/2012	9.523
10/07/2012	25.000



(a)



(b)

Figure A.3 Log$_{10}$ variance to mean ratio (Log$_{10}$ (s^2/x_m)) ratio *versus* Log$_{10}$ mean number (log$_{10}$ x_m) of individuals at all PAP 2012 stations. Poisson expectation are given in line (n= 7 in large dashed line, n =11 in dashed line, n = 13 in dots) with the upper confidence limit on top and the lower confidence limit on the bottom (a) for polychaete specimens, (b) for macrofauna specimens.

Table A.8 Dispersion coefficient s^2/x_m (variance to mean ratio), degree of freedom D_F, distribution given for $p < 0.05$ level of confidence for total polychaete (both families and functional groups) and total macrofauna specimens of PAP 2012 stations.

Fauna	Station	s^2/x_m	D_F	Distribution
Polychaetes	A1	1.600	5	random
	A2	0.944	4	random
	A3	1.625	4	random
	AA1	0.533	5	random
	B1	3.000	3	random
	B2	1.228	5	random
	B3	0.200	5	random
	BB1	0.666	3	random
	C1	1.000	2	random
	C2	3.066	3	random
	C3	0.000	3	random
	C4	0.666	3	random
	CC1	1.642	4	random
	D1	1.809	3	random
	D2	0.666	3	random
	D3	1.156	3	random
	D4	0.666	3	random
	D5	1.200	3	random
	DD2	0.745	5	random
	E2	1.190	3	random
	E3	1.000	3	random
Macrofauna	A1	1.981	5	random
	A2	1.491	4	random
	A3	4.822	4	aggregated
	AA1	1.493	5	random
	B1	6.207	3	aggregated
	B2	3.455	5	aggregated
	B3	2.805	5	aggregated
	BB1	2.214	3	random
	C1	3.957	2	random
	C2	4.197	3	aggregated
	C3	0.000	3	random
	C4	2.666	3	random
	CC1	0.346	4	random
	D1	3.266	3	random
	D2	0.666	3	random
	D3	0.439	3	random
	D4	2.493	3	random
	D5	5.630	3	aggregated
	DD2	0.610	5	random
	E2	4.407	3	aggregated
	E3	4.804	3	aggregated

A.4 Discussion

The distributions for total polychaete families could not be distinguished from random distributions at Sta. M and PAP on the investigated scales. The heterogeneity chi-squared tests using all families as replicates although considered to be more reliable to indicate departure from random distribution (Jumars, 1975b), did not support aggregation either. For total macrofaunal classes, aggregation was observed at both small and large scales. At

Sta. M, the macrofauna assemblage showed aggregation in 3 patches out of 12 and at 2 sites out of 3 with indication of discordant aggregation between the classes. In other words, where one class tended to be abundant, others tended to be rare. At PAP, the macrofauna appeared aggregated at 3 abyssal hill sites and one abyssal plain site, all with indications of discordance. Aggregation was however not found to be significantly different between hill and plain sites. Within a hill, aggregation occurred in 8 stations out of 21. Looking only at the individual family instead of total polychaete family, some families appeared aggregated at Sta. M and PAP (see annex on the data CD). Jumars (1974) also found that 2 polychaete species out of 57 exceeded the Poisson confidence limits and that 9 of these 12 species were more abundant in a single core tube. Jumars and Eckman (1983) concluded that random dispersion patterns could not be generalised and that no simple, typical deep-sea multispecies patterns emerge from all the studies (Gage, 1977, Hessler and Jumars, 1974, Jumars, 1975b, 1976, 1978) to date.

Total polychaete family lack of aggregation may be real or induced by insufficient sampling. Although aggregated distribution of benthic organisms in soft sediment has been recognised for a long time (Barry and Dayton, 1991), it has remained difficult to quantify (Gage, 1977, Hessler and Jumars, 1974, Jumars, 1975b, 1976, 1978, Jumars and Eckman, 1983, Lamont et al., 1995). Analyses of index of dispersion suffer from several issues. Firstly, low faunal densities have been shown to dramatically lower the power of the statistical tests performed (Jumars and Eckman, 1983). And deep-sea species densities are particularly low (Jumars, 1975a, 1976). Lamont et al. (1995) reported issues in spatial dispersion analysis of macrofauna in abyssal plain in the North East Atlantic due to low abundance. Low densities are particularly problematic for macrofauna. Compared to meiofauna, the macrofauna is less abundant at abyssal depths and requires higher sampling effort to obtain a similar number of specimens. Jumars (1981) stated that the samples required to detect non-random dispersion at local scale may be prohibitive for deep-sea macrofauna species even using a 0.25 m^2 box-corer. In the present study, core tubes were used, not box-corers. Megacorer and push-cores have been proven to reduce bow wave effect during the sampling compared to a box-corer leading to a greater number of animals being caught (Bett et al., 1994). However, the associated reduction in sampled areas increases the variance of the samples. In the present study, dispersion analyses within patch at Sta. M and within PAP 2012 megacorers were based on abundance found in 3 to 8 cores of less than 0.004 to 0.008 m^2. So for the within sampler analyses, the polychaete family densities may have been too low to meaningfully test for dispersion. Analyses of spatial dispersion between sites (by opposition to between cores) were less prone to low density issues. For macrofauna classes, although the densities were higher than polychaete family ones, they remained low and the detected trends should be interpreted with caution. Secondly, deep-sea macrofauna has been characterised by numerous spatially rare species (Snelgrove, 1998) which also may increase data variances. Thirdly, apparent aggregation may also be an artefact of analysing spatial dispersion in a 2D plan whereas animals live in a 3D structure of sediments. Abyssal macrofauna likely live at different sediment depths as a way to partition resources. Based on sediment content analyses, Danovaro et al. (2001) reported that at PAP central, animals in surface or sub-surface sediment likely experienced different diets and may have different adaptive mechanisms to exploit the different resources. However, vertical segregation of deep-sea macrofauna remained hard to assess as the transit time of the sample from the seafloor to the research vessel at PAP is couple of hours or more.

Total polychaete families appeared to have been aggregated at PAP central in the past. We conducted post hoc dispersion tests using polychaete data obtained from the time-series sampling of Sta. M and PAP central (see Laguionie-Marchais et al., 2013 for more details on macrofauna time series at both station). Because data were not collected at the same time as data in the present study, the post hoc test purposes were to investigate if different sampling intensities may change the results of the present study and if family and species-level studies differ as Sta. M polychaetes were identified to species level. Among the time series data, those with the most numerous replicates were chosen. Seven 0.25 m^2 box-corers were taken at PAP central in September 1996. At Sta. M, macrofauna was sampled with a Free-Vehicle Grab Respirometer (FVGR, Smith et al., 2001) at Sta. M. The FVGR is a sampling system comprised of four 413-cm^2 grabs separated by 25 cm (square design) collecting the top 15 cm of sediment. In June 1991, seven grabs were collected. Results showed that at Sta. M, the polychaete assemblage was not aggregated both at family ($s^2/x_m = 1.82$, 6 degrees of freedom, $p < 0.05$) and species levels ($s^2/x_m = 1.32$, 6 degrees of freedom, $p < 0.05$). However, some particular families and species had dispersion indexes above the Poisson distribution confidence limit: Paraonidae, Spionidae and species *Prionospio* sp. B and sp. E showing that family and species level spatial dispersion differed. Overall, dispersion could not be distinguished from random at Sta. M. At PAP, a significant aggregation was found between polychaete families in September 1996 ($s^2/x_m = 6.62$, 6 degrees of freedom, $p < 0.05$) at the scale of box-corer drop distance (100s m). The chi-squared test indicated that polychaete families were discordant ($\chi^2 = 478.83$, χ^2 pooled $= 39.73$, χ^2 heterogeneity $= 439.10$, $p < 0.001$).

Overall, the polychaete and macrofauna assemblages were not related to the distance between the samples. The use of multivariate analyses using spatial distances between samples (based on their coordinates) did not indicate aggregation at Sta. M and PAP. Multivariate analyses have an advantage over summary statistics such as the dispersion index that tend to dilute aggregation (Jumars and Eckman, 1983). Other studies have reported that spatial distance had little influence on shallow water in macrofauna communities compared to environmental factors (Ellingsen, 2002). The results of the multivariate tests are important in the context of temporal studies. Sta. M and PAP have been sampled since 1989 to assess inter-annual variability in abyssal benthic community (Ruhl and Smith, 2004, Billett et al., 2010, Laguionie-Marchais et al., 2013). The absence of correlation between macrofauna assemblages and samples distances suggested that spatial processes do not dominate temporal patterns.

A.5 Conclusions

Abyssal polychaete family spatial distribution did not appeared to be aggregated at 10s cm to 10s km at Sta. M and PAP. However, sampling design may not have been sufficient to detect any aggregation. At macrofauna level, classes were found to be discordantly spaced at several scales. Overall the faunal assemblages were not dependent of the spatial distances between the samples.

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Appendix B

Chapter 2 supplement information

Table B.1 Number of macrofauna and polychaete specimens collected during the between and among hill (BH) study and the within and surrounding a single hill (WH) study with details on the name of the site, gear deployment number (GDN) and number of cores (nc).

Study	Site	GDN	nc	Macrofauna	Polychaetes
BH	P1	JC062-16+98	8	35	16
	P1	JC062-20	4	16	7
	P1	JC062-28	4	35	18
	P1	JC062-36	4	27	8
	P1	JC062-37+97	4	21	17
	P3	JC062-65+70	4	37	22
	P3	JC062-100	4	25	15
	P3	JC062-67+101	5	39	12
	P3	JC062-68	4	43	13
	P3	JC062-69+131	4	40	19
	P4	JC062-73+133	6	44	15
	P4	JC062-111	5	7	6
	P4	JC062-75+112	8	56	26
	P4	JC062-76	1	10	2
	P4	JC062-77	2	16	7
	H1	JC062-52+115	5	38	19
	H1	JC062-53	1	3	2
	H1	JC062-56+114	6	36	22
	H1	JC062-60	3	17	14
	H1	JC062-61	1	13	3
	H2	JC062-91	2	26	15
	H2	JC062-92	2	15	9
	H2	JC062-88+117	5	18	9
	H2	JC062-89	6	61	29
	H2	JC062-90 + 129	6	29	17
	H3	JC062-105	2	22	7
	H3	JC062-106+116	6	56	33
	H3	JC062-108	2	17	8
	H3	JC062-109	3	18	12
	H3	JC062-110	3	8	3
	H4	JC062-123	2	16	9
	H4	JC062-128	2	26	12
	H4	JC062-125	2	15	9
	H4	JC062-126	2	16	12
	H4	JC062-127	2	16	6
WH	H3-A1	D377/8-29	6	56	25
	H3-A2	D377/8-20	5	28	10
	H3-A3	D377/8-31	5	44	21
	H3-AA1	D377/8-36	6	33	18
	H3-B1	D377/8-24	4	21	8

Table B.1 continued

Study	Site	GDN	nc	Macrofauna	Polychaetes
WH	H3-B2	D377/8-25	6	41	23
	H3-B3	D377/8-27	6	55	21
	H3-BB1	D377/8-35	4	22	11
	H3-C1	D377/8-14	3	26	12
	H3-C2	D377/8-15	4	45	22
	H3-C3	D377/8-22	3	31	13
	H3-C4	D377/8-23	4	33	14
	H3-CC1	D377/8-37	5	24	10
	H3-D1	D377/8-11	4	41	14
	H3-D2	D377/8-13	4	16	10
	H3-D3	D377/8-19	4	38	18
	H3-D4	D377/8-20	4	37	13
	H3-D5	D377/8-21	4	36	12
	H3-DD2	D377/8-40	6	26	15
	H3-E2	D377/8-18	4	41	21
	H3-E3	D377/8-17	4	31	9

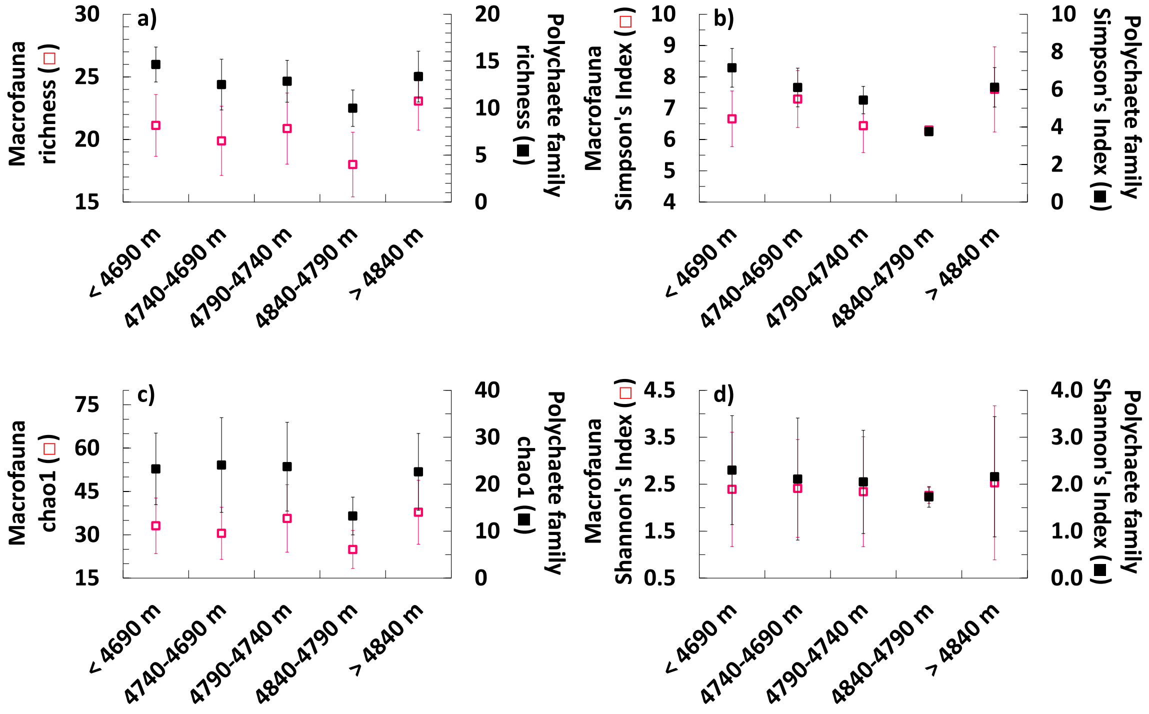


Figure B.2 Within and surrounding a single hill (WH) – depth band. Diversity indexes with associated standard errors for macrofauna (□) and polychaete families (■) at each depth band (a) estimated species richness (rarefied to 79 individuals for macrofauna and to 35 individuals for polychaete family), (b) Inverse Simpson's index (rarefied to 79 individuals for macrofauna and to 35 individuals for polychaete family), (c) asymptotic species richness chao1 (rarefied to 79 individuals for macrofauna and to 35 individuals for polychaete family), (d) Shannon's index rarefied to 79 individuals for macrofauna and to 35 individuals for polychaete family).

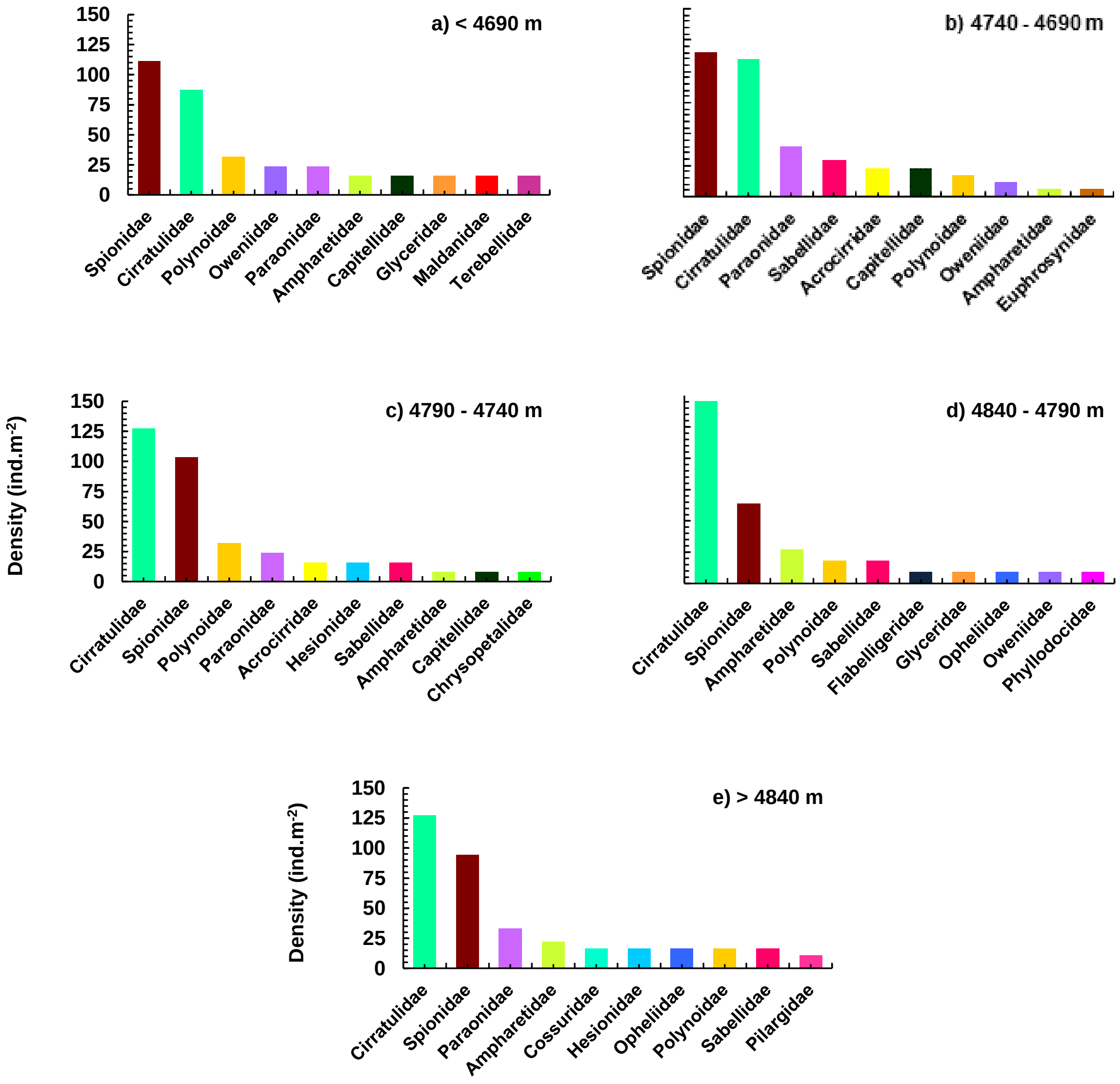


Figure B.3 Within and surrounding a single hill (WH) – depth band. Polychaete family rank abundance at each depth band. The most dominant families (rank 1) are on the left side and the 10Th dominant families (rank 10) are on the right side.

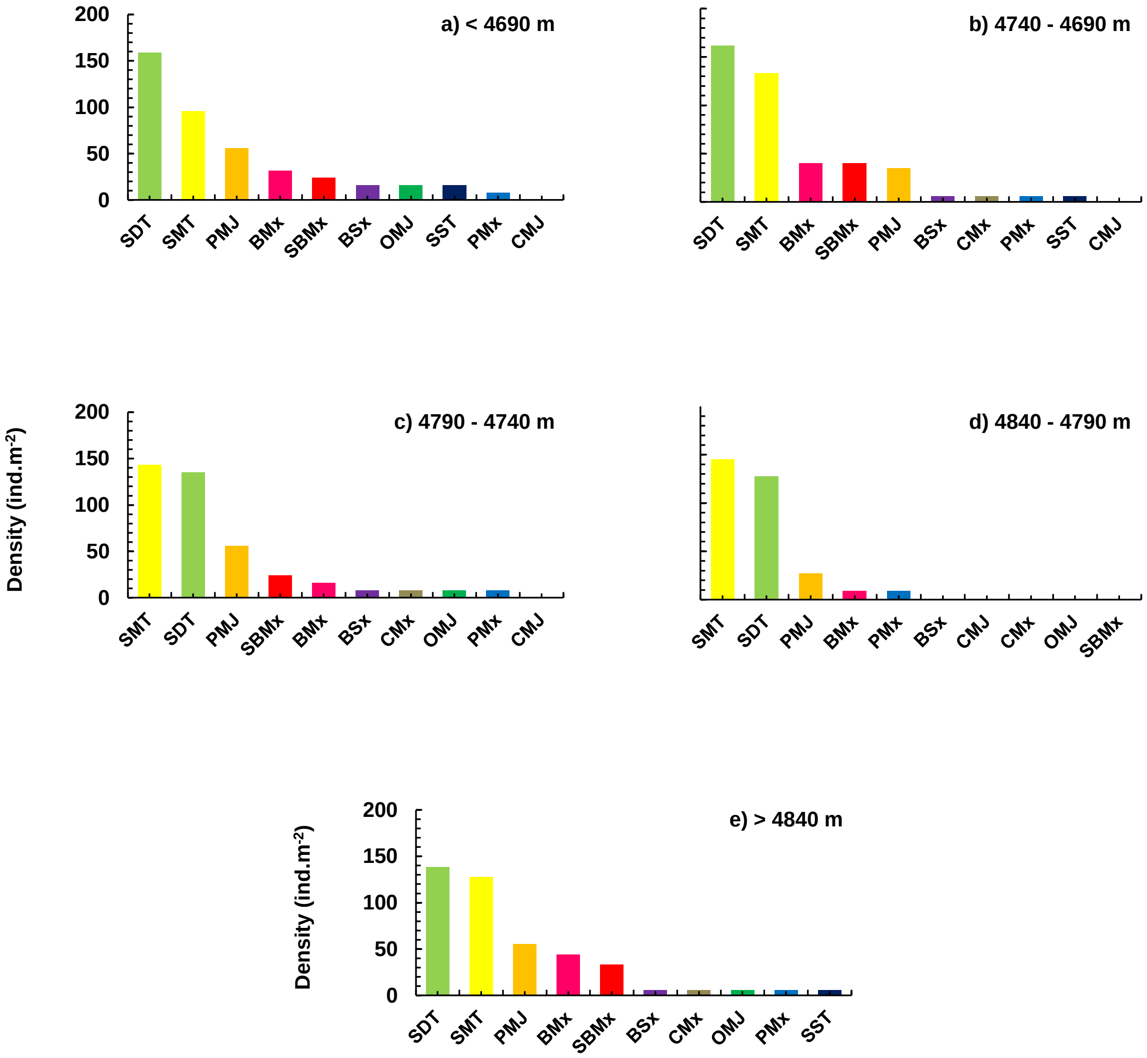
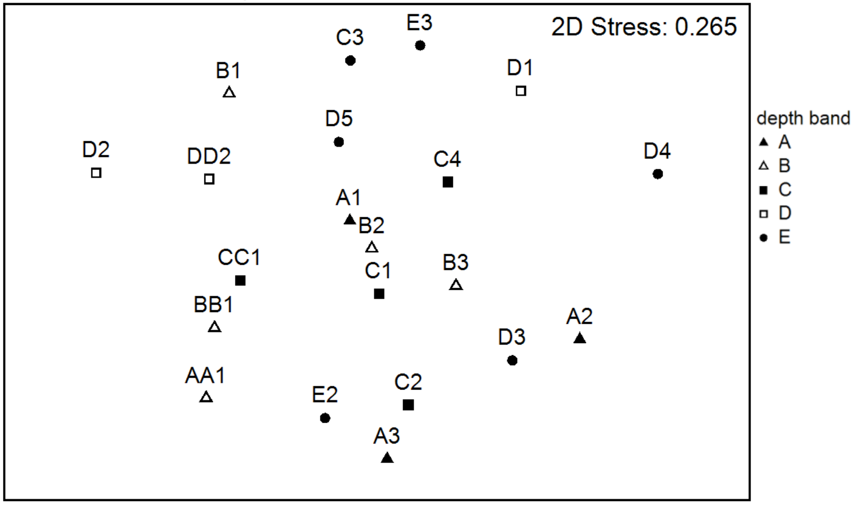
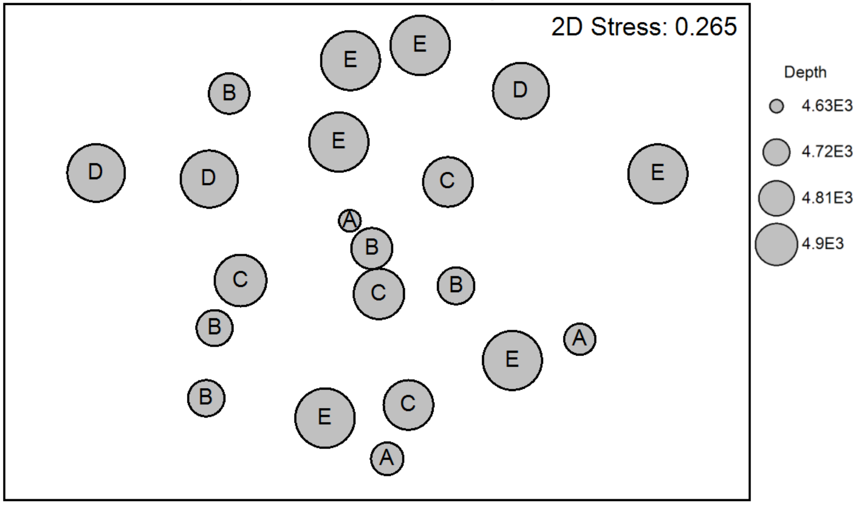


Figure B.4 Within and surrounding a single hill (WH) – depth band. Polychaete functional group rank abundance at each depth band. The most dominant functional groups (rank 1) are on the left side and the 10Th dominant functional groups (rank 10) are on the right side.

a) macrofauna - MDS



b) macrofauna - depth



c) macrofauna - % sand

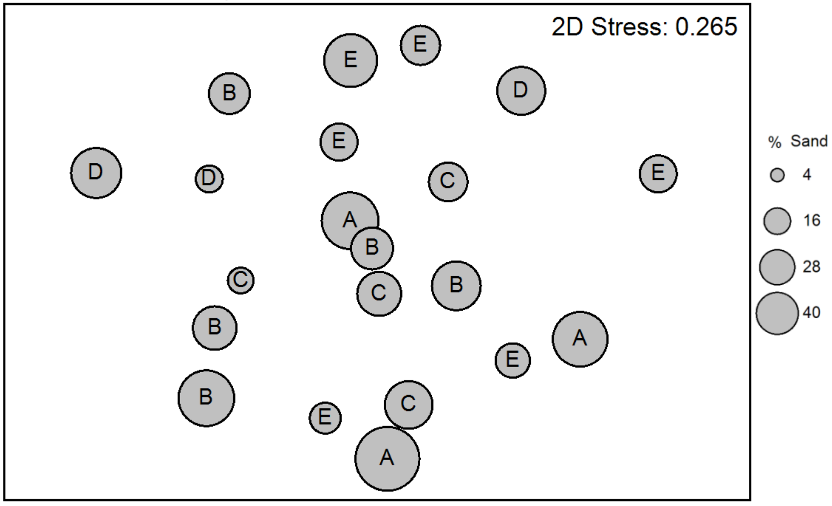
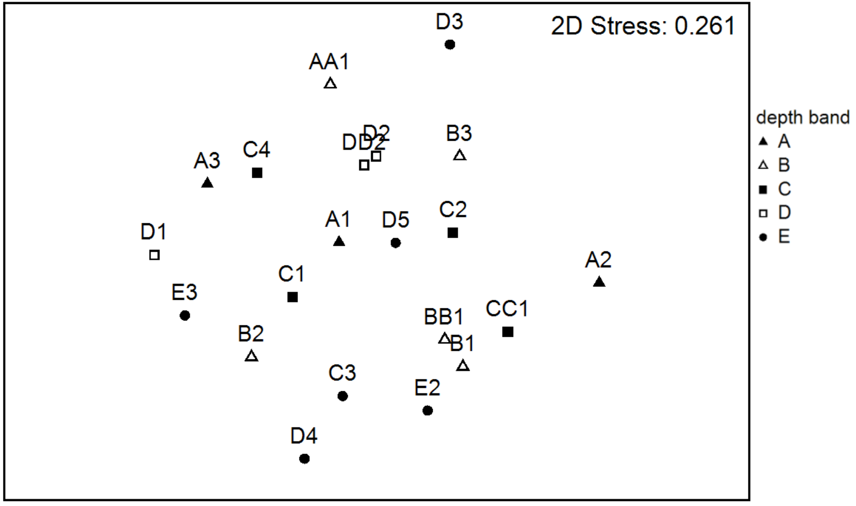
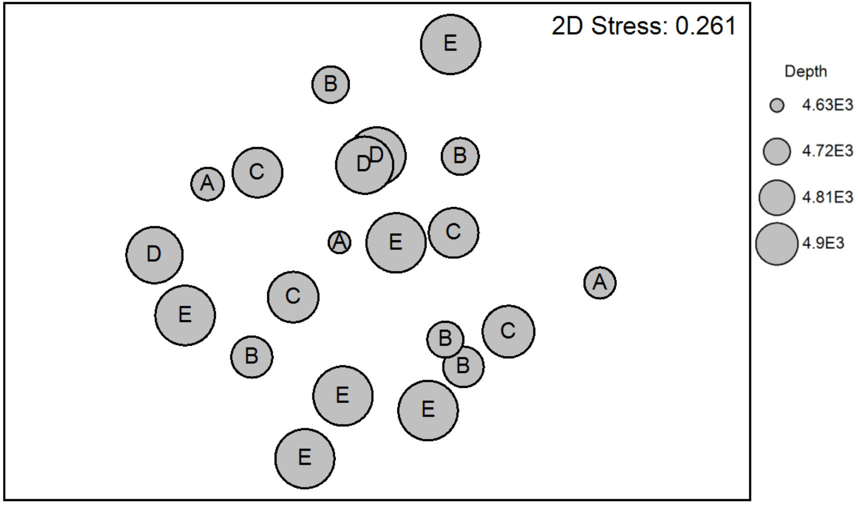


Figure B.5 Within and surrounding a single hill (WH) – depth band. Multi-Dimensional Scaling ordination for macrofauna taxa (a) by site with depth bands coded by symbols, (b) with depth as bubble plot and depth band as over-imposed letter, (c) with % sand as bubble plot and depth band as over-imposed letter. Depth band letter with A: < 4690 m, B: 4740-4690 m, C: 4790-4740 m, D: 4840-4790 m, E: > 4840 m.

a) polychaete family - MDS



b) polychaete family - depth



c) polychaete family - % sand

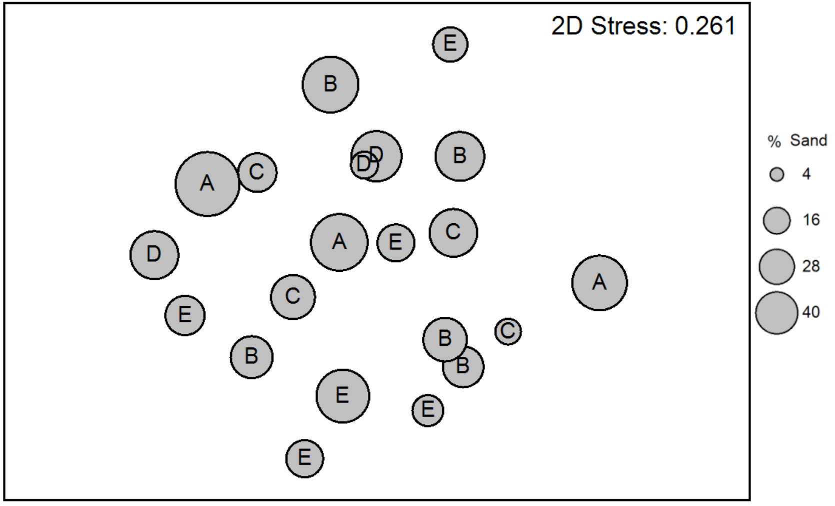
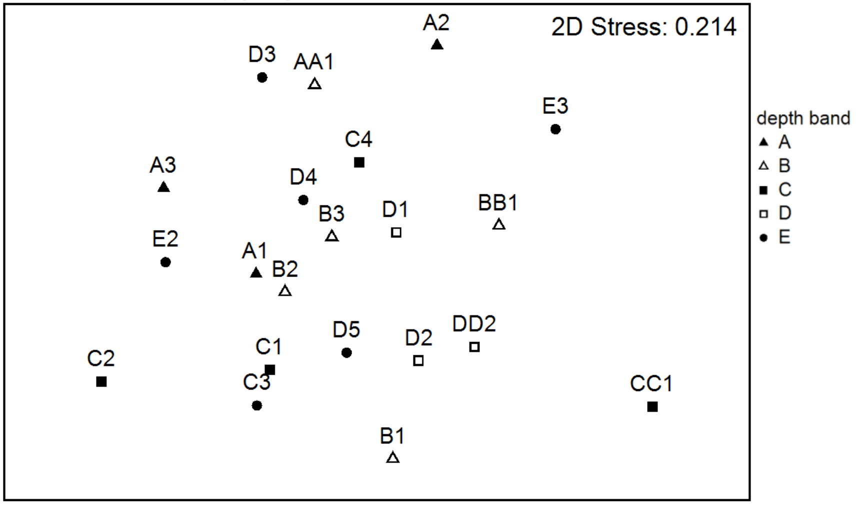
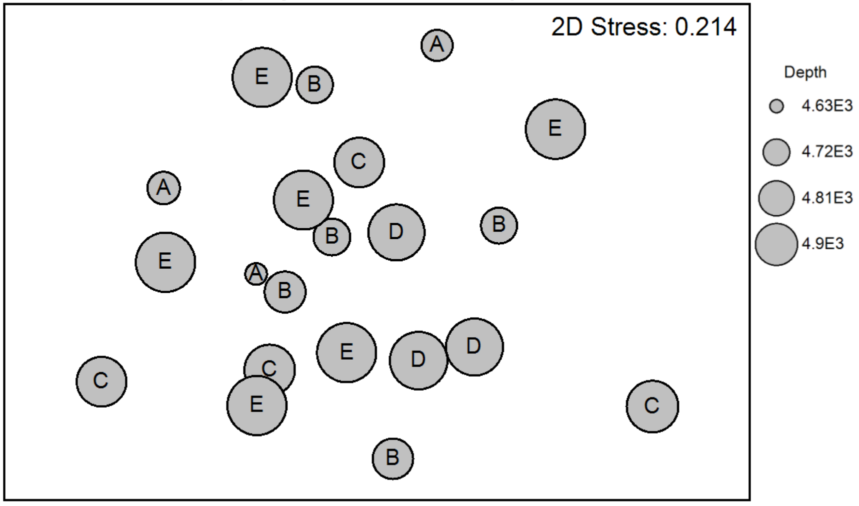


Figure B.6 Within and surrounding a single hill (WH) – depth band. Multi-Dimensional Scaling ordination for polychaete families (a) by site with depth bands coded by symbols, (b) with depth as bubble plot and depth band as over-imposed letter, (c) with % sand as bubble plot and depth band as over-imposed letter. Depth band letter with A: < 4690 m, B: 4740-4690 m, C: 4790-4740 m, D: 4840-4790 m, E: > 4840 m.

a) polychaete FG - MDS



b) polychaete FG - depth



c) polychaete FG - % sand

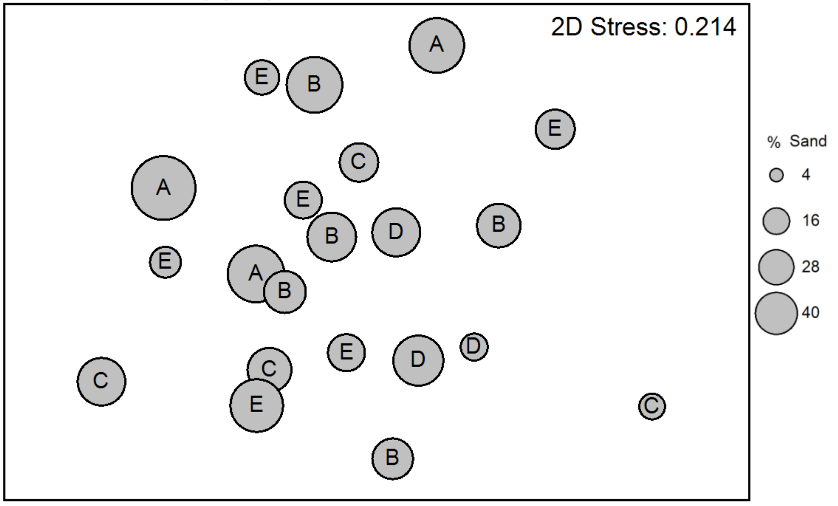


Figure B.7 Within and surrounding a single hill (WH) – depth band. Multi-Dimensional Scaling ordination for polychaete functional groups (a) by site with depth bands coded by symbols, (b) with depth as bubble plot and depth band as over-imposed letter, (c) with % sand as bubble plot and depth band as over-imposed letter. Depth band letter with A: < 4690 m, B: 4740-4690 m, C: 4790-4740 m, D: 4840-4790 m, E: > 4840 m.

Table B.8 Within and surrounding a single hill (WH) spearman rank correlation (r_s) with associated p-values between sediment % sand and various faunal groups, in relation to depth band. n is the number of data points used.

Grouping	Fauna	r_s	p	N
Sites	Ophiuroidea	-0.443	0.045	21
	Lumbrineridae	0.533	0.013	21
	Maldanidae	0.507	0.019	21
	BSx	0.507	0.019	21
Depth bands	Lumbrineridae	0.947	0.015	5
	Oweniidae	0.918	0.028	5
	Terebellidae	0.901	0.037	5
	SST	0.901	0.037	5

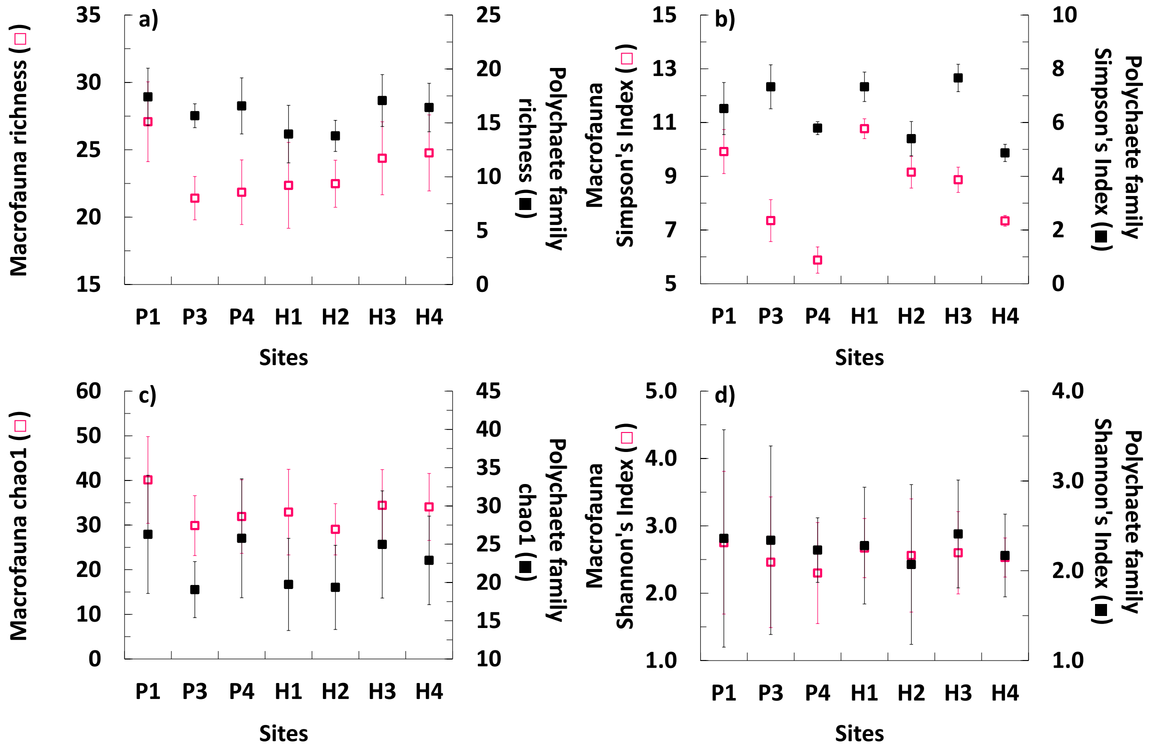


Figure B.9 Between and among hill (BH) diversity indexes with associated standard errors for macrofauna (□) and polychaete families (■) at each site (a) estimated species richness (rarefied to 93 individuals for macrofauna and to 45 individuals for polychaete family), (b) Inverse Simpson's index (rarefied to 93 individuals for macrofauna and to 45 individuals for polychaete family), (c) asymptotic species richness chao1 (rarefied to 93 individuals for macrofauna and to 45 individuals for polychaete family), (d) Shannon's index rarefied to 93 individuals for macrofauna and to 45 individuals for polychaete family).

Table B.10 Between and among hill (BH) spearman rank correlation (r_s) with associated p-values between sediment features (percent sand particles, % sand, total organic content, % TOC) and various faunal groups. n is the number of data points used. Significant correlations are in bold.

Sediment feature	Fauna	r_s	p	n
% TOC	Ampharetidae	-0.750	0.050	7
	Cirratulidae	**-0.930**	**0.002**	**7**
	Phyllodocidae	**-0.820**	**0.024**	**7**
	Spionidae	**0.811**	**0.027**	**7**
	PMx	**-0.820**	**0.024**	**7**
	SMT	**-0.904**	**0.005**	**7**
% sand	Cirratulidae	**0.814**	**0.026**	**7**
	Spionidae	-0.753	0.050	7
	OMJ	0.738	0.058	7
	PMx	0.719	0.069	7
	SMT	**0.805**	**0.029**	**7**

Appendix C

Key of Polychaeta species of Sta. M in the North East Pacific

A dichotomic key is given to help with the identification of Sta. M polychaete species. Each family is presented in alphabetical order. Every specimen was identified to the lowest level, usually species. These species were classified to existing species wherever possible otherwise a unique letter was assign to each species to differentiate the species from similar unclassifiable species in the same family. In some cases, there was not enough of a specimen and not enough individuals to even observed generic characters. For example, no branchiae was seen in Orbiniidae specimens and their size was too small to be able to see potential branchial scares. Therefore these specimens could not be assigned to a genus. In these cases, specimens with the same features were classified within the family and assigned a unique identifying letter.

Acrocirridae

1	Thin, smooth body; dark red prostomium	Acrocirridae sp. A
	Anteriorly robust body with rugose surface and round papillae; un-colour prostomium	Acrocirridae sp. B

Ampharetidae

1	Wing-like structures on the first abdominal chaetiger with ridges	Ampharetidae sp. B
	No wing-like structures on the first abdominal chaetiger with ridges	2
2	Hooded prostomium	*Glyphanostomum* sp. A
	Prostomium not hooded	3
3	Palea present	4
	Palea absent	5
4	Very long palea (more than 2-chaetiger long); 4 pairs of branchiae not clearly separated by a gap	Ampharetidae sp. D
	Long but shorter palea (less than 2-chaetiger long); 4 pair of branchiae clearly separated in 2 groups by median gap	Ampharetidae sp. F
5	Peristomium ventrally fringed (toothed)	Ampharetidae sp. E
	No peristomium ventrally fringed (toothed)	6

6	3 pairs of branchiae	7
	4 pairs of branchiae	8
7	15 abdominal chaetigers	Ampharetidae sp. C
	10 abdominal chaetigers	Ampharetidae sp. I
8	Branchiae clearly separated by median gap	Ampharetidae sp. H
	Branchiae not clearly separated by median gap	9
9	12 uncinigers, branchiae smooth and cylindrical, at least 11 abdominal chaetigers (not whole specimen); no elevated notopodium; (if papillose tentacle confirmed the genus will be *Asabellides*)	Ampharetidae sp. A
	Body otherwise (damaged)	Ampharetidae sp. G

Amphinomidae

1	Ventral cirri only well-developed in pre-branchial chaetigers; neurochaetae as aciculae with inflated tips, serrated fine capillaries and basally spurred serrated chaetae	*Paramphinome* sp. A
	Ventral cirri well-developed on all chaetigers; neurochaetae as aciculae with inflated tips, serrated fine capillaries	*Paramphinome* sp. B

Apistobranchidae

There was only one species: Apistobranchidae sp. A.

Capitellidae

1	Capillary chaetae on the first 3 chaetigers	*Capitomastus* sp. A
	Capillary chaetae on more than the first 3 chaetigers	2
2	Capillary chaetae on the first 4 chaetigers	3
	Capillary chaetae on more than the first 4 chaetigers	4
3	All first 4 chaetigers with only capillary chaetae	*Capitella* sp. A
	Chaetiger 4 with mixed chaetae	*Heteromastides* sp. A
4	Capillary chaetae on the first 5chaetigers	5
	Capillary chaetae on more than the first 5 chaetigers	7
5	Chaetiger 5 with mixed chaetae	*Capitella* cf. *syincola*
	Chaetiger 5 without mixed chaetae	6

6	All first 5 chaetigers only with simple capillary chaetae	*Heteromastus* sp. A
	All first 5 chaetigers with limbate capillary chaetae	*Heteromastus* sp. B
7	Capillary chaetae on the first 10 chaetigers	*Decamastus* sp. A
	Capillary chaetae on more than the first 10 chaetigers	8
8	Capillary chaetae on the first 11 chaetigers	9
	Capillary chaetae on more than the first 11 chaetigers	15
9	11th chaetiger with mixed chaetae	*Paraleiocapitella* sp. A
	11th chaetiger without mixed chaetae	10
10	No staining with methyl green	*Notomastus* cf. *latericeus*
	Staining with methyl green	11
11	Prostomium stained	12
	Prostomium not stained	14
12	Palpode stained as well as thorax	*Notomastus* sp. D
	Palpode not stained	13
13	Prostomium and first chaetiger stained, palpode not stained	*Notomastus* sp. A
	Prostomium and first chaetiger stained, palpode not stained and banding on the posterior part of the thorax	*Notomastus* sp. B
14	Thin rings of staining on the first 4 chaetigers and on the ridge of the abdominal section	*Notomastus* sp. C
	Wide large bands of staining on all the chaetigers of the thorax	*Notomastus* sp. E
15	Capillary chaetae on the first 12 chaetigers without mixed chaetiger	*Leiochrides* sp. A
	Capillary chaetae on the first 12 chaetigers with mixed chaetae on the 12th chaetiger	*Leiochrus* sp. A

Chaetopteridae

There was only one species: Chaetopteridae sp. A.

Chrysopetalidae

There was only one species: Chrysopetalidae sp. A.

Cirratulidae

1	Prostomium swollen	2
	Prostomium not swollen	3
2	Prostomium tip not blunt; peristomium with 3 annulations; body shape cylindrical without tapering; parapodia with distinct edges	*Aphelochaeta* sp. A
	Blunt prostomium tip; peristomium without annulation; body shape barrel-shaped, slightly tapering; parapodia without distinct edge	*Aphelochaeta* sp. B
3	Arrow-like prostomium	*Chaetozone* sp. E
	Pointed or rounded prostomium	4
4	Pointed prostomium	5
	Rounded prostomium	8
5	Short and hour-glass shaped peristomium	*Chaetozone* sp. A
	Cylindrical peristomium, not hour-glass	6
6	Erected chaetae in chaetiger 1, long capillary chaetae in thoracic area (more than 3-chaetiger width)	*Chaetozone* sp. B
	No erected chaetae in chaetiger 1, short capillary chaetae in thoracic area (less than 3-chaetiger width)	7
7	Short peristomium (about 2-chaetiger long)	*Chaetozone* sp. C
	Long peristomium (about 5-chaetiger long)	*Chaetozone* sp. F
8	Body shape widens quickly from chaetiger 3, widest at the boundary thorax-abdomen then tapers	*Chaetozone* sp. D
	Cylindrical body shape	9
9	Very short chaetae (1-chaetiger long) and few per bundle	*Chaetozone* sp. H
	Long chaetae (more than 1-chaetiger long) and numerous	*Chaetozone* sp. G

Cossuridae

1	Methyl-green on the edge not the tip of the prostomium; conical prostomium, rounded at the tip	*Cossura* cf. *rostrata*
	Methyl-green over all prostomium; pear-shaped prostomium	*Cossura* sp. A

Dorvilleidae

1	Short bi-articulated antennae (about 1-chaetiger long)	Dorvilleidae sp. A
	Long multi-articulated antennae (at least 2-chaetiger long)	Dorvilleidae sp. B

Eunicidae

1	Compound chaetae as bidentate falcigers	*Marphysa* sp. A
	Compound chaetae otherwise	*Marphysa* sp. B

Fabriciidae

1	Two types of thoracic notochaetae present	See Sabellidae
	One type of thoracic notochaetae present	Fabriciidae 2
2	Long abdomen (more than 30 chaetigers)	Fabriciidae sp. B
	Short abdomen (less than 30 chaetigers)	3
3	Collar not distinct	Fabriciidae sp. C
	Collar well developed	Fabriciidae sp. A

Fauveliopsidae

1	Fixed number of chaetigers (16); small interramal papillae	*Laubieriopsis brevis*
	Number of chaetigers varying between 30 and 45; interramal papillae prominent anteriorly	*Fauveliopsis* sp. A

Flabelligeridae

There was only one species: Flabelligeridae sp. A.

Glyceridae

There was only one species: Glyceridae sp. A.

Goniadidae

1	Long (more than 5-chaetiger long) and conical prostomium	*Bathyglycinde* cf. *sibogana*
	Short (2-chaetiger long) and pear-shaped prostomium	Goniadidae sp. A

Hesionidae

There was only one species: Hesionidae sp. A.

Lumbrineridae

1	Pseudo-compound or compound hooded hooks present in anterior part of the body; no modified hooded-hook resembling limbate chaetae in anterior part of the body	*Augeneria* sp. A
	Pseudo-compound or compound hooded hooks absent in anterior part of the body; presence of modified hooded-hook resembling limbate chaetae in anterior part of the body	2
2	One aciculae dark yellow to brown, pointed, with a short hair on the distal end, real hooded hooks starting around chaetiger13 (up to chaetiger 20)	*Abyssoninoe* sp. A
	Two aciculae light yellow to transparent, with a long thin hair on the distal end, real hooded hook starting between chaetigers 10 and 20	*Abyssoninoe* sp. B

Maldanidae

1	Multidentate neuro-hooks starts in chaetiger 1	Maldanidae sp. F
	Multidentate neuro-hooks starts in chaetiger 3 or after	2
2	Acicular spines present until chaetiger 4	Maldanidae sp. E
	Acicular spines present until chaetiger 3	3
3	Acicular yellow protruding high above the body surface	4
	Acicular uncoloured and protruding only slightly if at all (difficult to see)	5
4	Long chaetigers (more than 5 times longer than wide) with rounded edge; hook with pointed fang	Maldanidae sp. B
	Short chaetigers (about 3 times longer than wide) with sharpened edge; hook with rounded fang	Maldanidae sp. D
5	Neuro-hooks in chaetiger 4 numerous (more than 4); prostomium acutely pointed	Maldanidae sp. C
	Neuro-hooks in chaetiger 4 are 2 to 4 only; prostomium rounded and pygidium as plate with dorsal anus	Maldanidae sp. A

Nephtyidae

1	Well-developed involute branchiae	2
	Branchiae reduced to small button-like cirri	3
2	Branchiae starting in chaetiger 3, well-developed at chaetiger11-13	*Aglaophamus* sp. A
	Branchiae stating in chaetiger 2, well developed at chaetiger8	*Aglaophamus* sp. B
3	Small button-like branchiae present from chaetiger 2 to 5-7	*Micronephthys* sp. A
	Small button-like branchiae present from chaetiger 2 to 15 or more	*Micronephthys* sp. B

Nereididae

1	Double ventral cirri	*Ceratocephale* cf. *abyssorum*
	Simple ventral cirri	2
2	Ligules with stylodes	Nereididae sp. B
	Ligules without stylodes	3
3	Slender neuro-ligules	Nereididae sp. A
	Chubby neuro-ligules	4
4	Notopodial ligules greatly reduced; pigmentation on prostomium and chaetigers; notochaetae as several heterogomph spinigers (more than 2)	Nereididae sp. C
	Notopodial ligules not greatly reduced; no pigmentation on prostomium and chaetigers; notochaetae as 2 heterogomph spinigers in anterior part, then one	Nereididae sp. D

Onuphidae

1	Tentacular cirri present; branchiae in part pectinate; anterior parapodia not prolonged	*Onuphis* sp. A
	Tentacular cirri absent; no branchiae seen on 13 chaetigers (fragment only)	*Paraonuphis* sp. A

Opheliidae

1	Thick, large, grub-like body	2
	Thin, elongated body	4

2	Branchiae absent	*Kesun* sp. A
	Branchiae present	3
3	Branchiae on all the body except the first and last 6 chaetigers	*Travisia* sp. A
	Branchiae from chaetiger 5 with only 9 pairs	*Travisia* sp. B
4	Branchiae throughout the body or at least in anterior and middle areas	5
	Branchiae posteriorly only	8
5	Long anal funnel	*Ophelina farallonensis*
	No long anal funnel	*6*
6	Branchiae on all chaetigers	*Ophelina* sp. A
	Branchiae limited to anterior and mid-body chaetigers	*7*
7	Branchiae from chaetiger 4 with 6 to 7 pairs that end abruptly; pygidium scoop-shaped	*Ophelina aulogastrella*
	Branchiae on a least the first 25 chaetigers; anal funnel long and cylindrical	*Ophelina* sp. B
8	Branchiae in posterior chaetigers, 10 pairs, last 4 segments abranchiate	*Ammotrypanella* sp. A
	No branchiae in posterior chaetigers	*Ammotrypanella* sp. B

Orbiniidae

1	Absence of spines in specimen	Orbiniidae sp. B
	Presence of spines in specimen	2
2	Single long spine in posterior part of the body	Orbiniidae sp. C
	Several spines starting in anterior part of the body	3
3	Short stubby spines on most chaetigers	Orbiniidae sp. D
	Slender spines from chaetiger 1 to 7-10	Orbiniidae sp. A

Oweniidae

1	Chaetiger 1 and 2 with neurochaetae only, hooded prostomium	Oweniidae sp. A
	Notochaetae from chaetiger 1, prostomium collar-like	Oweniidae sp. B

Paraonidae

1	Presence of an antenna on the prostomium	2
	Absence of an antenna on the prostomium	10
2	Modified chaetae present in notopodia as one thick acicular spine with curved hair attached below terminal tip (bayonet chaetae)	*Cirrophorus branchiatus*
	Modified chaetae present in neuropodia as pseudo-compound, or hooked with sub-terminal spine	3
3	Branchiae absent	*Aricidea abranchiata*
	Branchiae present	*4*
4	Leaf-like branchiae	5
	Branchiae other shapes	6
5	Broad-based, short tapering antenna (not extending beyond chaetiger 2); broad leaf-like branchiae with a tapered tip, branchiae from chaetiger 4 up to 16; trilobate prostomium; tapering body shape	*Aricidea* sp. A
	Thin downward tapering antenna attached on the upper half of the prostomium; branchiae as leaf like, short with a tapered tip, folded on the body, branchiae from chaetiger 4 up to 12;heart-shaped prostomium	*Aricidea* sp. F
6	Rounded prostomium	*Aricidea* sp. B
	Prostomium other shapes	7
7	Quadrilobate prostomium	*Aricidea* sp. C
	Triangular prostomium	8
8	Prostomium without pigmented nuchal organs	*Aricidea* sp. G
	Prostomium with pigmented nuchal organs	9
9	Apple-shaped prostomium; very cylindrical body without any tapering; modified chaetae as 1 thick spine and 2 spines with aristae	*Aricidea* sp. E
	Triangular-shaped prostomium; tapering body shape; modified chaetae as spine with aristae	*Aricidea* sp. D
10	Modified chaetae present	11
	Modified chaetae absent	15
11	Modified chaetae in notopodia	12
	Modified chaetae in neuropodia as row of spines	14
12	Branchiae absent	*Paradoneis abranchiata*
	Branchiae present	13

13	Branchiae present from chaetiger 4; modified notochaetae as lyrate	*Paradoneis* cf. *lyra*
	Branchiae present from chaetiger 7; modified notochaetae as long straight aciculae ending with a small point	*Paradoneis* cf. *drachi*
14	Branchiae absent	*Levinsenia uncinata*
	Branchiae present	*Levinsenia* cf. *oligobranchiata*
15	Branchiae absent	16
	Branchiae present	17
16	Triangular prostomium somehow rounded on the anterior margin; cylindrical tapering body shape; bead-shaped chaetigers with defined rounded edges in thoracic area	*Paraonella abranchiata* sp. A
	Pointed prostomium; slightly dorso-ventrally thoracic area; constant body shape without distinctive edge of chaetigers	*Paraonella abranchiata* sp. B
17	Short (less than 1-chaetiger long) triangular branchiae with rounded tips, branchiae from chaetiger 4 to chaetiger 12; triangular prostomium somehow rounded on the anterior margin	*Paraonella rubriceps*
	Long (up to 2-chaetiger long) cylindrical branchiae with pointed tips, branchiae from chaetiger 7 up to chaetiger 17; rounded prostomium	*Paraonella* sp. C

Pholoidae

There was only one species: Pholoidae sp. A.

Phyllodocidae

1	Dorsal and ventral cirri rounded and short, highly pigmented	Phyllodocidae sp. B
	Dorsal and ventral cirri other shapes	2
2	Flat circular dorsal cirri with pigments	Phyllodocidae sp. E
	Dorsal cirri other shape	3
3	Ovoid dorsal cirri with a pointed end, at least 2/3 of parapodial length	Phyllodocidae sp. C
	Dorsal and ventral cirri other shapes	4

4	Dorsal cirri as cup, shorter rounded ventral cirri, both pigmented	Phyllodocidae sp. F
	Ovoid (leaf-like) dorsal cirri, short in anterior part and becoming longer in mid-body, with a rounded distal part and pigmented only at the base	Phyllodocidae sp. A

Pilargidae

1	No emergent hooks	*Pilargis* sp. A
	Emergent hooks	2
2	Small fine hooks on chaetiger 1 to 3 becoming erect after and visible until chaetiger 13	Genus A sp. A
	Emergent hooks starting on chaetiger 2 or after	3
3	Emergent hooks on chaetiger 6	*Ancistrosyllis* sp. A
	Emergent hooks on chaetiger 2 or 3	4
4	Emergent hooks on chaetiger 3	*Sigambra* sp. A
	Emergent hooks on chaetiger 2	*Sigambra* sp. B

Pisionidae

There was only one species: Pisionidae sp. A.

Poecilochaetidae

There was only one species: Poecilochaetidae sp. A.

Polynoidae

1	Presence of a unique wing-like structure on ventral side of lower lip projecting posteriorly on chaetiger 3	*Bruunilla* sp. nov.
	No wing-like structure on ventral side of lower lip projecting posteriorly on chaetiger 3	2
2	15 pairs of elytra	*Harmothoe* sp. A
	6 pairs of elytra	*Macellicephalinae* sp. A

Sabellidae

1	One type of thoracic notochaetae present	See Fabriciidae
	Two type of thoracic notochaetae present	2 (Sabellidae)
2	Collar well developed	3
	Collar not well developed	Sabellidae sp. D

3	Collar higher on ventral side	Sabellidae sp. B
	Collar not higher on ventral side	4
4	10 abdominal chaetigers	Sabellidae sp. E
	More than 10 abdominal chaetigers	5
5	Angular collar	Sabellidae sp. A
	Rounded collar	Sabellidae sp. C

Scalibregmatidae

1	Spines present in chaetigers 1 and 2	*Oligobregma* sp. A
	Spine absent	*Scalibregma* sp. A

Serpulidae

1	6 thoracic chaetigers; operculum on its own wrinkled stalk (cylindrical, no wing or pinnule)	Genus A sp. A
	5 thoracic chaetigers; operculum peduncle pinnulate	*Bathyditrupa* sp. A

Sigalionidae

1	Short (prostomium width) subulate median and lateral antenna	*Leanira* sp. A
	Long (more than prostomium width) tapering median and lateral antennas	*Leanira* sp. B

Sphaerodoridae

1	Dorsal and ventral surface smooth	*Levidorum* sp. A
	At least 2 rows of dorsal macrotubercles	2
2	Macrotubercles with terminal papillae; all chaetae composite except curved hooks in the first chaetiger	*Ephesiella* sp. A
	Macrotubercles distally rounded, sessile; all chaetae composite	3
3	Multiple and dense macrotubercles in alternating rows; hook present; body small, compact	*Sphaerodoropsis* sp. A
	4 rows of macrotubercles; hook absent; body elongated	*Sphaerodoropsis* sp. B

Spionidae

1	Chaetiger 5 with large modified neurochaetae	*Dipolydora* sp. A
	No modified neurochaetae in chaetiger 5	2
2	Branchiae absent; hooks in chaetiger 1	*Spiophanes* sp. A
	Branchiae present; no hooks in chaetiger 1	3
3	Antenna present	4
	Antenna absent	5
4	No indentation on anterior edge of prostomium	*Laonice* sp. A
	Indentation on anterior edge of prostomium	*Laonice* sp. B
5	Branchiae starting in chaetiger 3	*Aurospio dibranchiata*
	Branchiae starting in chaetiger 2	6
6	Branchiae from chaetiger 2 to 5	7
	Branchiae from chaetiger 2 to 4 or 6	13
7	Chaetae short (less than 2-chaetiger long, specimens not ‘hairy’)	8
	Chaetae long (more than 2-chaetiger long, specimens appear ‘hairy’)	11
8	Hooded hooked starting at or after chaetiger 18	*Prionospio* sp. F
	Hooded hooked starting before chaetiger 18	9
9	Hooded hooked starting before chaetiger 15	*Prionospio* sp. K
	Hooded hooked starting at chaetiger 15	10
10	No dorsal crest	*Prionospio* sp. E
	Dorsal crest in chaetiger 8 to 13	*Prionospio* sp. G
11	Dorsal crest in numerous chaetigers (more than 10)	*Prionospio* sp. A
	Dorsal crest in few chaetiger (less than 10)	12
12	Dorsal crest in chaetiger 6 to 7	*Prionospio* sp. H
	Dorsal crest in chaetiger 11	*Prionospio* sp. I
13	Branchiae from chaetiger 2 to 4	*Prionospio* sp. C
	Branchiae from chaetiger 2 to 6	14
14	No dorsal crest	*Prionospio* sp. B
	Dorsal crest present	15
15	Dorsal crest from 9 to 13	*Prionospio* sp. L
	Dorsal crest from 8 to 21 at least	*Prionospio* sp. M

Syllidae

1	Dorsal cirri flask-shaped	2
	Dorsal cirri other shapes	3
2	Palps fused at least on ¾ of the length; flask-shape dorsal cirri with a short (less than 2 times longer than the basal part) and rounded distal part	*Sphaerosyllis* sp. A
	Palps entirely fused (but junction between them is visible as a shallow demarcation); flask-shape dorsal cirri with a long (2 times longer than the basal part) and digitiform distal part	*Sphaerosyllis* sp. B
3	Short (about 1-prostomium long) palps fused all along	*Exogone* sp. A
	Long (1.5 to more than 2-prostomium long) palps partly or entirely fused	4
4	Palps fused at least from half to 2/3 of the length, slightly tapering at the distal end (with a rounded prostomium wider than long giving the anterior end an overall rabbit-head shape); rounded proventriculus with 15-22 rows of muscular cell	*Anguillosyllis* sp. A
	Palps entirely fused, with a thinner rounded distal part (with an inversed heart shape prostomium); heart-shape proventriculus with 10 to 15 rows of muscular cell	*Anguillosyllis* sp. B

Trichobranchidae

1	First special neurochaetae with tooth at 90 degrees to shaft often on chaetiger 5 or 6, other thoracic neurochaetae bidentate	*Terebellides* sp. A
	First special neurochaetae with tooth at 90 degrees to shaft only on chaetiger 5, other thoracic neurochaetae unidentate with fringe of small teeth behind	*Terebellides* sp. B

Appendix D

Taxonomic descriptions of the five density-dominant polychaete species of Sta. M

This appendix and chapter 4 are a modified version of paper in preparation: Laguionie-Marchais, C., Ruhl, H.A., Smith, K.L.Jr., Paterson, G.L.J. Descriptions and demographics of North East Pacific density-dominant abyssal polychaete species. Marine Ecology.

Abstract

Out of the 167 species found at Sta. M between 1991 and 2011 (Appendix D), five species belonging to 4 families dominated the polychaete assemblage in terms of density: Cirratulidae *Aphelochaeta* sp. A., the Cossuridae *Cossura* cf. *rostrata*, the Paraonidae *Levinsenia* cf. *oligobranchiata* and *Paradoneis* cf. *lyra* and the Syllidae *Sphaerosyllis* sp. A. Two species, *Aphelochaeta* sp. A and *Sphaerosyllis* sp. A are new species.

D.1 Introduction

The Cirratulidae are conspicuous inhabitants of sedimentary abyssal habitats (Glover et al., 2001, Paterson et al., 2009, Soto et al., 2010). The majority of deep-sea cirratulid species are new to science and known by provisional names (Blake and Grassle, 1994, Blake et al., 2009, Doner and Blake, 2009). Nothing is known about the life history of deep-sea cirratulids. In shallower systems, the cirratulids are free living polychaetes that burrow or crawl through the substratum (Blake, 1996a). They often extend their branchiae into the overlying water for aeration. Some bitentaculate species form vertical tubes composed of mucous and silts. The Cirratulidae are surface deposit feeders. Both non-selective and selective feedings have been reported for Cirratulidae (e.g. *Aphelochaeta marioni* is a selective feeder, Wolf, 1973, Fauchald and Jumars, 1979). In terms of reproduction, sexes of the Cirratulidae are usually separate but hermaphroditism has been reported (for an *Aphelochaeta* species by Petersen, 1994). Three types of larval development have been described among the cirratulid species: lecithotrophic, direct or viviparous. *Aphelochaeta marioni* has been described as a free spawner with either lecithotrophic larvae or entirely direct development (Wilson, 1991). Overall, Cirratulidae are poorly known (Blake, 1996a). The family comprises 11 genera (Magalhães and Bailey-Brock, 2013). The genus *Aphelochaeta* was established to include those cirratulids having only simple capillary chaetae restricting the genus *Tharyx* to species having serrated capillary chaetae (Blake, 1991). The genus *Aphelochaeta* is one of the most speciose genera collected on the continental slope sediments off Northern California (2400-3200 m, Doner and Blake, 2009). *Aphelochaeta* are a common component of deep-sea benthic infauna but few species have been described (Doner and Blake, 2009). Prostomial and peristomial characters, body shape and methyl green staining patterns are important taxonomic features for species discrimination (Doner and Blake, 2009).

The Cossuridae are small polychaetes living in mixed sandy and muddy sediments from shallow to abyssal depths (Hilbig, 1996). In the deep sea, cossurids can occur in high density and may be the numerically dominant species (Blake and Grassle, 1994, Hilbig, 1996). Studies in shallower systems have reported that most species appear to tolerate a wide range of sediment types (Hilbig, 1996). The Cossuridae are motile burrowers (Fauchald and Jumars, 1979) and most likely surface to sub-surface deposit feeders (Hilbig, 1996). Except from some mucus among the chaetae, cossurids are free of any surrounding or attached tube-like structure (Hilbig, 1996). Little is known about the reproduction of the Cossuridae except for some observations on *Cossura pygodactylata* (Bachelet and Laubier, 1994) and *C. longocirrata* (Fournier and Petersen, 1991, Blake, 1993). Eggs and sperms were observed in *C. longocirrata* specimens (Fournier and Petersen, 1991) as well as evidence of facultative hermaphroditism (Blake, 1993). Blake (1993) reported seasonal reproduction for this species off North Carolina. In terms of taxonomy, the Cossuridae are inconspicuous and relatively featureless. Rouse and Pleijel (2001) reported 2 genera: *Cossura* (18 species) and *Cossurella* (5 species). The presence of a single mid-dorsal filament that arises from one of the anterior segments is the main feature of the family. The scarcity of other external features useful for species discrimination has caused some confusion (Hilbig, 1996, Read, 2000). In addition, specimens often lack posterior body parts as most of the specimens are collected incomplete, making the description of new species all the more complicated (Hilbig, 1996, Liñero-Arana and Díaz-Díaz, 2010). The main features used to identify cossurid species are the segment of filament insertion, the number and thickness of chaetae, number of thoracic segments and the structure of the pygidium (Fauchald, 1972, Read, 2000).

The Paraonidae are small, elongated polychaetes reported worldwide in soft substratum (Blake, 1996b). In particular, paraonid species are among the dominant infauna in continental shelf and slope (Hilbig, 1994, Blake, 1996b). Knowledge of the Paraonidae life history comes from shallow systems. Paraonids live in mud or sand (Pettibone, 1982), in vertical burrows (Blake, 1996b). The Paraonidae can form fragile mucous tubes that are covered in silt and are likely temporary (Blake, 1996b). Some species twist their bodies into a tight corkscrew to facilitate water movement through the burrow (Gaston et al., 1992, Blake, 1996b). Paraonids are considered to be sub-surface feeders, having short, eversible, sac-like pharynges. However, other methods of feeding have been frequently reported, from surface deposit feeding (Fauchald and Jumars, 1979, Gaston et al., 1992) to carnivory (e.g. *Levinsenia oculata*, Fauchald and Jumars, 1979, Penry and Jumars, 1990). Virtually nothing is known about the reproduction and development of Paraonidae generally and particularly in the deep sea (Blake, 1996b). Eggs have been observed in some species and direct development has been proposed as larval development mode (Strezlov, 1973, Lȯpez-Jamar et al., 1987). The Paraonidae comprises eight genera and about 110 species (Read and Fauchald, 2014). The number of recorded species has increased since the review of Paraonidae systematics by Strezlov (1973) and the use of finer mesh screens (Blake, 1996b). The presence and shape of the antenna, the number, position and shape of branchiae, the position of modified chaetae as well as the number, shape, and starting chaetiger are important taxonomic features for species discrimination. Abundant species at Sta. M belonged to 2 genera: *Levinsenia* and *Paradoneis*. Some controversy exists about taxonomic position of *Paradoneis*. Some taxonomists include *Paradoneis* species within *Cirrophorus*, the latter being distinguished from the former by the presence of an antenna (Strezlov, 1973, Fauchald, 1977, McLelland and Gaston, 1994). However, most authors separate the two genera (Mackie, 1991, Blake, 1996b, Lovell, 2002, Aguirrezabalaga and Gil, 2009). Recent molecular analyses have shown that *Cirrophorus* and *Paradoneis* should be considered as synonyms as the antenna is a homoplastic character and that some *Paradoneis* species belong to a new genus (Reuscher, 2013). The name *Paradoneis* was kept for this study to facilitate comparison with previous studies and because no molecular study could be conducted on the specimens to determine if they belonged to *Cirrophorus* or the new genus.

The Syllidae are small polychaetes with various life styles from epibiota on hard surfaces or on metazoans to infauna in soft-bottom environments (Kudenov and Harris, 1995). The Syllidae is represented by only a few genera in deeper waters and their life history at great depth is unknown (Kudenov and Harris, 1995, San Martin, 2005). The family Syllidae is divided into 4 subfamilies: Eusyllinae Malaquin, 1893, Exogoninae Langerhans, 1879, Autolytinae Langerhans, 1879, and Syllinae Grube, 1850. Except for *Anguillosyllis* species, all syllid species found at Sta. M belong to the subfamily Exogoninae. Polychaetes of the subfamily Exogoninae are both found living interstitially in sand, mud, in crevices on corals and rocks, and at great depths in the sediment (San Martin, 2005). Syllids are highly mobile and are considered to be carnivorous (Kudenov and Harris, 1995). The Syllidae have eversible, often armed pharynx followed by a strong muscular pumping structure called a proventricle (Fauchald and Jumars, 1979). Some Exogoninae may be selective deposit feeders (Day, 1967, Fauchald and Jumars, 1979, Pettibone, 1982, Kudenov and Harris, 1995). Fauchald and Jumars (1979) reported that *Sphaerosyllis hystrix* and *S. pirifera* not only feed on detritus, being highly selective surface deposit feeders but are carrion-feeders or carnivores when opportunities arise. Syllid reproductive biology is complex and only known from shallow systems (Heacox, 1980, Heacox and Schroeder,1981a,b, Kudenov and Harris, 1995). Sexes are separate, but species can generally reproduce both asexually (stolon formation) and sexually with direct spawning (Kudenov and Harris, 1995). In Exogoninae, three reproductive methods have been reported (San Martin, 2005): dorsal incubation of eggs by means of capillary notochaetae on the females (Kuper and Westheide, 1998, Díaz-Castañeda and SanMartín, 2001, San Martin, 2005) or by means of compound notochaetae (San Martin, 2005), ventral incubation of eggs and development of attached juveniles (San Martin, 2005) and viviparity (Pocklington and Hutchenson, 1983, San Martín, 1991). The parental care of eggs and also sometimes of juveniles is thought to be a biological adaptation to interstitial life (Westheide, 1984, 1987). In the genus *Sphaerosyllis*, *S. bulbosa*, *S. erinaceus, S. hystrix* have been reported as brooding on the outside of the body with a direct development (Wilson, 1991). In terms of taxonomy, the Syllidae represent one of the most diverse and systematically challenging families of the Polychaeta, with about 70 genera and about 700 species (Fauchald, 1977, Pettibone, 1982, Kudenov and Harris, 1995, San Martin, 2003). Several reasons account for the complexity of assigning specimens to syllid species (Faultwetter et al., 2011): the lack of details in older descriptions (before 1970), the difficulty to observe certain characters in fixed material (Riser, 1991), the lack of comparison with type material, and ongoing discussions on the taxonomic value of some characters. Overall the most used species level characters are: pigmentation patterns, shape and distribution of such structures as antennae and eyes, palps, nuchal organs, pharynx, proventricle, peristomial cirri, occipital flap, parapodia, dorsal and ventral cirri, chaetae and aciculae (Kudenov and Harris, 1995).

D.2 Material and method

See sections 4.2.1 and 4.2.2 in Chapter 4.

D.3 Systematics

Phylum Annelida

Class Polychaeta

Family Cirratulidae Ryckholt, 1851

Genus *Aphelochaeta* Blake, 1991

Generic diagnosis (from Doner and Blake, 2009 and Magalhães and Bailey-Brock, 2013): prostomium conical; peristomium elongate with 1 to 4 achaetigerous annulations with pair of grooved dorsal tentacles arising either on or anterior to chaetiger 1; first pair of branchiae arising either on or anterior to chaetiger 1; thoracic region frequently expanded, with crowded segments; abdominal segments variable, sometimes moniliform; chaetae simple capillaries, with distinct serrations or saw-tooth edge not visible in light microscopy, but fibril endings sometimes seen with SEM; far posterior segments may be expanded or not, with or without dorsal and/or ventral grooves, tapering to simple pygidial lobe.

Species: *Aphelochaeta* sp.A

Diagnosis: bulbous peristomium with 3 annulations; 14 to 17 thoracic chaetigers, very long-capillary chaetae (4- to 6-chaetiger long) in notopodia in anterior and middle body area becoming longer in middle region (Fig. D.1).

Examined material: North East Pacific, Station M (~4 000 m deep, 50˚00 N, 123˚00 W), 149 specimens examined.

Description: all specimens incomplete; up to 35 mm long and 0.6 mm wide, longest specimen with more than 50 chaetiger for 35 mm long. Three reproductive female specimens observed; eggs from chaetiger 16 to 20 (broken after 20), egg round to oblong; 1st specimen egg size 120 ± 22 µm, 2nd specimen egg size 31 ± 8 µm, 3rd specimen egg size 33 ± 9 µm.

Body elongate, robust, with a slightly expanded anterior end and a tapering posterior end, divided in two areas (Fig. D.1a). Thoracic area broad, dorso-ventrally flattened; with 14 to 17 crowded chaetigers (Fig. D.1b, c), chaetigers 3 to 8 wider than other thoracic chaetigers, sometimes only slightly; thoracic chaetigers oblong to oval; without dorsal or ventral groove. Anterior parapodia developed, produced into low fleshy lobes; posterior parapodia less developed. Anterior abdominal chaetigers elongate, with sub-moniliform to nonmoniliform chaetigers, appearing moniliform in small specimens. Abdominal region narrower than thoracic area, with less chaetae, chaetigers wider than long; without dorsal or ventral groove.

Prostomium conical with a wider base (almost as bi-annulated) and a rounded tip, as long as wide to longer than wide; without eyes; nuchal organs not observed. Peristomium inflated, longer than wide, with 3 annulations, middle annulations slightly longer than the others; without dorsal crest. Pair of grooved dorsal tentacles at the posterior end of the peristomium at the edge of the junction (Fig. D.1d,e), longer than the thoracic area, coiled, 15 times the tentacle width (Fig. D.1d). First branchiae pair postero-lateral to tentacles (tentacles and first branchiae distance varied with specimens). Following branchiae with a gradual migration of position from a more dorsal position in anterior body to a more lateral position in posterior body, branchiae more visible anteriorly but present throughout; anterior branchiae as long filaments (more than 5-chaetiger long) with rounded tip, coiled, easily broken or lost; posterior branchiae not observed (only scars). Chaetae all capillaries, fibrils not observed in light microscopy. Anterior notopodia and neuropodia with about 6 capillaries per fascicles; anterior and middle notopodia with elongated capillary becoming longer in anterior abdominal chaetigers, at least 5-chaetiger long giving a “bottle brush” appearance to anterior end. Posterior chaetae shorter and less numerous (about 3 per bundle). Pygidium not observed.

Methyl green staining pattern: Body with overall blue-green colour, no pattern.

Remarks: The species could not easily be matched to previously described species. The number and length of peristomial annulations has not been described well enough in species reported prior to 2000 and Doner and Blake (2009) highlighted that these features warrant further investigation. In addition the shape of abdominal segments is dependent on the specimen maturity. Older descriptions have often described different stages of the same species as different species. In particular, immature specimens of some species may appear to have moniliform chaetigers (Blake, 1996a, Doner and Blake, 2009). The methyl green patterns of Cirratulidae may also vary depending on the archival storage time. The present species is different from: *A. bullata* (Doner and Blake; 2009) as the latter has a peristomium with 4 annulations and a dorsal crest, *A. guttata* (Doner and Blake, 2009), *A. monilaris* (Hartman, 1960), *A. tigrina* (Blake, 1996a), *A. williamsae* (Blake, 1996a), *A. petersenae* (Blake, 1996a) as these five species have distinct staining patterns; *A. glandaria* (Blake, 1996a), *A. arizonae* (Magalhães and Bailey-Brock, 2013), *A. honouliuli* (Magalhães and Bailey-Brock, 2013), *A. saipanensis* (Magalhães and Bailey-Brock, 2013) as these four species have their first pair of branchiae arising from chaetiger 1; *A. phillipsi*

(Blake, 1996a), *A. elongata* (Blake, 1996a) as both species have no annulation on the peristomium; *A. multifilis* (Moore, 1909) as the latter has the ventral segmental annuli of the thorax interrupted by a pair of grooves.

Distribution and habitat: Sta. M, North East Pacific, abyssal silty-clay sedimentary area (~4 000 m depth).

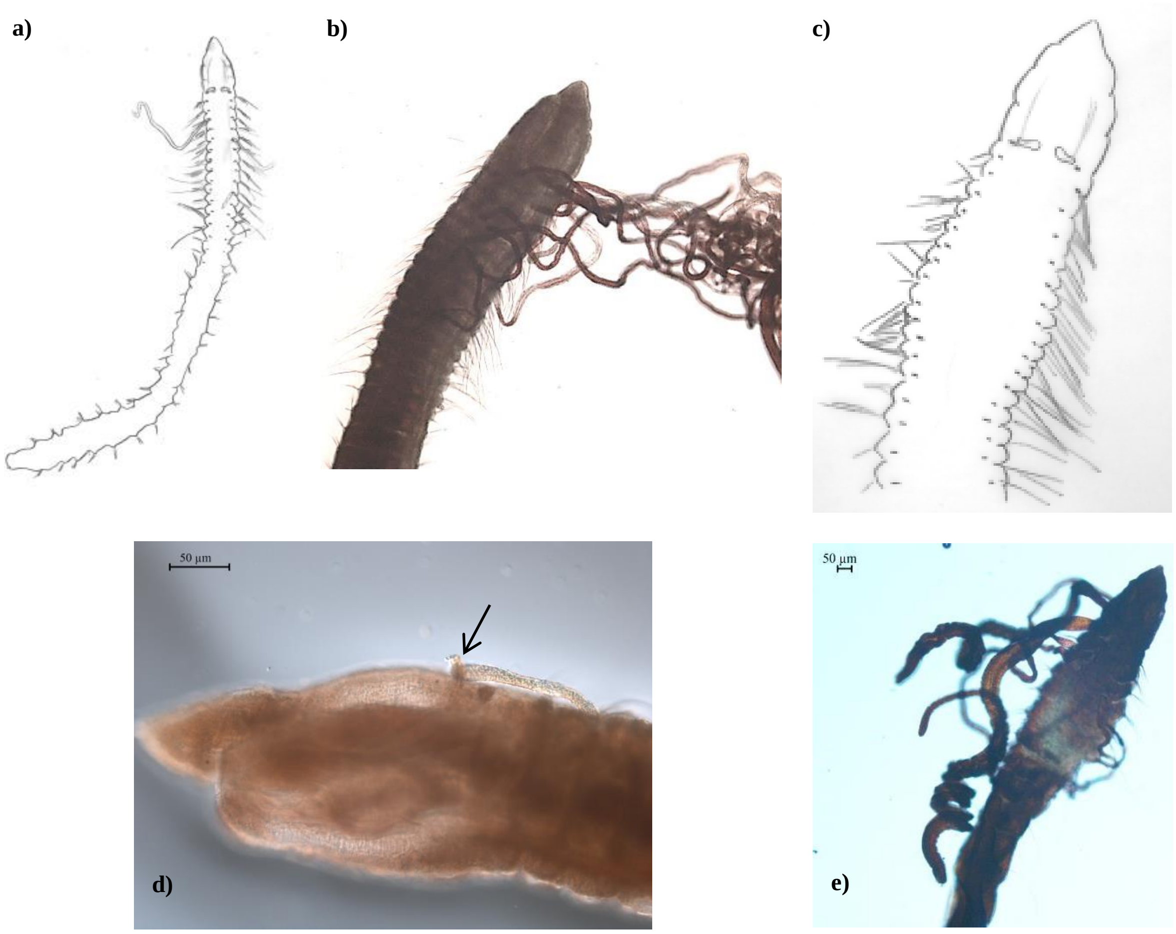


Figure D.1 *Aphelochaeta* sp. A (a) thoracic and abdominal area, (b) thoracic area with branchiae, (c) thoracic area with branchial and palps scars, (d) peristomium scars (black arrow), (e) palps.

Family Cossuridae, Day, 1963

Genus *Cossura* Webster and Benedict, 1887

Generic diagnosis (from Hilibig, 1996): Prostomium conical, without appendages or eyes, with more or less distinct, transverse prostomial furrow; peristomium consisting of single apodous achaetigerous segment. Body divided into thorax and abdomen. Thorax with crowded, dorso-ventrally flattened segments, chaetae emerging at anterior segmental borders. Abdomen usually with cylindrical, longer, often beaded segments, chaetae emerging from mid-length of segments. Single dorso-median filamentous gill arising from anterior segment (chaetigers 2 to 5). Parapodial lobes usually not developed. Aciculae absent. Chaetae capillary or bent and abruptly tapering to acute tips, sometimes appearing hirsute, limbate, or serrated. Pygidium with 3 anal cirri and occasionally additional papillae.

Species: *Cossura* cf. *rostrata* (Fauchald, 1972)
Diagnosis: two wide limbate chaetae in neuropodia from chaetiger 1 to 12, methyl-green pattern as green patch between each segment; conical prostomium, rounded at the tip; slightly dyed on lateral margins but not on the tip; filament at the junction between chaetiger 2 and 3 (Fig. D.2).
Material examined: North East Pacific, Station M (~4 000 m deep, 50˚00 N, 123˚00 W), 215 specimens examined.
Description (based on present specimens and Hilbig, 1996): all specimens incomplete; up to 2 mm long and 0.2 mm wide; longest specimen with 31 chaetigers for 2 mm long. No reproductive specimen observed.
Body fine, slender, with thoracic and abdominal areas without distinct transition (Fig. D.2a,f). Thoracic area dorso-ventrally flattened with shallow mid-dorsal groove. Abdomen not complete, with more cylindrical chaetigers.
Prostomium conical with a blunt tip, approximately as long as wide; prostomial furrow usually not well-defined. First chaetiger uniramous; following chaetigers all biramous. Thorax with 15-20 chaetigers; branchial filament arising from chaetiger 3 (at least 6-chaetiger long, no complete filament observed, Fig. D.2b). Anterior part of abdomen cylindrical, slightly wider than thorax. Posterior part of abdomen not observed here (Hilbig, 1996, reported posterior abdomen tapering towards pygidium with segments about as long as wide, beaded expect the last 5- or 6-crowded pre-pygidial chaetigers). Anterior neurochaetae capillaries plus 2 thick limbate capillaries, abruptly tapering to a filose tip, limbate with surficial hair on the concave side, limbate present until segments 10-12 (Fig. D.2c-e), limbate becoming more slender and more similar to capillaries in posterior thorax and abdomen. All notochaetae as capillaries, chaetae longer in mid-body.
Pygidium not observed (Hilbig, 1996 reported last few pygidial segments very short and crowded, pygidium with 3 anal cirri, no additional lobes or papillae present, anus terminal).

Figure D.2 *Cossura* cf. *rostrata* (a) body shape, (b) body methyl green staining pattern, (c) anterior parapodia with two limbate chaetae, (d-e) limbate chaetae, (f) specimen.

Methyl green staining pattern: methyl-green pattern as green patches between each segment; prostomium stained on lateral edges but not on the tip.

Remark: the present species is different from other species which have the filament arising from chaetiger 3 and reported at depth greater than 500 m (Fournier and Petersen, 1991). *C. abyssalis* (Hartman, 1967) has smooth limbate chaetae (*versus* pilose here), *C. brunnea* (Fauchald, 1972) has coarsely serrated limbate chaetae and longer thoracic area up to 30 chaetigers, *C. candida* (Hartman, 1955) has longer thoracic areas of 25-28 chaetigers, *C. dayi* (Hartman, 1976) does not have the first chaetiger uniramous. The species is referred as *Cossura rostrata* due to the peculiar limbate chaetae in neuropodia corresponding with the description of the neurochaetae given in Fauchald and Hancock (1981). However, the staining pattern differed from the one reported by Hilbig (1996). The difference may be due to the timing of staining and the fact that present specimens were conserved sometimes for 20 years before identification.

Distribution and habitat: Sta. M, North East Pacific, abyssal silty-clay sedimentary area (~4 000 m depth), *Cossura* cf. *rostrata* has already been reported in the North East Pacific (Hilbig and Blake, 2006). Hilbig (1996) found that *C. rostrata*, although occurs at depths from 6 to 3348 m, preferred water depths between 1000 and 1200 m in sediment mixed of silt and sand in the North East Pacific. Fauchald (1972) suggested that *Cossura* cf. *rostrata* distribution was apparently nearly worldwide in colder waters (but see Appendix E.12).

Family Paraonidae Cerruti, 1909

Genus Levinsenia Mesnil, 1897

Generic diagnosis (from Blake, 1996b): Body long, thin, threadlike. Prostomium lacking antenna; with terminal sensory organ; without prostomial ciliary bands; nuchal organs along posterior margin, distinct from peristomium; lateral sensory organs (check organs) present or absent on sides of prostomium. Pre-branchial segments 4-7. All notopodia with postchaetal lobes; neuropodial postchaetal lobe absent. Notochaetae capillaries; neurochaetae include capillaries and thick, curved, modified spines. Pygidium tapering with 2 anal cirri.

Species*:* *Levinsenia* cf. *oligobranchiata*

Diagnosis: palpode present. Branchiae from 6 to 8-12 (3-6 pairs), modified neurochaetae as large, short acicular spine (starting about segment 14), 1 to 7 by neuropodia, some long, curly, capillary chaetae after the branchial area (Fig. D.3).

Material examined: North East Pacific, Station M (~4 000 m deep, 50˚00 N, 123˚00 W), 154 specimens examined.

Description: no complete specimens; up to 6 mm long and 0.4 mm wide; longest specimen with 68 chaetigers for 6 mm long. Five reproductive specimens were observed, 2 specimens were too damaged; 3 female specimens with 1-3 eggs per chaetiger from chaetiger 22 (up to 32 but broken after); egg rounded;1st specimen with egg size 72 ± 10 µm, 2nd specimen with egg size 84 ± 19 µm, 3rd specimen with egg size 57 ± 12 µm. Body thin, long, slender, with overall short chaetae (Fig. D.3d,e). Body with two areas: change in segmentation marking thoracic/abdominal areas; thoracic segmentation stronger with posterior segments anteriorly wider; abdominal segmentation weak with segment of uniform width (Fig. D.3a,b). Thoracic area dorso-ventrally flattened. Abdominal area often missing, more rounded and coiled when present with indistinct segmentation.

Prostomium conical, rounded anteriorly, about as wide as long or longer than wide (1.5 times); ending in a cylindrical sensory organ, sometimes everted; lateral sensory organs not apparent; eyes and antenna absent; nuchal organs recurved, longitudinal slits. Posterior buccal lip with 5-6 longitudinal folds, extending to chaetiger 1.

Pre-branchial region with 5 chaetigers. Branchiae from chaetiger 6 to 8-12 (3-6 pairs), with larger specimens having more pairs; branchiae cylindrical, long (3 to 4 times longer than wide and half the chaetiger length), narrow, tapered, smaller in the first chaetiger and shorter/rounder in last branchial chaetiger.

Notopodial postchaetal lobes from chaetiger 1; small and digit shape, shorter than branchiae and hardly visible on branchial area, short and digitate in posterior area.

Notochaetae as simple capillaries, more numerous and in tight bundles in thoracic area; some long, curly, capillary chaetae after the branchial area, becoming shorter and less numerous in abdominal area. Modified neurochaetae spines with expanded node on shaft, narrowing to slightly curved, pointed tip, convex side of shaft with sheath but not reaching end of the chaetae; arranged in a single vertical row, up to 7 per fascicles, decreasing in size ventrally on the chaetiger; spines starting about chaetiger 14-16 with 2 to 4 accompanying capillary chaetae (Fig. D.3c).

Pygidium not observed.

Remark: There are six *Levinsenia* species with 5 pre-branchial chaetigers (Aguirrezabalaga and Gil, 2009). The present species differs from: *L. flava* (Strezlov, 1973) as the latter has longer postchaetal lobe in branchial chaetigers, only up to 6 shorter spines. In *L. gracilis* (Tauber, 1879), the number of pre-branchial chaetigers can vary from 5 and the modified neurochaetae start later (20-26); *L. gracilis minuta* (Hartman-Shröder, 1965) has more branchiae pairs (up to 11) and branchiae have an acute tip and modified neurochaetae starting later than the current species; *L. multibranchiata* (Hartman, 1967) differs from *Levinsenia* sp. A as the latter has more branchiae pairs and the branchiae are digitiform. *L. kantauriensis* differs by having spines with a thickened hood. *L. oculata* (Hartman, 1967) has 5-8 pre-branchial segments, branchiae with acute tip and spines without hood. Overall the present species is close to *Levinsenia oligobranchiata* (Strezlov, 1973) but with a fixed number of pre-branchial segments (5 rather than 5-7), modified neurochaetae starting slightly earlier (14-16 rather than 16-18) and up to 7 spines (rather than 6).

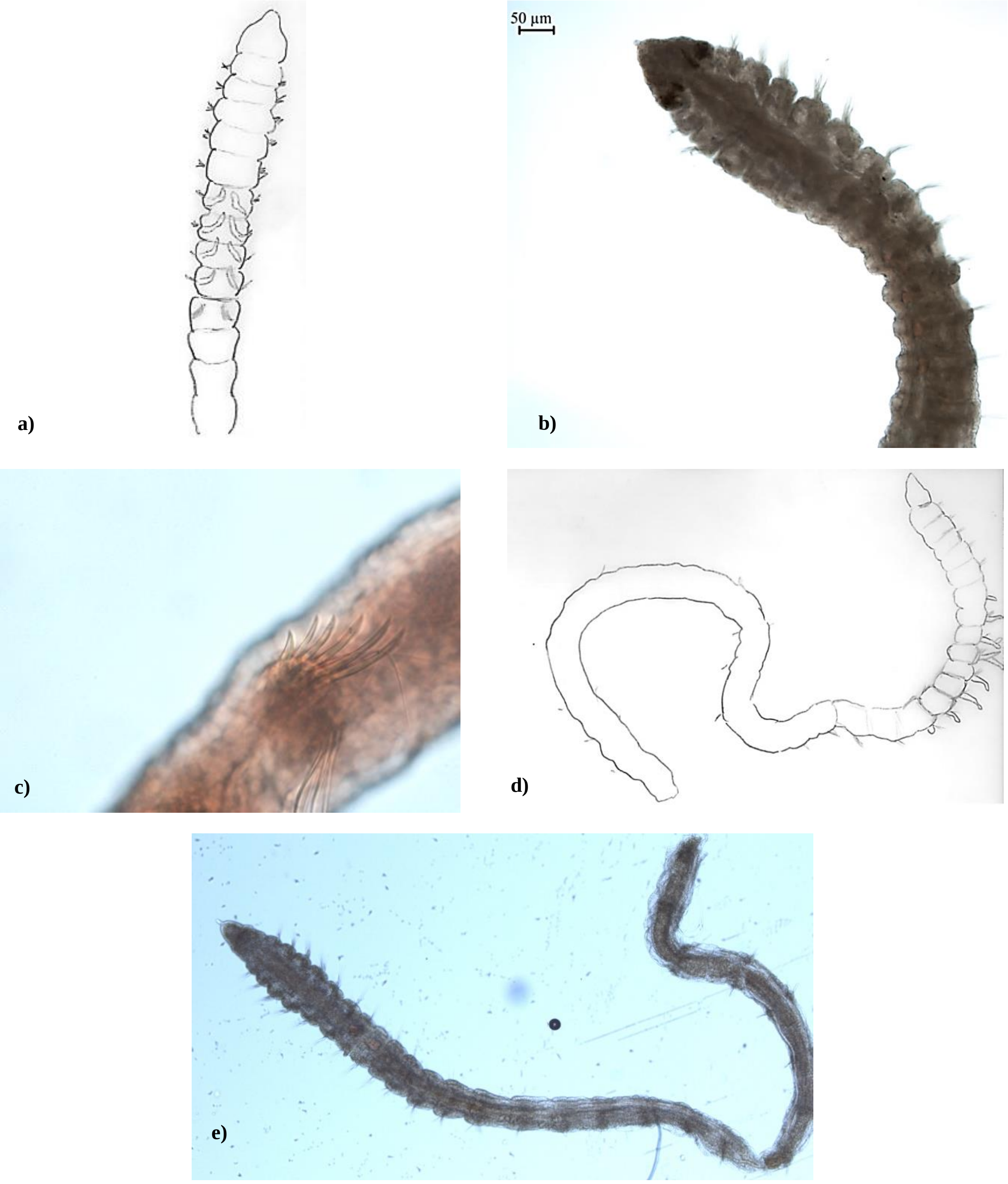


Figure D.3 *Levinsenia* cf. *oligobranchiata* (a-b) thoracic area, (c) abdominal spines, (d) specimen side view with thoracic and abdominal area, (e) specimen dorsal view.

Distribution and habitat: Sta. M, North East Pacific, abyssal silty-clay sedimentary area (~4 000 m depth).

Genus *Paradoneis* Hartman, 1965

Generic diagnosis (from Blake, 1996b): body long, thin, slightly enlarged anteriorly. Median antenna absent; prostomial ciliary bands absent; longitudinal nuchal grooves along posterior prostomial margin; peristomium indistinct; eyes present or absent. Three to five pre-branchial segments. All segments with notopodial postchaetal lobes; neuropodial lobes absent. Notochaetae include capillaries and either lyrate chaetae or modified simple spines; neurochaetae capillaries, without lateral fringe. Branchiae from chaetigers 4-6, numbering 6-30 or more pairs. Pygidium rounded terminally, with 3 anal cirri.

Species: *Paradoneis* cf. *lyra*

Diagnosis: Branchiae present from chaetiger 4; 6 to 13 pairs. Modified notochaetae lyrate (1 to 6 per notopodia) starting in chaetiger 17-19 (Fig D.4).

Material examined: North East Pacific, Station M (~4 000 m deep, 50˚00 N, 123˚00 W), 203 specimens examined.

Description: many incomplete specimens; up to 7.2 mm long and 0.7 mm wide; longest complete specimen with 48 chaetigers for 7.2 mm long. No reproductive specimen observed.

Body long, robust in anterior area, more fragile in posterior area (often lacking), with a very regular segmentation (Fig. D.4a,b). Thoracic area with branchiae on the posterior part; strong segmentation; enlarged pre-branchial segments.

Prostomium conical and anteriorly rounded, longer than wide (about 1.5/2 times); without eyes; without median antenna or palpode; oblique nuchal organ starting at the external region of mid prostomium and reaching the posterior end of peristomium (appearing as ciliated bands in larger specimens). Peristomium reduced to small lateral lobes. Proboscis not observed.

Branchiae from chaetiger 4 to 10/13/16 (6/10/13 pairs), cylindrical, basally thick, tapering at the tip, the longest one about inter-branchial width long, first and last 1-2 pairs smaller than the anterior pairs (Fig. D.4c,d). Notopodial postchaetal lobes, inconspicuous in chaetiger 1, short triangular in pre-branchial segments, becoming cirriform, clearly smaller than branchiae in branchial area, longer after branchial area shortening in the last 3 chaetigers.

Anterior notochaetae and neurochaetae capillaries; modified lyrate chaetae in notopodia, 1-6 per notopodia (mostly 2-4), starting around chaetiger 17-19; lyrate with one tine longer than the other one (1.3 to 1.5 times longer) with a thin filamentous tip, both tines equal in thickness, with inner edges spinulate (Fig D.4e,f). Pygidium rounded, slightly bilobed with one short medial cirri and two longer lateral cirri.

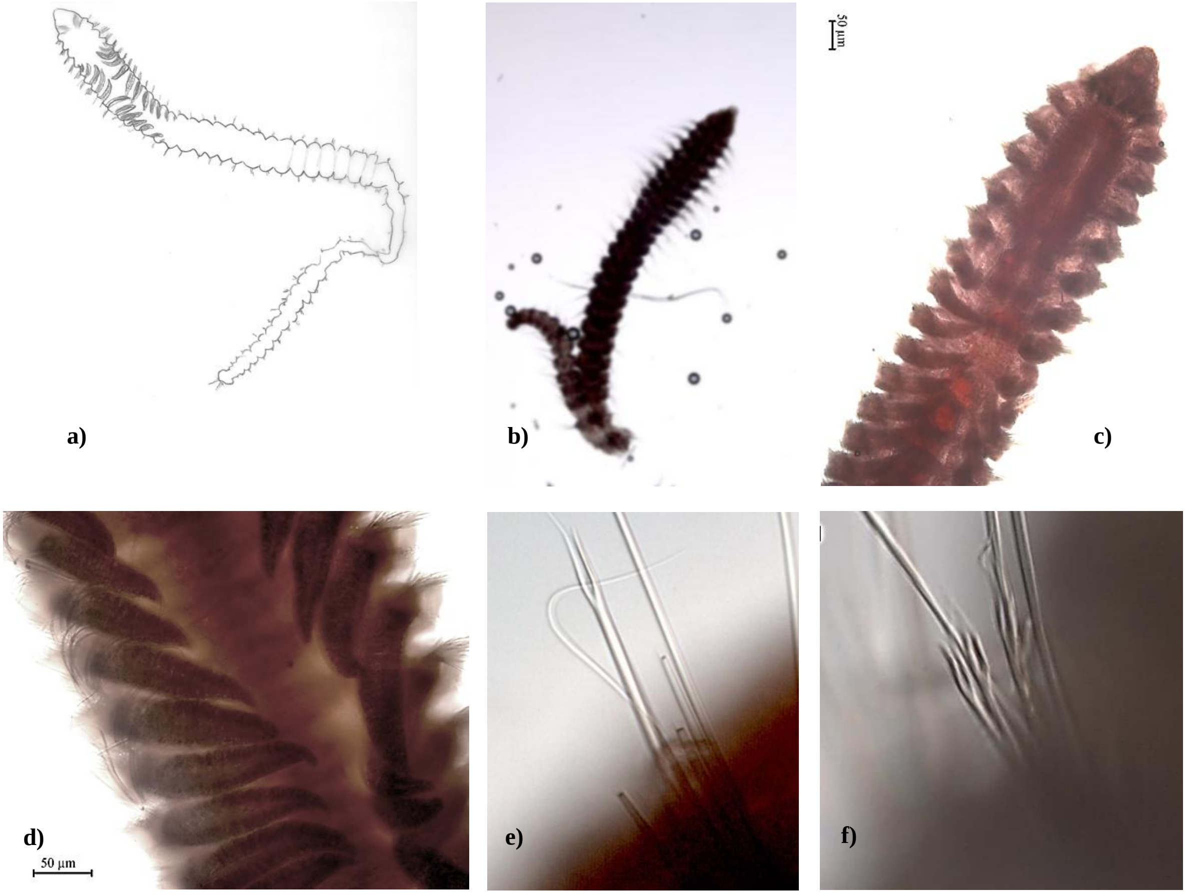


Figure D.4 *Paradoneis* cf. *lyra* (a-b) specimen in dorsal view, (c) anterior part, (d) branchiae, (e-f) modified lyrate chaetae in notopodia.

Remark: Several *Paradoneis* species have been reported having their branchiae starting in chaetiger 4 (Aguirrezabalaga and Gil, 2009). The present species is close to *P. armata* (Glemarec, 1966) in number of pre-branchial segments but does not have a modified acicular spine. *P. brunnea* (Hartman-Schröder and Rosenfeldt, 1988) and *P. nipponica* are also different of the present species as their notopodial postchaetal lobes do not become longer in posterior part of the body. *P. eliasoni* (Mackie, 1991) differs because it has acicular neurochaetae. *P. forticirrata* (Strezlov, 1973) is different due to its massive pre-branchial postchaetal lobes. *P. harpagonea* (Storcholker, 1967), *P. ilvana (*Castelli, 1985), *P. juvenalis* are also different because they have rounded branchiae. *P. perdidoensis* (McLelland and Gaston, 1994) and *P. perkinsi* (McLelland and Gaston, 1994) have less branchiae pairs (3 to 4 only) than the present species. *P. lyra capensis* (Day, 1955) differs as lyrate chaetae are present in the last few branchial segments. Overall, the present species is close to *P. lyra* (Mackie, 1991).

Distribution and habitat: Sta. M, North East Pacific, abyssal silty-clay sedimentary area (~4 000 m depth).

Family Syllidae Grube, 1850

Sub family Exogoninae Langerhans, 1879

Sub family diagnosis (from Kudenov and Harris, 1995): body rather compact, less than 8 mm long, 0.8 mm wide. Palps fused dorsally for at least one-half to all their length. Nuchal organs usually inconspicuous. Tentacular cirri usually numbering 1-2 pairs; may be absent. Antennae, tentacular cirri and dorsal cirri smooth. Ventral cirri present. Pharynx usually straight, with a mid-dorsal tooth or unarmed.

***Genus Sphaerosyllis* Claparède, 1863**

Generic description (*sensu* Kudenov and Harris, 1995): Prostomium with 3 antennae. Palps fused dorsally for most or entire length. One pair of tentacular cirri. Nuchal organ inconspicuous. Pharynx with a single anterior mid-dorsal tooth. Antennae, tentacular cirri and dorsal cirri usually flask-shaped (pyriform). Intergument usually with glandular adhesive papillae.

Species: *Sphaerosyllis* sp. A

Diagnosis: 18 to 22 chaetigers; short pharynx, sinuous an anterior part when non-everted; barrel shape proventriculus with 12-14 rows of muscle cells; no dorsal cirri on chaetiger 2, other dorsal cirri with papillae on the bulbous part of the cirri, aciculae distally bulbous with a short tip and posterior parapodia with a second aciculae distally bent at right angle, no papillae on body (Fig D.5).

Examined material: North East Pacific, Station M (~4000 m deep, 50˚00 N, 123˚00 W), 207 specimens examined.

Description: Complete specimens with 18 to 22 chaetigers, up to 1.2 mm long and 0.3 mm wide. Sixteen specimens observed with reproductive tissues. Thirteen with chaetiger 10 and 11 full of reproductive tissue (Fig. D.5c); granulate and more darkly stained than other tissues. Three specimens with eggs, 2 per chaetiger in chaetiger 10, 11 and 12; round shape; 1st specimen with egg size 29 ± 5 µm, 2nd specimen with egg size 21 ± 6 µm, 3rd specimen with egg size 12 ± 3 µm.

Body short, slender, dorso-ventrally flattened, tapering at the posterior end (Fig. D.5a,b). Papillae not observed on dorsal or ventral side (if present scattered and few). Parapodia conical and distally blunt.

Prostomium ovoid, wider than long; without eyes. Median antennae short, extending beyond edge of prostomium but not beyond the palps, median antenna inserted posteriorly to lateral antennae; bowling-pin shape. Lateral antennae inserted on anterior margin of the prostomium, bowling-pin shape. Palps short, fused all along their length, with a distal median notch as furrow, slightly bent ventrally. Peristomium as long as the following chaetigers, fused to the prostomium, visible dorsally as fold covering the posterior half of prostomium. Tentacular cirri small, shorter than antennae, inserted ventro-laterally to lateral antenna, bowling-pin shape. Pharynx thin, extending to 1-2 first chaetigers, dark and appearing sinuous in anterior part when non-everted in preserved specimens - pharyngeal tooth relatively large, conical, on anterior rim (Fig D.5h,i). Proventriculus barrel shaped, longer and wider than pharynx, 3-chaetiger long, with 12-14 cell rows, usually present from chaetiger 2 to 4 (Fig. D.5b).

Dorsal cirri absent on chaetiger 2; short on anterior segments (shorter than parapodia), slightly longer on mid-body and posterior segments; bowling-pin shape; papillae on the basal part of the cirri, rounded and small (Fig. D.5g). Parapodial gland not observed. Ventral cirri short, cylindrical, not extending beyond parapodia.

Anterior parapodia with 4 heterogomph compound chaetae with a dorso-ventrally graduation in blade length. Solitary dorsal simple chaetae, long, unidentate and apparently smooth. Number of compound chaetae increasing to 6-7 in mid-body and decreasing to 3-2 in posterior body (Fig. D.5d-f). Compound chaetae with unidentate blades. Chaetae with short shaft in proventriculus area, blade and shaft becoming longer in mid-body, then becoming shorter in posteriormost chaetigers. Uppermost compound chaetae with relatively elongated, unidentate blade with well-developed marginal serration. Posterior chaetigers with one ventral simple chaetae, unidentate (starting in chaetiger 9-12). Anterior parapodia with one aciculae distally bulbous with a short tip, just protruding and posterior parapodia with a second protruding aciculae distally bent at right angle.

Last segment achaetigerous. Pygidium hemispherical, somehow flattened, with 2 long, lightly clavate anal cirri.

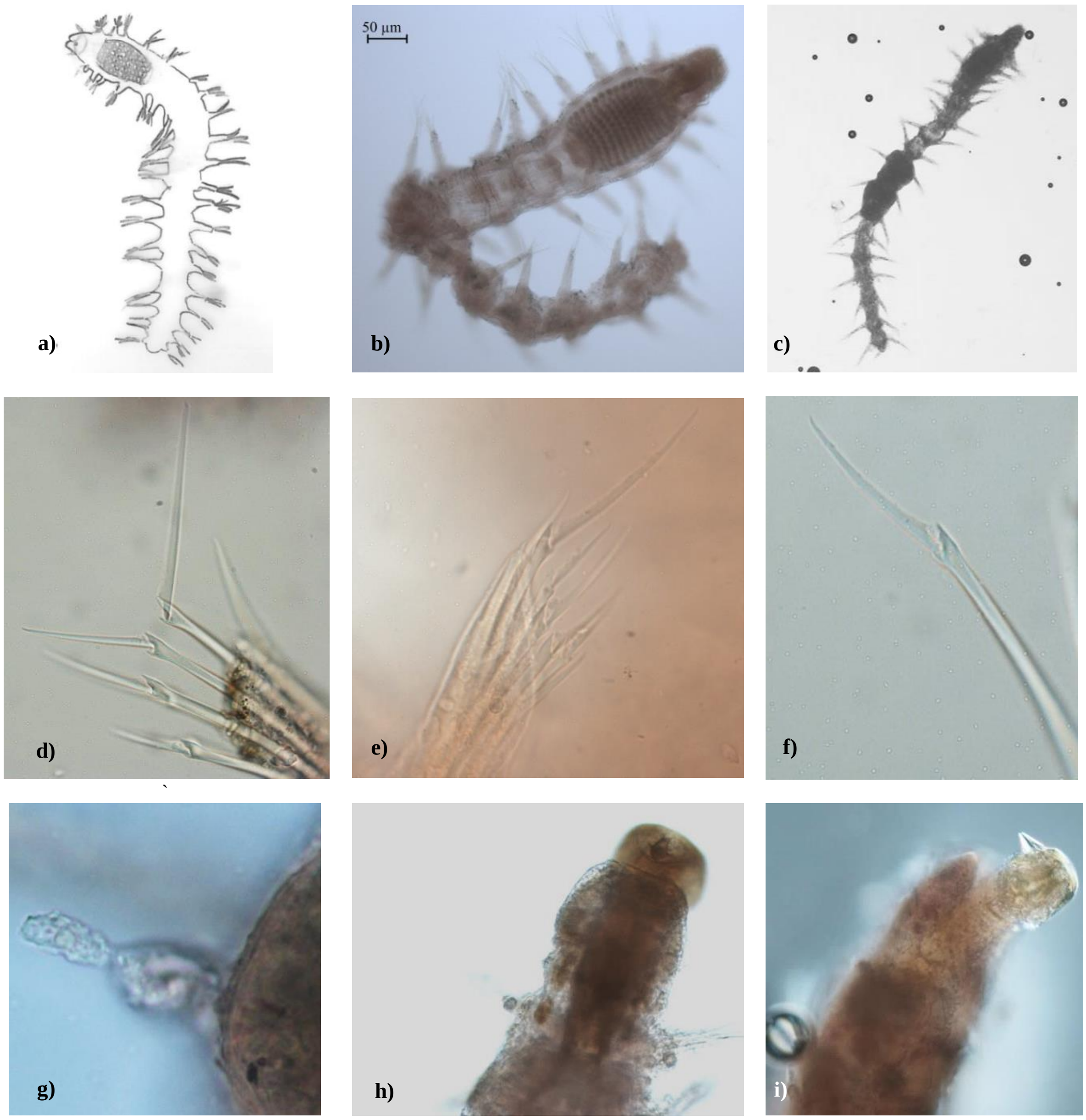


Figure D.5 *Sphaerosyllis* sp. A (a-b) specimen in dorsal view, (c) specimen with reproductive tissues in segments 10 and 11, (d-f) compound chaetae, (g) bowling-pin shape dorsal cirri, (h) everted pharynx with pharyngeal tooth in dorsal view, (i) everted pharynx with pharyngeal tooth in side view.

Remark: The absence of dorsal cirri on chaetiger 2 has been reported for numerous *Sphaerosyllis* species and was used by San Martin (1984) to define 2 subgenera: *Prosphaerosyllis* for species with dorsal cirri on chaetiger 2 and *Sphaerosyllis* for species without it. Riser (1991) stated that exogonine syllids having dorsal cirri on chaetiger 2 as adults, usually lack dorsal cirri on chaetiger 2 as juveniles. In a more recent review of Australian Exogoninae polychaetes, San Martin (2005) used reproductive character to differentiate between *Prosphaerosyllis* and *Sphaerosyllis*. Such reproductive characters could not be used for the present deep-sea species. Based on San Martin (2005) key, *Prosphaerosyllis* is unlikely as the pharyngeal tooth is usually located far from anterior margin which is not the case in the specimens from Sta. M; *Erinaceusyllis* is also unlikely as the bowling-pin shape of the dorsal cirri is not reported in this genus; *Parapionosyllis* is different as it has dorsal cirri on chaetiger 2. *Sphaerosyllis sensu* Kudenov and Harris (1995) is close to the present species except for the papillae on the body. If the genus is confirmed, this species is close to *S. bulbosa* (Southern, 1914) in having no papillae on the body and particular aciculae shape. However, *S. bulbosa* has some papillae on parapodia and anal segment as well as 4 strongly pigmented eyes.

Distribution and habitat: Sta. M, North East Pacific, abyssal silty-clay sedimentary area (~4 000 m depth).

D.4 Discussion

The five density-dominant species at Sta. M belonged to genera found in other deep-sea systems and extended the bathymetric range of 4 of them in the North East Pacific (Table D.6). *Aphelochaeta* species have been reported in the North East Pacific as a dominant genus at Sta. M in 2007 (Jeffreys et al., 2013) and as one of the most diverse cirratulids in the deep water of Northern California (2400-3200 m, Doner and Blake, 2009). In the Atlantic, *Aphelochaeta* was also one of the most diverse genera at the Porcupine Abyssal Plain (PAP, Soto, 2009) and species were also found in the Madeira Abyssal Plain (MAP), the Tagus Abyssal Plain (TAG), EUMELI Oligotrophic sites (EOS) in the North East Atlantic (Glover, 2000). Overall, *Aphelochaeta* distribution appears to be worldwide (Appendix E.12). *Cossura* species have been reported in Atlantic abyssal stations but were not among the dominant species (PAP, Soto, 2009). The present record of *Cossura* cf. *rostrata* at Sta. M increased the bathymetric range of the genus in the North East Pacific. *Levinsenia* species has been reported worldwide at > 1 000 m depth (Appendix E.12). In the Atlantic *Levinsenia* was one of the dominant paraonid genera at the PAP (Soto, 2009) and species were also found at TAG but were less dominant (Glover, 2000). In the North East Pacific, one species in particular, *Levinsenia gracilis*, was found to be cosmopolitan from shallow subtidal to more than 3000 m. The present record of *Levinsenia* species at Sta. M increased the bathymetric range and distribution of the genus in the North East. *Paradoneis* species have been reported in the North East Pacific, from 1750 to 3100 m (Blake, 1996b, Hilbig and Blake, 2006). Overall, *Paradoneis* was found worldwide at > 1000 m depth (Appendix E.12). But, at abyssal depths, this genus was not a dominant species (e.g. Soto, 2009). Our records extended the distribution of the genus in the North East Pacific. However, recent molecular analyses showed that *Paradoneis* and *Cirrophorus* genera were similar albeit some *Paradoneis* species belonged to a different genus (Reuscher, 2013). These distributions will need to be reassessed in the view of molecular analyses in order to clarify distinction for our samples. *Sphaerosyllis* have been found in the North East Pacific at 2400-3100 m (Hilbig and Blake, 2006, Blake et al., 2009). Overall, fewer records of S*phaerosyllis* have been reported at greater depths (> 1000 m, Appendix E.12). S*phaerosyllis* were not observed at PAP. Among the sub-family Exogoninae, the *Exogone* has been most often reported at abyssal depths (PAP, Soto, 2009, TAP, MAP, EOS, Glover, 2000). The present record of *Sphaerosyllis* at Sta. M increased the bathymetric range of the genus in the North East Pacific.

Table D.6 Records in literature of the genera of the five density dominant species of Sta. M, with location, depth and source. Only record deeper than 1000 m were kept. Nr stands for not reported.

Genus	Location	Depth (m)	Source
Aphelochaeta	Weddell Sea, Antarctic Ocean	1000-2400	Hilbig, 2002
	Antarctic Ocean	1000-4000	Fütterer et al., 2003, Blake and Narayanaswamy, 2004
	Arctic Ocean	1018-1654	Kronke, 1994
	Hausgarten observatories, Arctic Ocean	2450	Bergmann et al., 2011
	Faroe Shetland Channel, Atlantic-Arctic boundary	1000	Gontaki et al., 2011
	Porcupine Abyssal Plain, North East Atlantic	4850	Soto, 2009
	Madeira Abyssal Plain, North East Atlantic	5400	Glover, 2000
	Tagus Abyssal Plain, North East Atlantic	5035	Glover, 2000
	EUMELI Oligotrophic sites, North East Atlantic	4500-4600	Glover, 2000
	Condor Seamount off Azores, North East Atlantic	1006	Bongiorni et al., 2013
	Carolina continental slope, North West Atlantic	600-3000	Hilbig, 1994
	Sigsbee Basin, North Western Gulf of Mexico	200-3760	Perez-Mendoza et al., 2003
	Off Mauritania, Tropical North East Atlantic	3100-4600	Cosson-Sarradin et al., 1998
	Angola Basin, South East Atlantic	5433-5494	Fiege et al., 2010
	Off Farallones Island, North East Pacific	1500-4600	Hilbig and Blake, 2006, Blake et al., 2009, Doner and Blake, 2009
	Station M,. Abyssal sedimentary area, North East Paific	~4000	Jeffreys et al., 2013
	Chatham Rise, off New Zealand, Subtropical front	2285-2330	Propert et al., 2009
	Oman Margin, North West Arabian Sea, Indian Ocean	400-1250	Levin et al., 2000
Cossura	Reykjanes Ridge	1815	Mironov and Gebruk, 2007
	Santa Cruz Basin, North East Pacific	1670	Bernardino et al., 2010
	Off Farallones Island, North East Pacific	400-3000	Hilbig and Blake, 2006, Blake et al., 2009
Levinsenia	Weddell Sea, Antarctic Ocean	1000-2400	Hilbig, 2002, 2004
	Porcupine Abyssal Plain, North East Atlantic	4850	Soto, 2009

Table D.6 continued

Genus	Location	Depth (m)	Source
Levinsenia	Tagus Abyssal Plain, North East Atlantic	5035	Glover, 2000
	Nazaré and Setúbal canyons, North East Atlantic	1000-4300	Cunha et al., 2011, Paterson et al., 2011
	Carolina continental slope and rise, North West Atlantic	200-3000	Blake and Grassle, 1994, Hilbig, 1994
	Sigsbee Basin, North Western Gulf of Mexico	200-3760	Perez-Mendoza et al., 2003
	Gulf of Mexico	200-1000	Wei et al., 2010
	Angola Basin, South East Atlantic	5433-5494	Fiege et al., 2010
	Ionian Sea, Mediterranean Sea	300-3000	Terlizzi et al., 2008
	Santa Catalina Basin, North East Pacific	1240	Smith et al., 1986
	Off Farallones Island, North East Pacific	1000-1500, 2000-3000	Hilbig and Blake, 2006, Blake et al., 2009
	Abyssal Peru Basin, South East Pacific	4122-4201	Borowski, 2001
	Chatham Rise, off New Zealand, Subtropical front	1000	Propert et al., 2009
	Arabian basin, Western Indian Ocean	1524-2546	Ingole et al., 2010
	Oman Margin, North West Arabian Sea, Indian Ocean	850-3400	Levin et al., 2000
Paradoneis	Antarctic Ocean	1108-6319?	Blake and Narayanaswamy, 2004
	Porcupine Abyssal Plain, North East Atlantic	4850	Soto, 2009
	Condor Seamount off Azores, North East Atlantic	1006	Bongiorni et al., 2013
	Off South US, North West Atlantic	2000	Brown, 1991
	Carolina continental slope and rise, North West Atlantic	200-3000	Blake and Grassle, 1994, Hilbig, 1994
	Lacaze-Duthiers, Planier and Fox submarine cabyon, North East Mediterranean Sea	550-1195	Sarda, 2009
	Off Farallones Island, North East Pacific	600-3100	Blake, 1996b, Hilbig and Blake, 2006, Blake et al., 2009
	Seamounts, Indian Ocean	nr	Wafar et al., 2011
	Oman Margin, North West Arabian Sea, Indian Ocean	1000-3400	Levin et al., 2000
Sphaerosyllis	Weddell Sea, Antarctic Ocean	1000-2300	Hilbig, 2002, 2004, Blake and Narayanaswamy, 2004
	Antarctic continental slope and south Atlantic basin	1950.3	Wilmsem and Schüller, 2011
	Carolina continental slope and rise, North West Atlantic	200-3000	Hilbig, 1994
	Lacaze-Duthiers, Planier and Fox submarine cabyon, North East Mediterranean Sea	550-1195	Sarda, 2009
	Santa Catalina Basin, North East Pacific	1240	Smith et al., 1998
	Off Farallones Island, North East Pacific	2400-3100	Hilbig and Blake, 2006, Blake et al., 2009
	North West Sea of Japan	470-1490	Alalykina, 2013

At least two of the five density dominant species at Sta. M may be new species: *Aphelochaeta* sp. A and *Sphaerosyllis* sp. A. So far, Sta. M specimens were preserved in formaldehyde making molecular analyses more challenging. Since 2012, some samples have been preserved in ethanol and future studies of Sta. M polychaete taxonomy will include molecular analyses. However, polychaete phylogenetic relationships are far from being resolved and species/genus level analyses remain scarce (Reuscher, 2013). Overall, a considerable revision work on polychaete taxonomy is now required for deep-sea polychaetes including new research in phylogenetic relationship between species to resolve polyphyletic issues (Paterson et al., 2009).

Reference of appendix D

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Appendix E

Chapter 4 supplement information

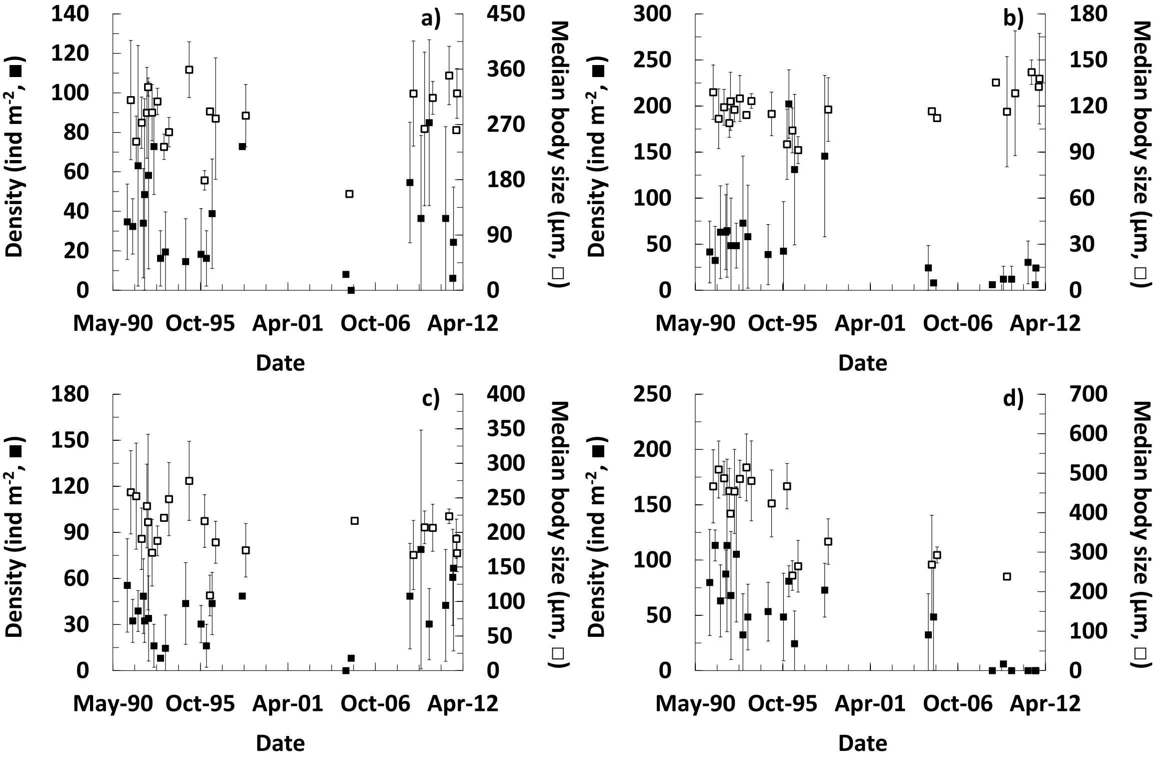

Figure E.1 Mean densities (■, ind.m^{-2}) and median body size (□, µm) over year with 95% confidence interval for (a) *Aphelochaeta* sp. A, (b) *Cossura* cf. *rostrata*, (c) *Levinsenia* cf. *oligobranchiata*, (d) *Paradoneis* cf. *lyra*. *Aphelochaeta* sp. A density was maximum in May 2010 with 84.93 ± 21.06 ind.m^{-2} and absent in June 2005 and its median body size was the smallest in February 2005 with 157 µm and was the highest in February 1995 with 376.96 µm. *Cossura* cf. *rostrata* density was highest in June 1996 with 202.22 ± 21.40 ind.m^{-2} and the lowest in November 2010 with 6.07 ± 6.07 ind.m^{-2}. In terms of median body size, it was the smallest in February 1996 with 81.89 µm and was the biggest in May 2011 with 149.62 µm. *Levinsenia* cf. o*ligobranchiata* had the highest density in November 2009 with 78.87 ± 38.84 ind.m^{-2} and was absent in February 2005. *Levinsenia* cf. o*ligobranchiata* had the smallest median body size in November 2011 with 157.36 µm and had the biggest body sizes in February 1995 with 299.85 µm. *Paradoneis* cf. *lyra* highest density was found in July 1992 with 113.24 ± 45.04 ind.m^{-2} and was absent in February 2009 and from May 2010 to November 2011. *Paradoneis* cf. *lyra* median body size was the smallest in June 1996 with 228.76 µm and was the biggest in July 1993 with 567.31 µm.

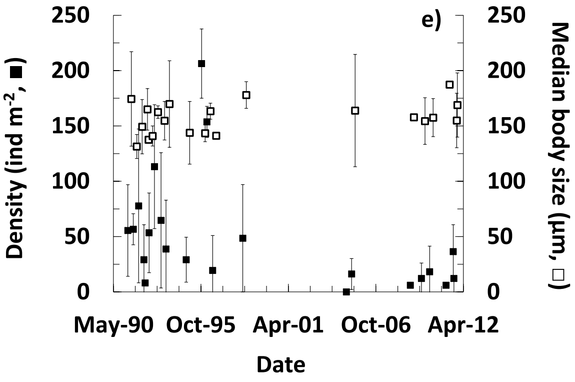

Figure E.2 Mean densities (■, ind.m^{-2}) and median body size (□, µm) over year with 95% confidence interval for *Sphaerosyllis* sp. A. *Sphaerosyllis* sp. A had a maximum density in February 1996 with 218.70 ± 24.26 ind.m^{-2} and was absent in February 2005. Its median body size was the smallest in February 1992 with 133.50 µm and was the biggest in May 2011 with 187.29 µm.

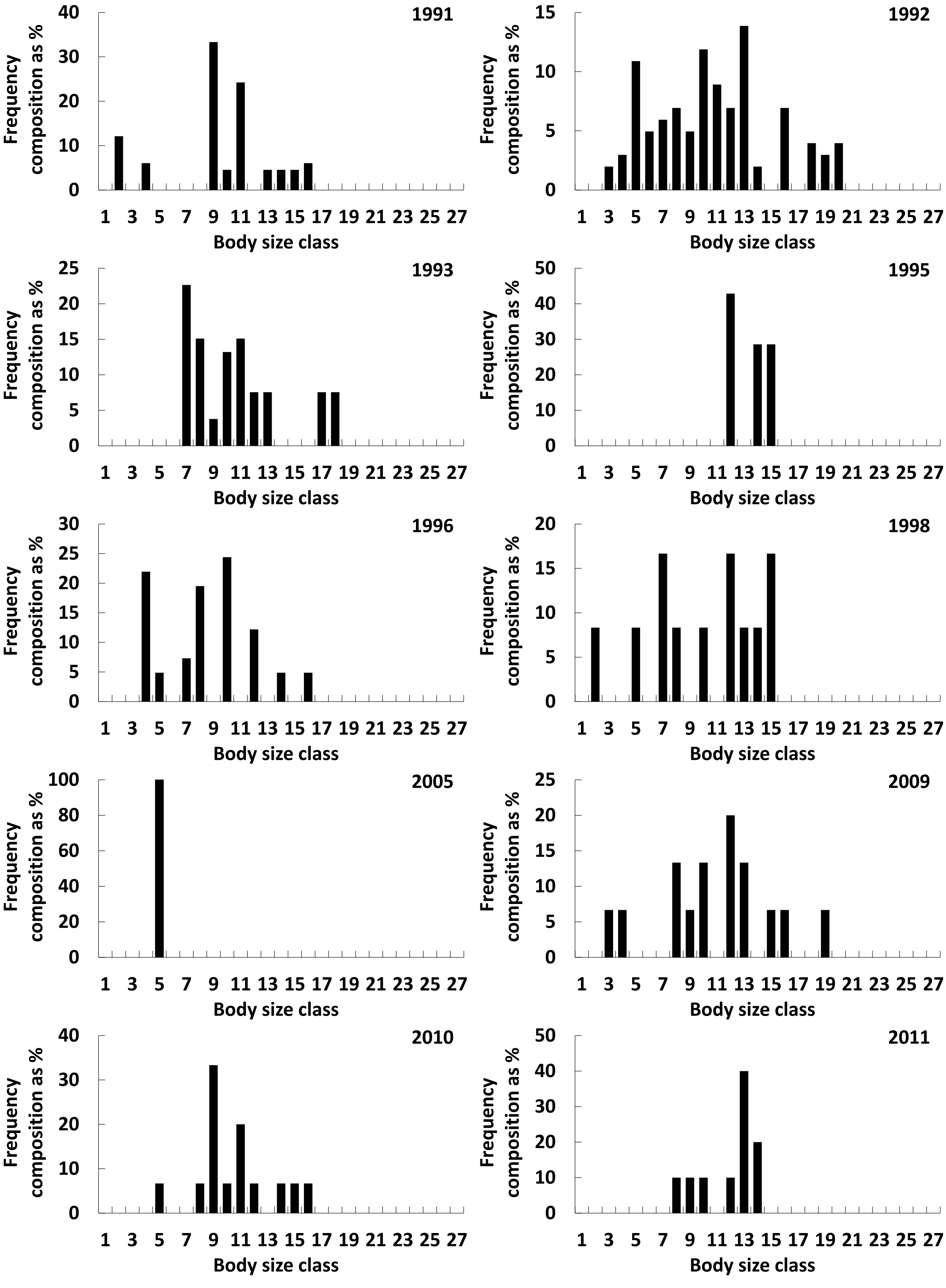

Figure E.3 Density body size spectra for each sampled year of *Aphelochaeta* sp. A. Figures are sequentially ordered.

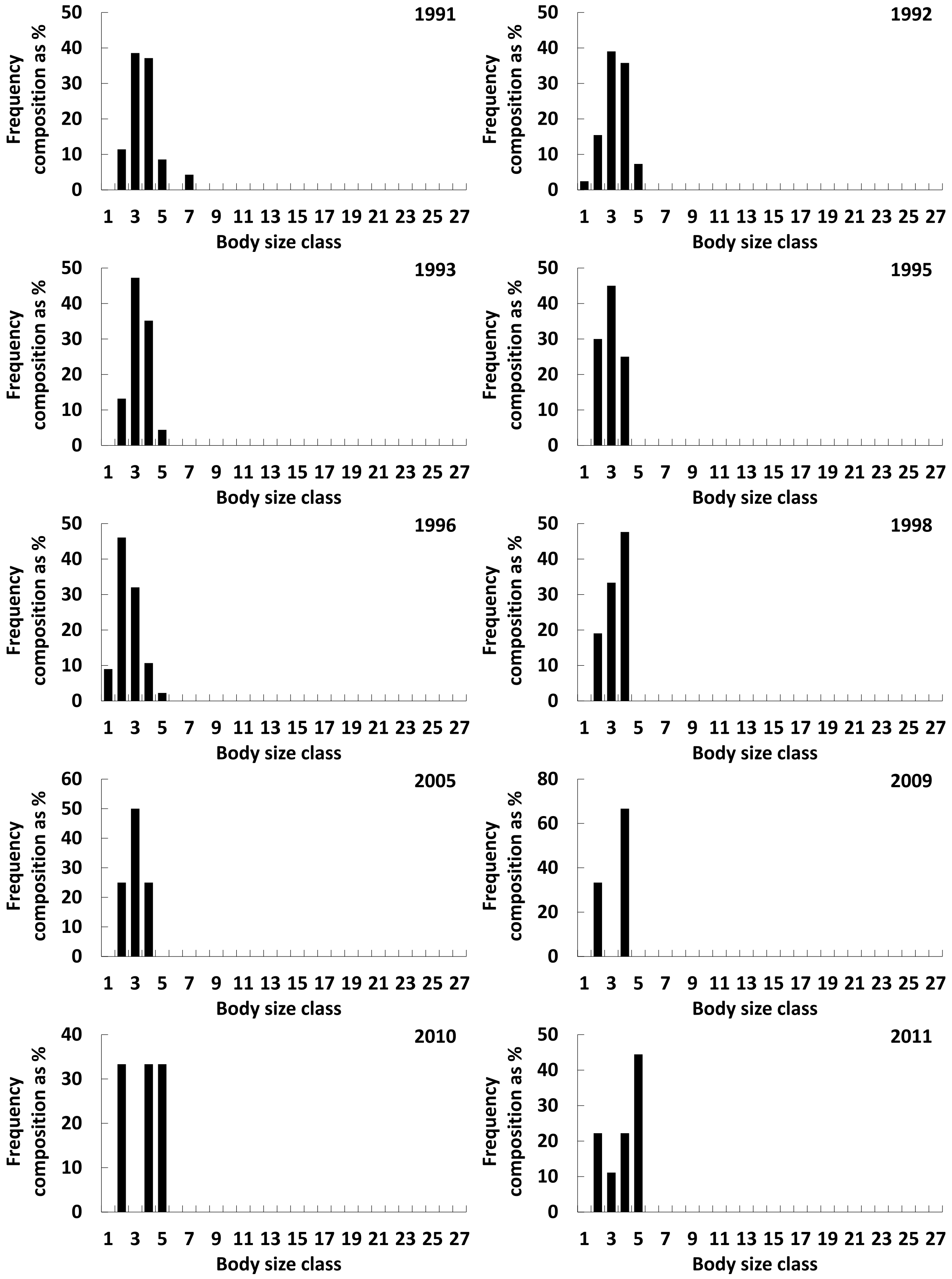

Figure E.4 Density body size spectra for each sampled year of *Cossura* cf. *rostrata*. Figures are sequentially ordered.

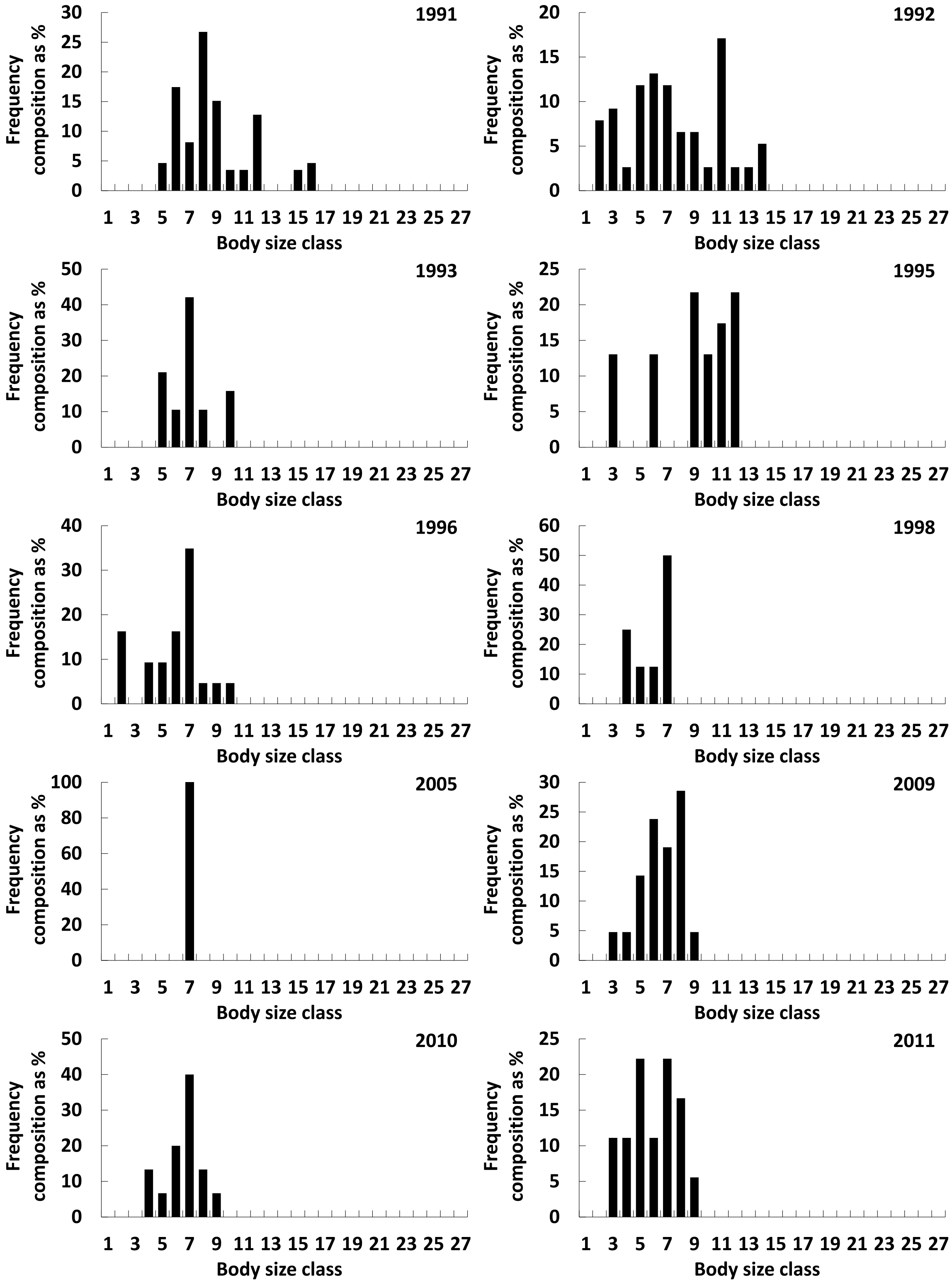

Figure E.5 Density body size spectra for each sampled year of *Levinsenia* cf. *oligobranchiata*. Figures are sequentially ordered.

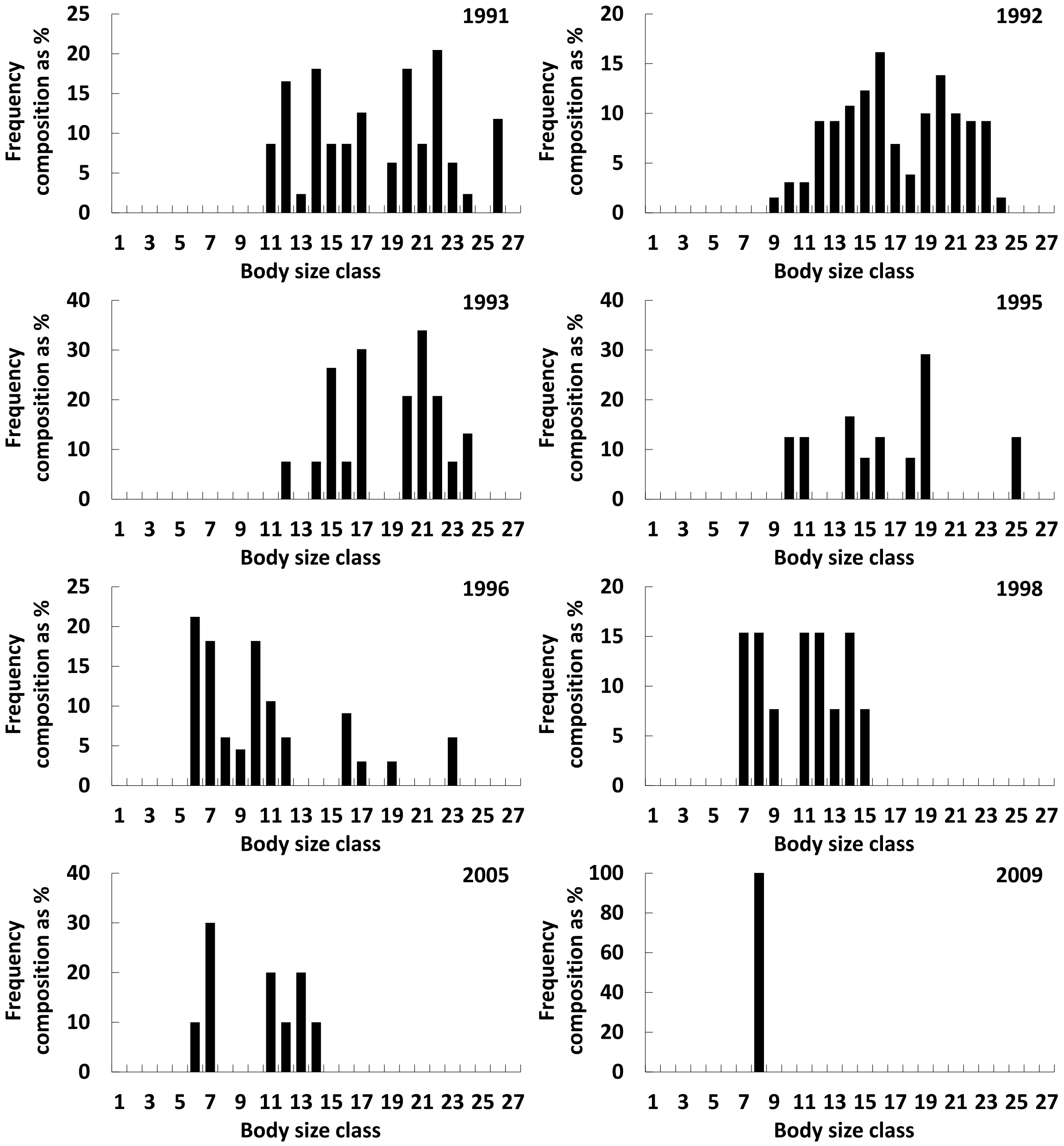

Figure E.6 Density body size spectra for each sampled year of *Paradoneis* cf. *lyra*. Figures are sequentially ordered.

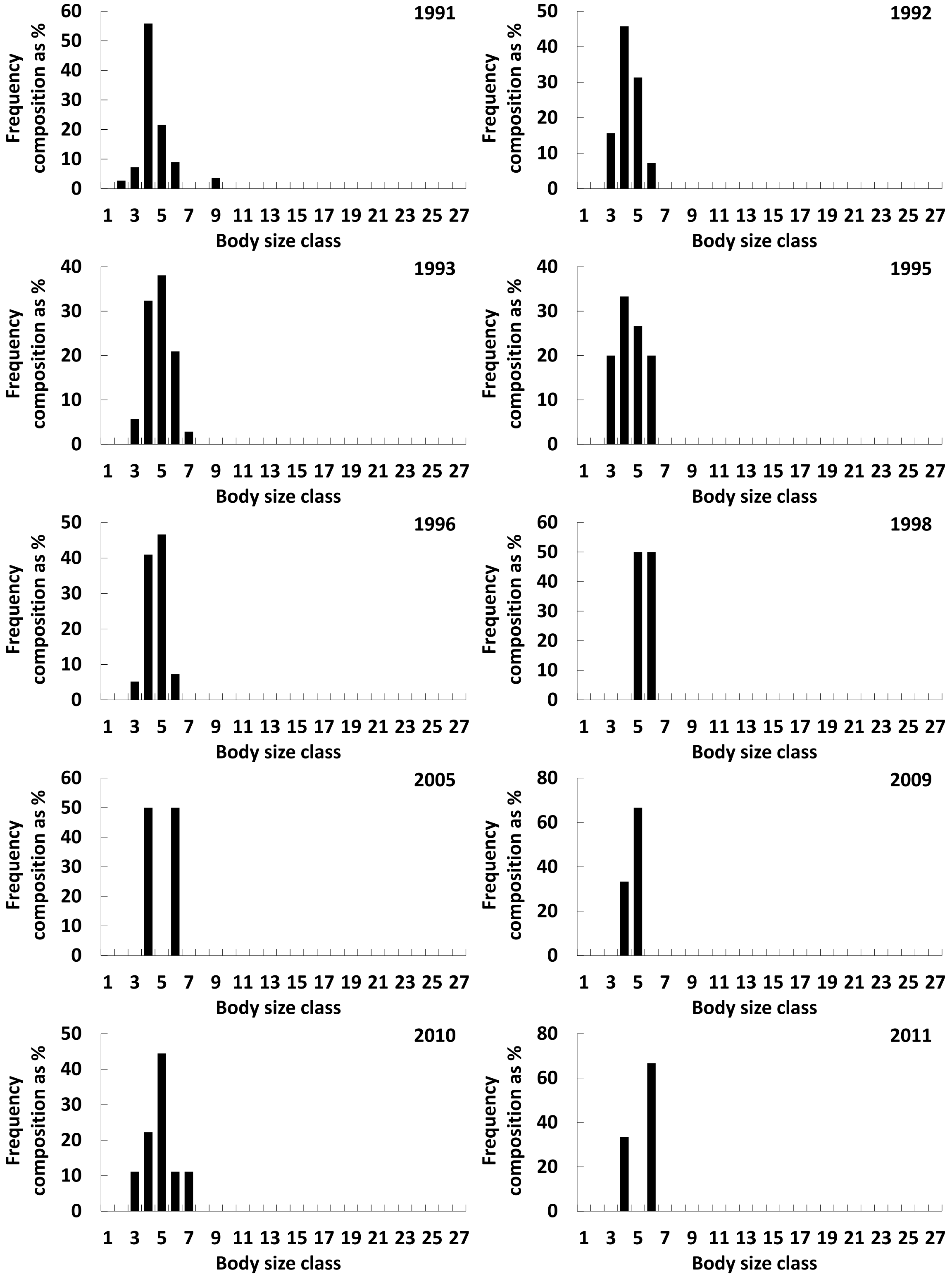

Figure E.7 Density body size spectra for each sampled year of *Sphaerosyllis* sp. A. Figures are sequentially ordered.

Table E.8 Records of polychaete specimens with reproductive tissues at Sta. M over 1991-2011: family, genus, species, pulse (research cruise reference), station, date, number of the grab of the Free-Vehicle Grab Respirometer (Smith et al., 2001), specimen reference number.

Family	Genus	Species	Pulse	Station	Date	Grab	Sample #
Capitellidae	*Heteromastus*	sp. A	6	616	Feb-91	4	18
	Heteromastus	sp. A	54	5401	Feb-09	3	4117
	Heteromastus	sp. A	56	5601	May-10	2	4480
	Notomastus	cf. *latericeus*	11	1107	Feb-92	2	624
	Notomastus	cf. *latericeus*	12	1205	Jun-92	1	825
	Notomastus	cf. *latericeus*	18	1818	Nov-93	2	1553
	Notomastus	sp. B	30	3002	Jun-96	4	2306
Cirratulidae	*Aphelochaeta*	sp. A	8	802	Jul-91	2	364
	Aphelochaeta	sp. A	31	3109	Oct-96	4	2423
	Aphelochaeta	sp. A	34	3405	Apr-98	3	2615
	Chaetozone	sp. A	7	706	Jun-91	3	182
	Chaetozone	sp. A	8	802	Jul-91	2	376
	Chaetozone	sp. A	24	2403	Feb-95	4	1759
	Chaetozone	sp. A	59	5901	Nov-11	2	5060
	Chaetozone	sp. G	54	5401	Feb-09	1	4019
	Chaetozone	sp. G	58	5801	May-11	4	4975
Fabriciidae	*Fabriciidae*	sp. C	16	1604	Feb-93	3	1326
Fauveliopsidae	*Fauveliopsis*	sp. A	7	720	Jun-91	4	301
	Indet.	fragment	31	3109	Oct-96	3	2383
Nephtyidae	*Micronephthys*	sp. A	11	1107	Feb-92	2	653
Nereididae	*Nereididae*	sp. B	11	1120	Feb-92	3	721
	Nereididae	sp. C	15	1505	Oct-92	4	1337
Opheliidae	*Ophelina*	*farallonensis*	6	616	Feb-91	4	31
	Ophelina	*farallonensis*	7	706	Jun-91	3	203
	Ophelina	*farallonensis*	7	720	Jun-91	2	333
	Ophelina	*farallonensis*	7	720	Jun-91	2	344
	Ophelina	*farallonensis*	11	1107	Feb-92	4	693
Paraonidae	*Aricidea*	*abranchiata*	56	5601	May-10	2	4496
	Aricidea	sp. A	55	5502	Nov-09	4	4375
	Aricidea	sp. A	57	5701	Nov-10	3	4735
	Aricidea	sp. B	57	5701	Nov-10	4	4774
	Aricidea	sp. B	58	5801	May-11	2	4890
	Aricidea	sp. D	59	5901	Nov-11	4	5190
	Levinsenia	cf. *oligobranchiata*	24	2403	Feb-95	1	1727
	Levinsenia	cf. *oligobranchiata*	54	5401	Feb-09	2	4065
	Levinsenia	cf. *oligobranchiata*	57	5701	Nov-10	1	4627
	Levinsenia	cf. *oligobranchiata*	58	5801	May-11	4	4980
	Levinsenia	cf. *oligobranchiata*	58	5801	May-11	4	4981

Table E.8 continued

Family	Genus	Species	Pulse	Station	Date	Grab	Sample #
Phyllodocidae	*Phyllodocidae*	sp. A	8	802	Jul-91	2	381
	Phyllodocidae	sp. A	18	1807	Nov-93	3	1513
	Phyllodocidae	sp. A	24	2403	Feb-95	1	1720
	Phyllodocidae	sp. A	31	3109	Oct-96	4	2449
	Phyllodocidae	sp. A	54	5401	Feb-09	1	4030
	Phyllodocidae	sp. A	56	5601	May-10	4	4555
	Phyllodocidae	sp. B	19	1904	Feb-94	2	1677
	Phyllodocidae	sp. B	30	3002	Jun-96	4	2304
	Phyllodocidae	sp. B	54	5401	Feb-09	4	4165
	Phyllodocidae	sp. F	47	4715	Jun-05	3	3062
Pilargidae	*Ancistrosyllis*	sp. A	16	1604	Feb-93	2	1235
	Indet.	indet.	19	1904	Feb-94	3	1667
	Pilargis	sp. A	59	5901	Nov-11	4	5157
Serpulidae	Genus nov.	sp. A	24	2403	Feb-95	4	1754
Sphaerodoridae	*Sphaerodoropsis*	sp. A	18	1818	Nov-93	2	1567
Spionidae	*Prionospio*	sp. B	15	1515	Oct-92	1	1138
	Prionospio	sp. M	58	5801	May-11	4	4993
Syllidae	*Anguillosyllis*	sp. A	18	1807	Nov-93	4	1492
	Anguillosyllis	sp. B	7	720	Jun-91	1	290
	Anguillosyllis	sp. B	15	1505	Oct-92	3	1081
	Anguillosyllis	sp. B	18	1807	Nov-93	2	1479
	Anguillosyllis	sp. B	34	3405	Apr-98	4	2689
	Anguillosyllis	sp. B	46	4607	Feb-05	3	3018
	Exogone	sp. A	16	1604	Feb-93	2	1284
	Sphaerosyllis	sp. A	6	616	Feb-91	4	45
	Sphaerosyllis	sp. A	16	1604	Feb-93	3	1303
	Sphaerosyllis	sp. A	18	1818	Nov-93	3	1611
	Sphaerosyllis	sp. A	24	2408	Feb-95	1	1793
	Sphaerosyllis	sp. A	29	2909	Feb-96	1	1902
	Sphaerosyllis	sp. A	29	2909	Feb-96	2	1943
	Sphaerosyllis	sp. A	29	2909	Feb-96	3	2005
	Sphaerosyllis	sp. A	29	2909	Feb-96	3	2002
	Sphaerosyllis	sp. A	30	3002	Jun-96	2	2130
	Sphaerosyllis	sp. A	30	3002	Jun-96	4	2310
	Sphaerosyllis	sp. A	34	3405	Apr-98	4	2663
	Sphaerosyllis	sp. A	34	3405	Apr-98	4	2673
	Sphaerosyllis	sp. A	35	3503	Aug-98	1	2726
	Sphaerosyllis	sp. A	35	3503	Aug-98	1	2718
	Sphaerosyllis	sp. A	35	3503	Aug-98	1	2773
	Sphaerosyllis	sp. A	35	3503	Aug-98	1	2900

Table E.9 Record of polychaete juveniles specimens for identified species/morphotypes at Sta. M over 1991-2011: family, genus, species, pulse (research cruise reference), station, date, number of the grab of the Free-Vehicle Grab Respirometer (Smith et al., 2001), specimen reference number.

Family	Genus	Species	Pulse	Station	Date	Grab	Sample #
Amphinomidae	*Paramphinome*	sp. A	10	1005	Oct-91	3	490
	Paramphinome	sp. A	16	1604	Feb-93	2	1248
	Paramphinome	sp. A	19	1904	Feb-94	3	1642
	Paramphinome	sp. A	24	2408	Feb-95	1	1798
	Paramphinome	sp. A	24	2408	Feb-95	1	1806
	Paramphinome	sp. A	29	2909	Feb-96	3	1996
	Paramphinome	sp. A	55	5502	Nov-09	4	4354
	Paramphinome	sp. A	56	5601	May-10	3	4512
	Paramphinome	sp. A	56	5601	May-10	4	4565
	Paramphinome	sp. A	57	5701	Nov-10	2	4662
Capitellidae	*Heteromastides*	sp. A	54	5401	Feb-09	3	4127
Cirratulidae	*Aphelochaeta*	sp. A	56	5601	May-10	3	4525
	Aphelochaeta	sp. B	34	3405	Apr-98	3	2608
	Chaetozone	sp. B	10	1005	Oct-91	1	484
	Chaetozone	sp. D	34	3405	Apr-98	4	2697
	Chaetozone	sp. F	55	5502	Nov-09	2	4267
Cossuridae	*Cossura*	cf. *rostrata*	35	3503	Aug-98	1	2897
	Cossura	cf. *rostrata*	36	3601	Dec-98	2	2576
Fabriciidae	Fabriciidae	sp. C	15	1505	Oct-92	4	1214
Fauveliopsidae	*Laubieriopsis*	cf. *brevis*	54	5401	Feb-09	2	4070
	Laubieriopsis	cf. *brevis*	54	5401	Feb-09	4	4167
	Laubieriopsis	cf. *brevis*	57	5701	Nov-10	4	4759
Lumbrineridae	*Abyssoninoe*	sp. A	59	5901	Nov-11	4	5152
	Abyssoninoe	sp. B	7	706	Jun-91	1	146
	Abyssoninoe	sp. B	11	1107	Feb-92	4	691
	Abyssoninoe	sp. B	16	1604	Feb-93	2	1251
	Abyssoninoe	sp. B	19	1904	Feb-94	2	1683
	Abyssoninoe	sp. B	30	3002	Jun-96	4	2294
Nereididae	*Ceratocephale*	cf. *abyssorum*	11	1120	Feb-92	4	803
Opheliidae	*Ophelina*	*farallonensis*	56	5601	May-10	4	4566
	Ophelina	*farallonensis*	59	5901	Nov-11	4	5169
Paraonidae	*Aricidea*	*abranchiata*	54	5401	Feb-09	4	4172
	Aricidea	sp. A	7	706	Jun-91	3	227
	Aricidea	sp. A	55	5502	Nov-09	4	4375
	Aricidea	sp. A	56	5601	May-10	4	4569
	Aricidea	sp. A	57	5701	Nov-10	3	4735
	Aricidea	sp. B	7	720	Jun-91	4	420
	Aricidea	sp. B	57	5701	Nov-10	3	4733
	Aricidea	sp. F	56	5601	May-10	4	4572
	Cirrophorus	*branchiatus*	10	1005	Oct-91	3	491

Table E.9 continued

Family	Genus	Species	Pulse	Station	Date	Grab	Sample #
Paraonidae	*Cirrophorus*	*branchiatus*	35	3503	Aug-98	1	2770
	Levinsenia	cf. *oligobranchiata*	24	2403	Feb-95	4	1788
	Levinsenia	cf. *oligobranchiata*	54	5401	Feb-09	1	4017
	Levinsenia	cf. *oligobranchiata*	30	3002	Jun-96	3	2247
	Paradoneis	*abranchiata*	7	706	Jun-91	4	243
	Paradoneis	*abranchiata*	10	1005	Oct-91	1	491
	Paradoneis	*abranchiata*	17	1714	Jul-93	4	1458
	Paradoneis	cf. *drachi*	59	5901	Nov-11	4	5184
	Paradoneis	cf. *lyra*	12	1218	Jun-92	3	969
	Paraonella	*rubriceps*	12	1205	Jun-92	3	894
	Paraonella	*rubriceps*	16	1604	Feb-93	3	1306
	Paraonella	*rubriceps*	24	2403	Feb-95	4	1769
	Paraonella	*rubriceps*	29	2909	Feb-96	2	1970
	Paraonella	*rubriceps*	29	2909	Feb-96	2	1971
	Paraonella	*rubriceps*	29	2909	Feb-96	3	2006
	Paraonella	*rubriceps*	30	3002	Jun-96	3	2237
	Paraonella	*rubriceps*	30	3002	Jun-96	3	2218
	Paraonella	*rubriceps*	30	3002	Jun-96	4	2297
	Paraonella	*rubriceps*	31	3109	Oct-96	3	2393
	Paraonella	sp. C	7	720	Jun-91	2	348
	Paraonella	sp. C	14	1401	Jul-92	2	1051
Phyllodocidae	Phyllodocidae	sp. B	15	1505	Oct-92	4	1107
	Phyllodocidae	sp. C	34	3405	Apr-98	3	2613
Pilargidae	*Ancistrosyllis*	sp. A	29	2909	Feb-96	3	2013
	Ancistrosyllis	sp. A	30	3002	Jun-96	2	2133
	Ancistrosyllis	sp. A	31	3109	Oct-96	4	2447
	Sigambra	sp. A	34	3405	Apr-98	3	2633
	Sigambra	sp. A	58	5801	May-11	1	4819
Scalibregmatidae	*Asclerocheilus*	sp. A	54	5401	Feb-09	3	4121
	Oligobregma	sp. A	54	5401	Feb-09	4	4174
	Oligobregma	sp. A	59	5901	Nov-11	1	5014
Sphaerodoridae	*Ephesiella*	sp. A	29	2906	Feb-96	2	1986
	Sphaerodoropsis	sp. B	31	3109	Oct-96	3	2413
	Sphaerodoropsis	sp. B	31	3128	Oct-96	3	2487
Spionidae	*Prionospio*	sp. H	10	1005	Oct-91	3	509
	Prionospio	sp. M	58	5801	May-11	4	4993
Syllidae	*Sphaerosyllis*	sp. A	10	1005	Oct-91	1	459
	Sphaerosyllis	sp. A	29	2909	Feb-96	3	2003

Table E.10 Significant ($p < 0.05$) Spearman rank correlations (r_s) between monthly polychaete species and monthly megafauna species for the period 1991-2005. The type of polychaete data used: D for density, B for body size. Megafauna species as defined in Kuhnz et al. (2014).

Polychaete species	Feature	Megafauna species	r_s	p
Aphelochaeta sp. A	B	*Abyssocucumis abyssorum*	0.552	0.041
Cossura cf. *rostrata*	D	*Oneirophanta mutabilis*	-0.708	0.005
	B	*Oneirophanta mutabilis*	-0.534	0.049
	B	*Scotoplanes globosa*	0.673	0.008
Paradoneis cf. *lyra*	B	*Elpidia* sp. nov.	-0.547	0.043
	B	*Abyssocucumis abyssorum*	0.582	0.029

Table E.11 Records of juveniles for unidentified specimens at Sta. M over 1991-2011: family, genus if determined, pulse (research cruise reference), station, date, number of the grab of the Free-Vehicle Grab Respirometer (Smith et al., 2001), specimen reference number.

Family	Genus	Species	Pulse	Station	Date	Grab	Sample #
Amphinomidae	*Paramphinome*	indet.	6	616	Feb-91	4	72
	Paramphinome	indet.	46	4607	Feb-05	1	2981
	Paramphinome	indet.	46	4607	Feb-05	1	2983
Cirratulidae	Indet.	indet.	6	616	Feb-91	4	48
	Indet.	indet.	10	1005	Oct-91	3	521
	Indet.	indet.	11	1107	Feb-92	1	619
	Indet.	indet.	11	1120	Feb-92	3	751
	Indet.	indet.	17	1714	Jul-93	2	1445
	Indet.	indet.	18	1818	Nov-93	2	1568
	Indet.	indet.	24	2403	Feb-95	1	1723
	Indet.	indet.	29	2909	Feb-96	3	2038
	Indet.	indet.	31	3109	Oct-96	3	2412
	Indet.	indet.	34	3405	Apr-98	3	2641
	Indet.	indet.	47	4715	Jun-05	3	3077
	Indet.	indet.	54	5401	Feb-09	1	4024
	Indet.	indet.	54	5401	Feb-09	2	4057
	Indet.	indet.	54	5401	Feb-09	4	4171
	Indet.	indet.	55	5502	Nov-09	2	4269
	Indet.	indet.	56	5601	May-10	1	4411
	Indet.	indet.	56	5601	May-10	1	4414
	Indet.	indet.	56	5601	May-10	3	4524
	Indet.	indet.	56	5601	May-10	4	4580
	Indet.	indet.	58	5801	May-11	2	4871
	Indet.	indet.	58	5801	May-11	2	4878
	Indet.	indet.	58	5801	May-11	4	4969
	Indet.	indet.	58	5801	May-11	4	4974
	Indet.	indet.	59	5901	Nov-11	4	5175
	Indet.	indet.	59	5901	Nov-11	4	5177
	Indet.	indet.	59	5901	Nov-11	4	5182
Dorvilleidae	Indet.	indet.	57	5701	Nov-10	4	4782
Fauveliopsidae	*Fauveliopsis*	indet.	57	5701	Nov-10	1	4613
	Laubieriopsis	indet.	54	5401	Feb-09	2	4070
	Indet.	indet.	7	706	Jun-91	3	214
	Indet.	indet.	54	5401	Feb-09	1	4034
	Indet.	indet.	56	5601	May-10	1	4404
Indet	Indet.	indet.	35	3503	Aug-98	2	2879
Lumbrineridae	Indet.	indet.	11	1107	Feb-92	1	602
	Indet.	indet.	18	1807	Nov-93	4	1495
	Indet.	indet.	35	3503	Aug-98	1	2771

Table E.11 continued

Family	Genus	Species	Pulse	Station	Date	Grab	Sample #
Nephtyidae	Indet.	indet.	9	906	Jul-91	1	447
	Indet.	indet.	10	1005	Oct-91	1	486
	Indet.	indet.	35	3503	Aug-98	4	2794
	Indet.	indet.	35	3503	Aug-98	1	2932
	Indet.	indet.	35	3503	Aug-98	1	2933
	Indet.	indet.	58	5801	May-11	4	4964
	Indet.	indet.	59	5901	Nov-11	1	5017
Opheliidae	Indet.	indet.	34	3405	Apr-98	4	2652
Orbiniidae	Indet.	indet.	30	3002	Jun-96	1	2089
	Indet.	indet.	58	5801	May-11	2	4871
Paraonidae	*Aricidea*	indet.	9	906	Jul-91	1	428
	Aricidea	indet.	18	1807	Nov-93	4	1505
	Aricidea	indet.	24	2403	Feb-95	4	1772
	Aricidea	indet.	29	2909	Feb-96	2	1968
	Aricidea	indet.	29	2909	Feb-96	3	2019
	Aricidea	indet.	31	3109	Oct-96	3	2394
	Aricidea	indet.	34	3405	Apr-98	4	2691
	Aricidea	indet.	34	3405	Apr-98	4	2692
	Aricidea	indet.	59	5901	Nov-11	4	5186
	Aricidea	indet.	59	5901	Nov-11	4	5196
	Paraonella	indet.	14	1401	Jul-92	3	1105
	Paraonella	indet.	34	3405	Apr-98	4	2669
	Paraonella	indet.	35	3503	Aug-98	4	2813
	Paraonella	indet.	59	5901	Nov-11	4	5191
Phyllodocidae	Indet.	indet.	18	1807	Nov-93	3	1515
Pilargidae	*Ancistrosyllis*	indet.	54	5401	Feb-09	1	4033
Sabellidae	Indet.	indet.	35	3503	Aug-98	1	2771
Sigalionidae	*Leanira*	indet.	6	616	Feb-91	4	38
	Leanira	indet.	7	720	Jun-91	2	340
	Leanira	indet.	7	720	Jun-91	4	344
	Leanira	indet.	10	1005	Oct-91	1	485
	Leanira	indet.	11	1107	Feb-92	4	708
	Leanira	indet.	15	1505	Oct-92	4	1144
	Leanira	indet.	24	2403	Feb-95	1	1730
	Leanira	indet.	24	2408	Feb-95	2	1817
	Leanira	indet.	30	3002	Jun-96	2	2184
	Leanira	indet.	35	3503	Aug-98	1	2721
	Leanira	indet.	35	3503	Aug-98	1	2944
	Leanira	indet.	58	5801	May-11	1	4808
Spionidae	Indet.	indet.	54	5401	Feb-09	3	4110
	Indet.	indet.	57	5701	Nov-10	2	4667

References of appendix E

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