UNIVERSITY OF SOUTHAMPTON

Scavengers & Submarine Canyons:
Studies on facilitators of secondary production in the deep sea

by

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A thesis submitted in partial fulfillment for the
degree of Doctor of Philosophy

in the
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Ocean and Earth Science

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Declaration of Authorship

I, Grant Andrew Duffy, declare that this thesis titled, '*Submarine Canyons: Studies on facilitators of secondary production in the deep sea*' and the work presented in it are my own. I confirm that:

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- Where I have consulted the published work of others, this is always clearly attributed.
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- I have acknowledged all main sources of help.
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"La mer est tout! Elle couvre les sept dixièmes du globe terrestre. Son souffle est pur et sain. C'est l'immense désert où l'homme n'est jamais seul, car il sent frémir la vie à ses côtés. La mer n'est que le véhicule d'une surnaturelle et prodigieuse existence; elle n'est que mouvement et amour."

"The sea is everything. It covers seven tenths of the terrestrial globe. Its breath is pure and healthy. It is an immense desert, where man is never lonely, for he feels life stirring on all sides. The sea is only the embodiment of a supernatural and wonderful existence. It is nothing but love and emotion."

Jules Gabriel Verne (1828–1905)
Twenty Thousand Leagues Under the Sea

UNIVERSITY OF SOUTHAMPTON

Abstract

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Scavenging amphipods and submarine canyons are often identified as important facilitators to secondary production in the deep sea. The findings presented here provide new insight into the ecology of submarine canyons and of scavenging amphipods in the wider deep-sea environment. The primary study of scavenging amphipod assemblages of Iberian submarine canyons was augmented by studies on scavenging amphipods from the Mid-Atlantic Ridge and benthic megafauna communities from submarine canyons in Southern California. Data from scavenging amphipod studies throughout the North Atlantic were combined in a synthesis examining scavenging amphipod distributions.

Scavenging amphipods were more abundant and communities had lower evenness in submarine canyons compared to communities from non-canyons. This may be an effect of the high-nutrient canyon environment. Population analysis of *Paralicella caperesca* showed strong evidence for semelparity. Canyon cohorts had larger mean body lengths and expressed sexual characteristics earlier than their counterparts from non-canyon environments. This is thought to be due to the increased food availability in submarine canyons, a hypothesis supported by population analysis of *Abyssorchomene abyssorum* populations under differing trophic conditions at the Mid-Atlantic Ridge. Cohorts of female *A. abyssorum* from north of the Charlie-Gibbs Fracture had consistently smaller average body lengths than those from the more-productive south.

The effects of depth on community composition were observed in benthic megafauna of the Southern Californian submarine canyon systems, surveyed using video survey techniques. The synthesis of studies of scavenging amphipod communities of the North Atlantic revealed the wide environmental tolerance of common scavenging amphipod species. Significant differences in community composition were seen between abyssal plains and between depth zones, the possible reasons for this are discussed.

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Dedicated to the memory of the 379 268 amphipods
that gave their lives that this thesis might live.

Chapter 1

Introduction

> "…the remarkable diversity of deep-sea fauna is difficult to explain and continues to challenge contemporary ecological and evolutionary theory…"
>
> Etter et al. (2005)

The deep-sea environment was once thought to be a homogenous expanse with limited disparity across space and time (Christiansen, 1996) but we now know this to be untrue. The variance seen both temporally and spatially within the deep-sea is well documented in literature (see Gage & Tyler, 1991; Rex & Etter, 2010, for comprehensive reviews). Instead of being a large homogenous expanse, the deep sea comprises of numerous environments ranging from hydrothermal vents and cold-seeps, housing chemosynthetic organisms, to the continental margins, which are reliant on organic carbon inputs from the overlying surface waters. Such heterogeneity results in a plethora of unique and interesting environments being found in the deep sea, each with the potential to house distinct faunal assemblages and unique ecosystems.

In the past the deep sea was believed to have a very low biodiversity but more in-depth research has demonstrated that the deep sea has surprisingly high levels of biodiversity, at least on a local scale (Grassle & Maciolek, 1992; Hessler & Sanders, 1967; Rex & Etter, 2010; Sorbe, 1989). Some estimates place deep-sea biodiversity at levels far above those of shallow seas and traditionally diverse areas such as tropical rainforests (Grassle & Maciolek, 1992), although this claim is highly controversial (Gray, 1997; Rex & Etter, 2010). One synthesis of nematode diversity data identified that while local diversity of this taxon in deep-sea sediments is high, regional diversity is modest in comparison to shallower marine environments (Lambshead & Boucher, 2003). There is great variation in biodiversity of deep-sea environments with both depth and latitude (Bett, 2001; Etter et al., 1999; Hecker, 1990, 1994; Howell et al., 2002; Levin et al., 2001, 2000; Rex, 1981), however the highest levels of biodiversity are frequently observed in the benthos (Angel, 1993; Hessler & Sanders, 1967). Coastal and bathyal regions have been found to contain elevated levels of biodiversity in comparison to non-coastal regions, this is most probably a result of the higher numbers of small-scale habitats causing increased heterogeneity (Etter et al., 2005; Gray, 1997).

The bathymetry of the deep sea may influence biotic and abiotic factors that increase local biodiversity and drive divergence and speciation via selective and nonselective processes (Etter et al., 2005; Grassle & Sanders, 1973). The relative temporal stability of the deep-sea environment may also have contributed further to the development of the heightened biodiversity observed in the deep sea (Sanders, 1968), limiting the number of environmental bottlenecks that greatly reduce diversity in other environments (Etter et al., 2005).

Regional biodiversity in the deep sea is difficult to assess and cannot be easily extrapolated from our current knowledge of local diversity (Rex & Etter, 2010). Patterns of biodiversity vary greatly across oceans and between taxonomic groups however one common pattern of deep-sea biodiversity is that of the diversity-depth pattern (Bett, 2001; Hecker, 1990, 1994; Howell et al., 2002; Levin et al., 2001, 2000; Rex, 1981). This demonstrates that the majority of taxonomic groups follow a trend of increasing biodiversity with depth as one progresses toward the bathyal zone, where biodiversity peaks and begins to decline towards the abyss. This unimodal pattern, with low diversity in the abyss, is thought to be a result of low population densities negatively affecting species richness (Rex & Etter, 2010). Some authors have suggested this pattern may be an artefact of the Mid-Domain Effect (Colwell & Lees, 2000; Colwell et al., 2004), whereby geometric constraints, rather than physiological limits, cause a peak in richness in mid-domains. The effects and existence of the Mid-Domain effect are both poorly understood and greatly debated (Hawkins et al., 2005; McClain & Etter, 2005).

Past studies of deep-sea biodiversity have focussed primarily on the European and North American margins due to the concentration of research institutes in these regions and ease of access from the coast (Bailey et al., 2007). Once the region of study has extended, with efforts targeting other regions, one would expect our understanding of deep-sea biodiversity to be greatly improved. It is also expected that a further understanding of the genetic component of biodiversity will yield higher levels of deep-sea biodiversity (Etter et al., 1999).

1.1 Productivity in the deep sea

One of the defining aspects of the deep-sea environment is the lack of direct solar input. Owing to the attenuation of light in water sunlight dissipates rapidly with increasing depth (Beer, 1852; Gage & Tyler, 1991; Lambert, 1760). Although the depth of sunlight penetration is highly variable dependent upon water turbidity, even in the open ocean no sunlight reaches deeper than the upper 1 000 m of the water column (Gage & Tyler, 1991). This isolation from any solar radiation means that deep-sea ecosystems are driven by productivity systems that differ substantially from their shallow-water and terrestrial counterparts. Primary productivity via photosynthesis is almost non-existent in the deep sea and a range of deep-sea ecosystems are supported by chemosynthetic primary producers with no reliance on solar radiation (Corliss et al., 1979; Jannasch & Wirsen, 1979; Lonsdale, 1977). Many other deep-sea ecosystems are less isolated from photosynthesis driven production. The reliance of input from overlying surface waters is a common feature in the majority of ecosystems below 1 000 m (Jannasch & Taylor, 1984) and as such most deep-sea environments are less isolated from their overlying surface waters than was previously theorised (Drazen et al., 2012; Ruhl & Smith, 2004). Dependence on nutrient input from above does however result in relatively poor nutrient conditions across a large area of the deep sea, with patches of high productivity providing localised nutrient hotspots.

1.1.1 Primary productivity

Of all the currently known deep-sea ecosystems, hydrothermal vents and cold seeps have garnered the most interest and attention because of their complete independence from sunlight-driven production (e.g. Beatty et al., 2005; Kelley et al., 2001; Lonsdale, 1977; Ramirez-Llodra et al., 2010; Sheader et al., 2000; Van Dover et al., 1996; Vetter &

Smith, 2005; Weaver et al., 2009; Yurkov et al., 1999). While there is limited evidence for photosynthesis at hydrothermal vents (Beatty et al., 2005; Van Dover et al., 1996; Yurkov & Beatty, 1998; Yurkov et al., 1999), primary productivity in the deep sea relies almost exclusively on chemosynthesis. Chemosynthetic primary production utilises the oxidation of hydrogen gas (H_2), hydrogen sulphide (H_2S), ammonia (NH_3), or methane (CH_4) as an energy source for organic carbon fixation (Jones et al., 1983; Sorokin, 1964).

Chemosynthesis is carried out by bacteria, often as part of a symbiosis with larger fauna such as siboglinid tube worms (Cavanaugh et al., 1981; Felbeck, 1981; Gage & Tyler, 1991; Thornhill et al., 2008) and *Rimicaris* shrimp (Petersen et al., 2010; Van Dover et al., 1988). Due to the need for a reducing energy source, chemosynthetic systems are limited in their distribution by the location of physical features in the deep sea that provide an ample supply of hydrogen gas, hydrogen sulphide, ammonia, or methane. Tectonically active areas provide sites for the most characteristic deep-sea chemosynthetic communities with hydrothermal vents found on active ocean ridges around the world (VENTS programme, PMEL, NOAA, USA). Beyond these areas of geothermic activity other sources of energy utilised by chemosynthetic organisms include cold-seeps, gas-hydrates, and methane seeps (Gage & Tyler, 1991; Ramirez-Llodra et al., 2010; Vanreusel et al., 2010). Areas of chemosynthetic primary production in the deep sea are very much hotspots of production in this usually low-nutrient environment.

1.1.2 Secondary production

Secondary production is the incorporation of biogenic energy stores into heterotrophic organisms (Soliman & Rowe, 2008), where the energy source is effectively recycled carbon from detrital sources (Jannasch & Taylor, 1984). With primary productivity in the deep sea limited to a few specific hotspots, heterotrophic organisms feeding on input from surface waters form the basis of a large majority of deep-sea ecosystems. The nutrient input to the the deep sea is patchy and dictated by variations in local oceanographic conditions, surface productivity, and sea floor topography. As such, there are areas of low secondary production and hotspots of high secondary production which are now of interest to deep-sea ecologists. In recent years an increasing number of studies have focused on other areas such as submarine canyons, non-vent mid-ocean ridge areas, continental slopes, and cold-water reefs. In the North Atlantic, research on these areas of the deep sea have been primarily driven by the EC-funded HERMES (Hotspot Ecosystem Research on the Margins of European Seas; Weaver & Gunn, 2009) and HERMIONE (Hotspot Ecosystem Research and Mans Impact on European Seas; Weaver et al., 2009) projects.

The particulate organic carbon (POC) that eventually reaches the deep sea reflects the productivity of the associated surface waters (Drazen et al., 2012; Johnson et al., 2007; Lutz et al., 2002; Ruhl & Smith, 2004). This means that the POC input to deep-sea ecosystems varies both spatially and temporally, with climate events such as El Niño having a noticeable effect down to at least abyssal depths ($>$ 4 000 m deep; Ruhl & Smith, 2004). This mirroring of surface-water productivity also means that there is some degree of seasonality in the deep sea. Coupling between surface productivity and deep-sea secondary production results in hotspots with heightened secondary production. These hotspots can be areas located under highly productive surface waters or may be areas where down-falling material is concentrated owing to oceanographic and topographic conditions.

1.2 Submarine canyons

Shepard & Dill (1966) identified eight different types of submarine valley, only one of which they considered to be a ‘true’ submarine canyon. ‘True’ submarine canyons are said to resemble terrestrial valleys with a V-shaped profiles and high, steep walls with rocky outcrops. They generally have meandering courses and numerous tributaries incised into the continental shelf. Examples of typical submarine canyons are the Nazaré Canyon, off the coast of Portugal, the Monterey Canyon, off the Californian coast, and the Tokyo Canyon at the entrance to Tokyo Bay. Canyon categories are broad and by no means discrete, with the identification of several hybrid canyons. However, quantitative classification of canyon systems, as proposed by Goff, 2001, is complicated and rarely applied in practice.

Due to their position on the shelf, submarine canyons intercept a large proportion of the sediment that is laterally transported along the continental shelf (Cúrdia et al., 2004). Canyons, such as Nazaré Canyon, Portugal, which penetrate almost the entire width of the continental shelf, intercept a greater amount of sediment than those with reduced shelf penetration (Van Weering et al., 2002). This sediment interception results in almost all canyons having very high levels of organic matter. Like continental margins, the amount of organic matter found within canyons depends upon the production of associated surface waters. Macrophyte communities, such as the kelp forests found near the Californian canyons, contribute substantially to the total organic matter entering the canyon system (Vetter & Dayton, 1998).

The high levels of organic matter that accumulate in submarine canyons result in increased food for resident detritivores (Sorbe, 1999) making them hotspots of secondary production (De Leo et al., 2010; Gage & Tyler, 1991; Jannasch & Taylor, 1984; Soliman & Rowe, 2008; Van Oevelen et al., 2011; Vetter, 1995). The heightened levels of secondary production within canyons may have resulted in the development of distinct faunal assemblages with high faunal and biomass densities relative to other deep-sea ecosystems at comparable depths (Ormond et al., 1999). Organisms that are able to alter their feeding strategies and take advantage of any feeding opportunities that may arise generally thrive in the unpredictable canyon environment (Cúrdia et al., 2004). Canyons not only catch sediment but also channel it down from the continental shelf to the abyssal plain. Although inactive canyons have little role in sediment transportation, active canyons act as vital conduits for organic matter, expediting its movement from the continental shelf to the abyssal plain (Vetter & Dayton, 1998). This channelling of falling sediment, from gentle ‘rain’ into torrential ‘rivers’, provides a substantial supply of organic carbon to the abyss.

Episodic events, although rare, have the potential to impact the environment within the canyon on both short and long-term scales (Griggs et al., 1969; Okey, 1997). The most commonly occurring canyon events are submarine landslides and the associated turbidity currents (Nisbet & Piper, 1998); these can be caused by a number of factors, such as earthquakes (Garfield et al., 1994), storms, cyclic loading, and under-consolidation of sediments (Terrinha et al., 2003). There is also some evidence to suggest that the presence of gas hydrates (Nisbet & Piper, 1998), changes in sea level (Weaver et al., 1992), and trawling at canyon heads (Puig et al., 2012) may also cause or contribute to landslides within submarine canyons. The Great Lisbon Earthquake of 1755, which measured an estimated 9 on the Moment Magnitude scale, has been linked to historical landslide scars found within the Nazaré canyon off of Portugal’s west coast (Koho et al., 2007; Thomson & Weaver, 1994).

1.3 Scavenging in the deep sea

Organisms in the deep sea have adopted a range of foraging and feeding strategies in order to survive. One such strategy is that of scavenging, relying upon falls of carcasses from overlying surface waters as a means of sustenance. Large food falls are a valuable energy source in the deep sea. The arrival of carcasses to the deep-sea floor provides a concentrated input of energy to areas that generally experience low organic matter supply (Klages et al., 2003). In spite of recent advances in deep-sea exploration, naturally occurring food falls are rarely observed (Klages et al., 2001; Smith & Hessler, 1987; Soltwedel et al., 2003; Stockton & DeLaca, 1982). This is primarily a result of the unpredictability of food falls in time and space and rapid consumption by scavengers resulting in a short residence time (Stockton & DeLaca, 1982), although residence time varies greatly depending on size and type of carrion (Lampitt et al., 1983). A limited number of naturally occurring whale carcasses have been found by chance (Amon et al., 2013; Soltwedel et al., 2003), in particular along known migration routes (Smith et al., 1989), however the majority of studies on scavenging fauna rely upon the artificial placement of food falls (Britton & Morton, 1994; Jones et al., 1998; Kemp et al., 2006; Klages et al., 2001; Smith et al., 1989).

The use of scavenging as a feeding strategy has been documented to varying degrees in many taxa inhabiting the deep sea. The abundance of highly motile scavengers within the deep sea is a testament to their abilities in rapidly locating and consuming food falls soon after their arrival (Dayton & Hessler, 1972). In areas with high densities of motile scavengers, less motile organisms rarely reach new food falls in time to sufficiently capitalise upon the resources that they provide. Due to their reliance on food falls, scavenger populations are not thought to be evenly distributed. Aggregations of scavengers form in areas with more frequent large food falls (Isaacs & Schwartzlose, 1975). While sightings of carcasses in the deep sea are rare, macrophyte detritus is frequently observed during photographic and video surveys of the deep-sea benthos. The use of landers baited with macrophyte material has demonstrated that at least some scavenging species of fish (Jeffreys et al., 2010) and amphipods (Lawson et al., 1993) will attend such vegetation-falls. Enzymes recovered from the guts of deep-sea scavenging amphipods imply the ability to assimilate nutrients from plant matter (Kobayashi et al., 2012).

Scavenging organisms are of particular importance in the deep sea where they play a pivotal role in the degradation and distribution of organic matter (Christiansen & Diel-Christiansen, 1993; Smith & Baco, 2003). In the deep sea primary production is limited to a few very specific locations, such as cold seeps and hydrothermal vents, and food supply is often a limiting factor (Dayton & Hessler, 1972). As detritivores, scavengers reintegrate organic carbon from food falls into the deep-sea food web. This makes it available for other deep-sea organisms that subsequently prey upon them. Research focussing on the dumping of radioactive waste into the deep sea highlighted the central role played by scavengers in deep-sea food webs, connecting trophic levels and driving secondary production (Figure 1.1; Charmasson & Calmet, 1989). This secondary production is vital in deep-sea food webs with scavengers acting as a mediator, facilitating energy transfer across trophic boundaries from carcasses to organisms in the upper trophic echelons (Payne & Moore, 2006).

Scavengers also act as a means of dispersal of deep-sea food falls. While the majority of nutrients will benefit a very localised area in the immediate vicinity of the fall, faeces and moults from scavengers attending the fall will result in enrichment of a wider area once feeding activity has ceased and scavengers begin to disperse (Jones et al., 1998). Although wide-spread enrichment is comparatively low compared to the enrichment at the site of the original fall, in the relatively energy poor environment of the deep sea it will still most likely provide a substantive augmentation of organic carbon (Stockton & DeLaca, 1982).

1.3.1 Scavenging amphipods

Of all of the scavenging organisms, members of the order Amphipoda (Crustacea, Malacostraca) are some of the most abundant and successful scavengers in the deep sea. Evidence suggests that scavenging has independently evolved on numerous occasions within this order (Dahl, 1979; De Broyer et al., 2004). With the exception of the Mediterranean Sea where scavenging activity is anomalously low (Dumser & Türkay, 2008; Jones et al., 2003), scavenging amphipods are almost always found within baited traps upon their retrieval from deep-sea deployments. Barring a few isolated examples (Fujii et al., 2010), exclusively amphipods are found at food falls in the deepest locations (Hessler et al., 1978).

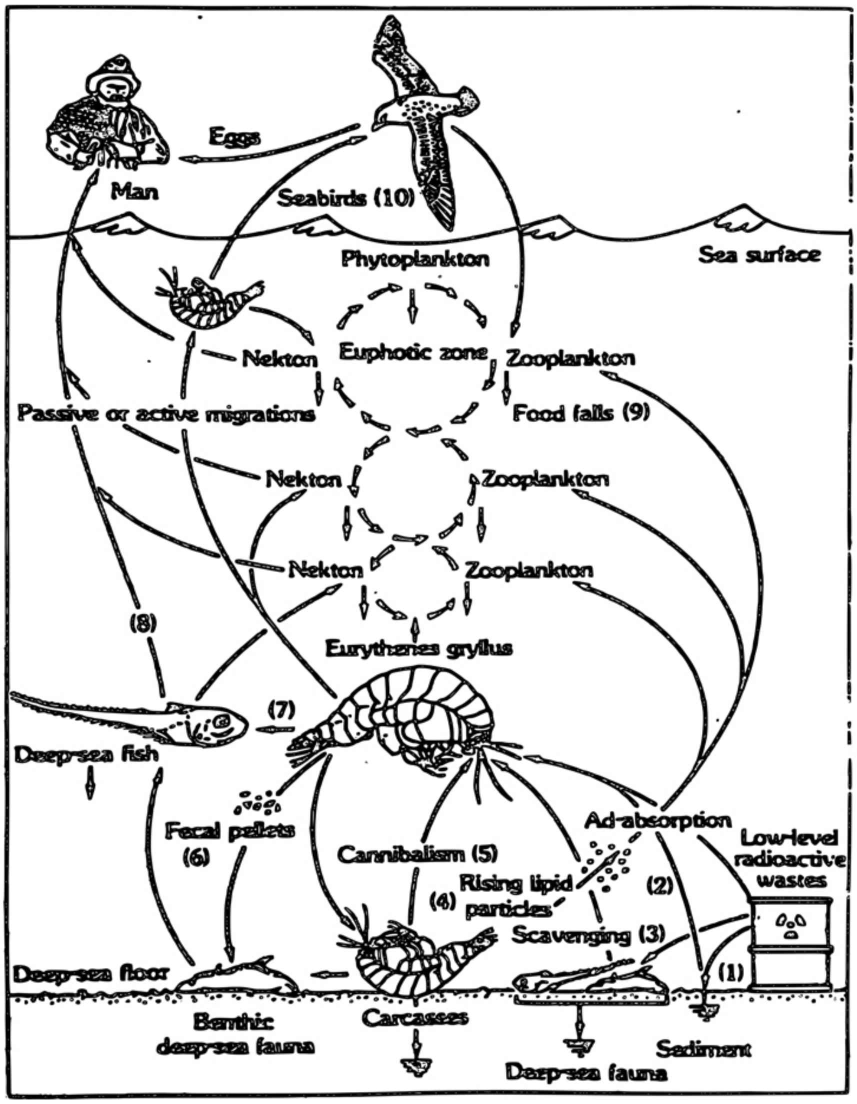


FIGURE 1.1: Theoretical pathway by which radionuclides could be transferred from deep-sea nuclear dumping grounds into the wider marine food chain via the vector *Eurythenes gryllus*. From Charmasson & Calmet, 1989.

Most amphipods recovered from baited traps belong to the super-family Lysianassoidea, containing the largest amphipod family Lysianassidae (De Broyer et al., 2004). Lysianassoids are one of the most abundant and ubiquitous macro-invertebrate groups in the marine environment (Slattery & Oliver, 1986). Many lysiannasoid species have cosmopolitan distributions, with little evidence to suggest that endemism occurs in geographically separated abyssal plains (Thurston, 1990). Some species, such as *Eurythenes gryllus* Lichtenstein, 1822, have been found in all of the world's oceans at a wide range of depths (De Broyer et al., 2004), although recent evidence suggests *E. gryllus* represents a species complex divided by depth (Havermans et al., 2012).

The success of scavenging amphipods is undoubtedly a result of a number of behavioural, anatomical, and physiological adaptations that they possess in order to capitalise on the limited resources available in the deep sea (Jannasch, 1978). Although there are still substantial gaps in our knowledge of some of these adaptations, a number of studies have been completed that give at least a basic understanding of what makes scavenging amphipods so successful in the deep sea.

The anatomical and physiological adaptations of lysianassoid amphipods provide them with an arsenal of sensing abilities in order to detect and localise food falls and the stimuli associated with them. It is believed that scavenging amphipods rely on three main receptor systems detecting mechanical, chemical, and photic stimuli (Dahl, 1979; Hallberg et al., 1980; Smith & Baldwin, 1984) in order to locate food falls, although only two of these stimuli are likely to be found in the deep sea. As well as detecting stimuli produced by the food fall itself, amphipods may also utilise these sensing systems to detect the presence of conspecifics already attending the fall. *Ex situ* experimentation indicates that these gregarious organisms rely on the presence of other amphipods over direct cues when making nearfield foraging decisions (Ingram & Hessler, 1983). Each sensing system has its own merits and limitations of usage within the deep-sea environment.

1.3.1.1 Detecting a food fall

Within crustaceans, chemoreception is the most studied of the three main sensory systems (Atema, 1986; Vanleeuwen & Maly, 1991; Yen et al., 1996). Chemosensing is also believed to be the system that scavenging amphipods rely upon the most when attempting to locate a food fall (Premke et al., 2003). The primary apparatus for chemoreception by amphipods is located on the antennae within sensing organs called callynophores. These are composed of aesthetascs, dense arrays of small hair-like projections covered in numerous chemosensing neurones (Kauffman, 1994). The dispersal of chemical stimuli from the site of the food fall is dependent upon local currents affecting the direction and distance that an odour plume can travel. Dissolved chemicals originating from the food fall track local fluid conditions (Vickers, 2000). Following the trail created by these plumes upstream (Bozzano & Sardà, 2002; Busdosh et al., 1982; Thurston, 1979), organisms with a chemosensing ability are able to respond to and locate food falls upon their arrival on the seabed.

Ex situ tests using both fish broth and isolated amino acids have demonstrated that both can act as feeding stimuli (Ide et al., 2006; Meador, 1989). This suggests that amino acids are the primary attractant of a food fall. When certain peptides are also present there is a potent synergy effect, which causes a heightened behavioural response (Ide et al., 2006). The cocktail of chemical stimuli released by a food fall solicits more of a response than free amino acids that may come from other sources. Individuals raised in an environment with reduced background levels of amino acids are particularly sensitive when exposed (Ide et al., 2006). This may mean that deep-sea scavengers have a heightened sensitivity to amino acids in nutrient poor areas.

Detecting chemicals associated with food falls also carries the potential to provide vital information regarding the quantity and quality of food available (Rittschof, 1980; Zimmer-Faust & Case, 1982). The ratio of amino acids to ammonia decreases with decomposition and bottom time of a food fall, and could be used to determine the current nutritional value of the fall (Zimmer-Faust, 1987). It is currently unknown whether scavenging amphipods use this information to preferentially attend food falls based upon their distance and the quality of food on offer (Premke, 2003). Previous studies have shown a rudimentary preference of scavenging fauna towards carcasses of round fishes over those of flat fishes or elasmobranchs (Jannasch, 1978; Witte, 1999). This is most probably due to the softer tissues of this bait type and not necessarily reflective of a preference based on chemical cues but rather the ease of assimilation upon arrival. There is some evidence to suggest that shallow water scavenging amphipods show a more specialised degree of bait preference (Moore & Wong, 1995; Morritt, 2001), but it is not known if deep-sea scavenging amphipods practice such prejudice when a low quality food source may be the only food source available.

The relative density of water means that sound is capable of travelling much faster and further than it does in air. This makes the use of sound to navigate a worthwhile endeavour for many marine organisms. The ability of amphipods to detect and interpret acoustic stimuli has been tested to a very limited degree. It is theorised that acoustic cues signalling a food fall could arise from either the initial impact of the fall onto the seabed (Klages et al., 2002) or via the feeding activity of scavenging organisms already attending the fall (Smith & Baldwin, 1984).

While a fall can be detected at great range, there is little evidence that amphipods can determine location or distance using acoustic stimuli alone (Klages et al., 2002), searching for a food fall without the necessary information could result in wasting resources trying to reach distant food falls or falls of indeterminate location. For this reason it is theorised that scavenging amphipods utilise acoustic signals to indicate the arrival of a food fall and then more accurately assess and locate it using chemical cues (Premke, 2003).

Most deep-sea scavenging amphipods possess functioning eyes (Bowman & Manning, 1972) and bioluminescent bacteria have been associated with food falls (Gillibrand et al., 2006). However, there is currently no substantive evidence to either support or oppose the theory that scavenging organisms in the deep sea use visual cues to aid their foraging efforts.

1.3.1.2 Reaching a food fall

Identifying the location of a food fall is of little use unless a scavenger is able to reach the site of a fall while it still has sufficient nutritional value. The anatomy of many deep-sea scavenging amphipods is well developed to facilitate swimming and increase mobility (Boudrias, 2002). *Eurythenes gryllus* has been observed swimming at speeds in excess of 18 cm s^{-1} (Laver et al., 1985), the equivalent of a 182 cm ($\sim$ 6 feet) tall human swimming at 25 km h^{-1}. This mobility allows scavenging amphipods to take full advantage of the heightened sensing ability awarded by their physiological adaptations.

The mean swimming speed of *E. gryllus* has been recorded as 8.05 cm s^{-1} (Laver et al., 1985), but other species have been recorded as having far lower swimming speeds (*P. caperesca*, Chevreux, 1908, 2.46 cm s^{-1}; *Orchomene* sp. Kröyer, 1846, 3.06 cm s^{-1}; Smith & Baldwin, 1982). This variance in speed could be due to a number of factors including body size, morphology, water temperature, testing conditions, and level of excitation.

1.3.1.3 Feeding and food storage

Scavenging amphipods have adopted a number of notable feeding behaviours in order to capitalise on any food that is available. Some lysianassoids are thought to be obligate scavengers, relying on large food falls as their sole food source, while others are facultative scavengers, turning to scavenging when required or when an opportunity arises (Klages et al., 2001; Sainte-Marie, 1984; Sainte-Marie et al., 1989). While it was once believed that obligate scavenging was infeasible in the marine environment (Britton & Morton, 1994), models using even the most conservative estimates have suggested otherwise (Ruxton & Bailey, 2005; Ruxton & Houston, 2004). The majority of these obligate scavengers follow a bingeing strategy, consuming as much food as possible as quickly as possible. This takes advantage of resources if and when they become available and allows for maximum exploitation of large food falls.

The behavioural adaptations of scavenging lysianassoids would be of little use without the anatomical adaptations required in order to practice bingeing behaviour (Dahl, 1979; Smith & Baldwin, 1982). Obligate scavengers are equipped with mandibles designed for shearing, with a broad, sharpened incisor (De Broyer et al., 2004; Steele & Steele, 1993) and enlarged *corpus mandibulae* (Shulenberger & Barnard, 1976). They also possess guts capable of growing 3-5 times their usual size to accommodate large meals (Figure 1.2; Dahl, 1979), taking on a bloated appearance (Shulenberger & Barnard, 1976). Large guts allows the practice of a ‘batch reactor’ mode of feeding, where large meals are consumed and processed as one discrete action with food evenly distributed throughout the gut (Hargrave et al., 1995; Shulenberger & Barnard, 1976). This ensures organisms are ready to consume large amounts of matter when the next food fall arrives. Coupled with a high assimilation efficiency, demonstrated by empty guts but little defecation following feeding (Hargrave et al., 1995), this mode of feeding allows obligate scavengers to make the most of what food is available. This in turn reduces foraging time requirements and the associated risk of predation (Kaïm-Malka, 2003).

Once a food fall has been successfully located, consumed, and assimilated, nutrients are stored as lipids within the body (Smith & Baldwin, 1982; Wirsen & Jannasch, 1983). The next challenge facing scavenging scavenging amphipods is surviving until the next meal arrives. To do this scavenging amphipods have adopted a metabolic strategy that is adaptive based upon food availability. Between meals, many species of

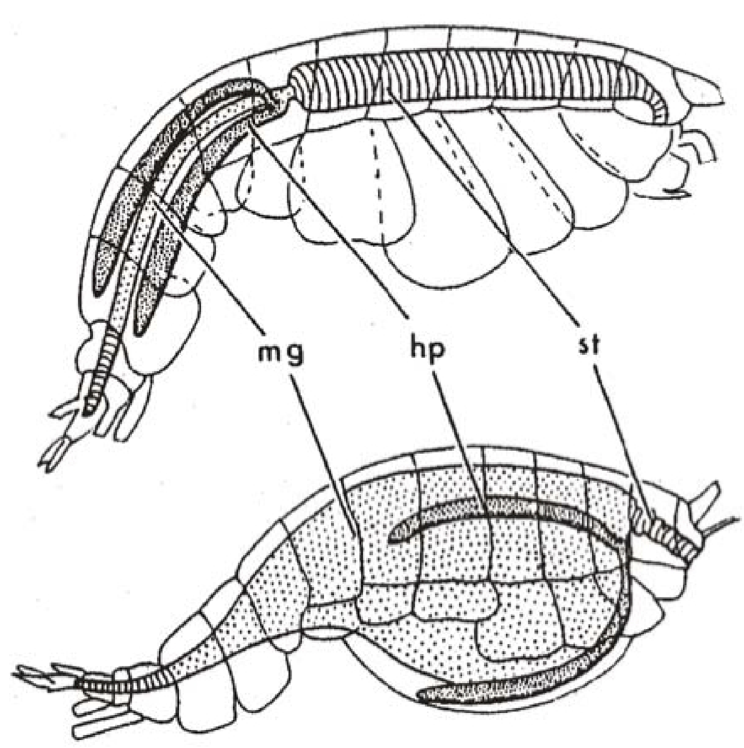


Figure 1.2: Diagrammatic sketch of modification of the intestinal tract for food storage in lysianassoid amphipods. Above; *Orchomene* with non expandable midgut, Below; expandable midgut storage as found in *Eurythenes gryllus*, *Paralicella* spp., and *Hirondellea* spp.. mg = midgut, hp = hepatopancreatic caeca, st = stomodaeum. From Premke, 2003, modified from Dahl, 1979.

scavenging amphipod enter a resting stage with decreased metabolic activity, respiration, and oxygen consumption (Christiansen & Diel-Christiansen, 1993; Smith & Baldwin, 1982).

A period of dormancy, when amphipods depend wholly upon their lipid reserves for sustenance (Chapelle et al., 1994), dramatically extends the period of time that they are able to survive before the next meal arrives (Premke & Graeve, 2009). The length of extension that this rest period affords varies from species to species and is tied to body size (Premke & Graeve, 2009). Upon detection of chemical cues from a new food fall, the resting stage is substituted with an active stage with an increased rate of oxygen consumption (Atema, 1998; Carr, 1988) and a metabolic regime more suited to actively searching for food falls (Smith & Baldwin, 1982). When exposed to chemical cues produced by living individuals this searching response is not observed (Tamburri & Barry, 1999).

1.3.2 Sampling Methodology

The lack of knowledge about the behaviour and ecology of deep-sea scavenging amphipods is in part due to the inherent difficulties associated with studying any deep-sea organisms (Gage & Tyler, 1991). The difficulties of deep-sea sampling are exacerbated by the mobility and small size of many amphipod species. Heightened mobility makes scavenging amphipods difficult to catch using towed trawls or more modern techniques such as remotely operated vehicle (ROV) surveys. Deep-sea trawling, a technique that is often used in studies on many organisms inhabiting the abyssal plain and continental shelf, is impractical for the sampling of deep sea scavenging amphipods and produces poor yields (Christiansen & Martin, 2000). Some highly motile organisms are able to escape trawls (Thurston, 1990). Trawling is also impractical and potentially destructive when targeting sites with complex topography such as submarine canyons (Farnsworth et al., 2007; Harvey et al., 2007). Remotely operated vehicles provide an extremely flexible option for imaging and sampling the deep sea but their prohibitive cost and limited sampling capacity make them a poor choice for sampling large numbers of small organisms.

Priede & Merrett (1998) suggested baited landers, with either cameras or traps affixed, as an alternative to trawling in deep-sea canyons. The use of baited landers provides at least an elementary level of understanding of submarine canyon ecology. Via the exploitation of their natural feeding behaviour (Legezynska et al., 2000), this method allows for the capture and study of large aggregations of scavenging organisms residing within the wider vicinity of the trap (Bailey et al., 2007; Jamieson et al., 2006). Baited traps can be used to obtain a snapshot of deep-sea scavenging amphipod communities. Sampling in understudied areas, such as submarine canyons and mid-ocean ridges, can provide us with important information regarding diversity, distribution, and abundance of these important deep-sea organisms.

1.4 Aims and objectives

The overarching aims of this research are to further our understanding of submarine canyon ecology and add to our knowledge of scavenging amphipod ecology and life histories. This increased understanding of deep-sea ecology can be achieved through the completion of a number of objectives examining the various aspects of this complex ecosystem. These objectives are:

- Identify the species composing scavenging amphipod communities in submarine canyons of the Iberian Peninsula and compare communities of scavenging amphipods from submarine canyons with those of the adjacent abyssal plains.
- Identify if the canyon environment affects the structure of populations of scavenging amphipods and determine if differing trophic conditions can alter the population structure of deep-sea scavenging amphipods.
- Use multivariate statistics to identify which environmental factors impact scavenging amphipod community composition in the North Atlantic and apply existing statistical models to identify the factors affecting taxon-level distributions in order to produce habtat suitability maps for scavenging amphipod taxa found in the North Atlantic
- Identify factors affecting benthic megafauna distributions within deep-sea submarine canyons.

Chapter 2

Deep-sea scavenging amphipod communities from submarine canyons of the Western Iberian Peninsula

2.1 Introduction

Large submarine canyons are complex, poorly understood, topographical features (Shepard & Dill, 1966). They experience heightened levels of sediment input, with active submarine canyons acting as downward conduits for matter that has been transported along the continental shelf (Vetter & Dayton, 1998). This effect is often amplified in the presence of contributory river systems (Cúrdia et al., 2004; Van Weering et al., 2002). Elevated sediment input carries with it substantial quantities of organic matter (Kiriakoulakis et al., 2011), providing food for deep-sea scavengers (Sorbe, 1999). Many submarine canyons have been identified as hotspots of secondary production (De Leo et al., 2010; Gage & Tyler, 1991; Jannasch & Taylor, 1984; Soliman & Rowe, 2008; Van Oevelen et al., 2011; Vetter, 1995). One section of the Nazaré Canyon, on the Iberian Peninsula, contains an estimated biomass of megabenthic invertebrates that is 2–3 orders of magnitude greater than that found on open slopes at similar depths (Van Oevelen et al., 2011). Biomass in the Kaikoura Canyon, off the coast of New Zealand is estimated to be an order of magnitude greater again (De Leo et al., 2010).

Scavenging organisms are particularly important in the deep sea (Britton & Morton, 1994). In an environment where food-supply is often a limiting factor, they play a pivotal role in the degradation and redistribution of organic matter (Christiansen & Diel-Christiansen, 1993). Scavengers breakdown, disperse, and reintegrate organic carbon from food-falls into the deep-sea food web via predator-prey interactions (Payne & Moore, 2006) and by faecal enrichment of sediments (Jones et al., 1998; Stockton & DeLaca, 1982).

Members of the order Amphipoda (Crustacea, Malacostraca) have been found to be some of the most abundant and successful scavenging organisms in the deep sea (De Broyer et al., 2004; Hessler et al., 1978). Morphological evidence suggests that scavenging has evolved independently on numerous occasions within this order, with the majority of scavenging amphipods being members of the super-family Lysianassoidea (Dahl, 1979; De Broyer et al., 2004; Lowry & Stoddart, 2009, 2011). Many deep-sea scavenger species have cosmopolitan distributions and there is little evidence of endemism in individual abyssal plain communities (Thurston, 1990). Some species, such as *Eurythenes gryllus* Lichtenstein, 1822 have been found in all of the World's oceans and over a wide range of depths (Christiansen et al., 1990; De Broyer et al., 2004). There is, however, a growing body of evidence to support the theory that discrete populations inhabit the Atlantic and Pacific oceans. The extent of this separation has yet to be determined with some indication that populations are on the verge of speciation (Thurston et al., 2002, and references therein).

Whole assemblages of scavenging amphipods in submarine canyons have been poorly studied and factors affecting the composition of these communities are yet to be identified. Previous studies of scavenging amphipods from canyon systems have focused on single species collected from relatively shallow deep-sea sites (e.g., Kaïm-Malka, 2003, 2004, 2005; Soliman & Rowe, 2008) . This study aims to determine if scavenging amphipod communities in submarine canyons differ from those in other locales and identify factors that may potentially be affecting community composition and species distributions. It is hypothesised that submarine canyons house scavenging amphipod communities that are significantly different to those of the abyssal plains and have the potential to house species that are new to science.

2.2 Methods

2.2.1 Study areas

Three submarine canyons on the Iberian Margin, off of the west coast of Portugal, were studied; Nazaré, Setúbal, and Cascais (Figure 2.1). All canyons in this study are situated on the Western Iberian Margin, off of the west coast of Portugal. This is reflective of the study areas targeted by the HERMES and HERMIONE projects.

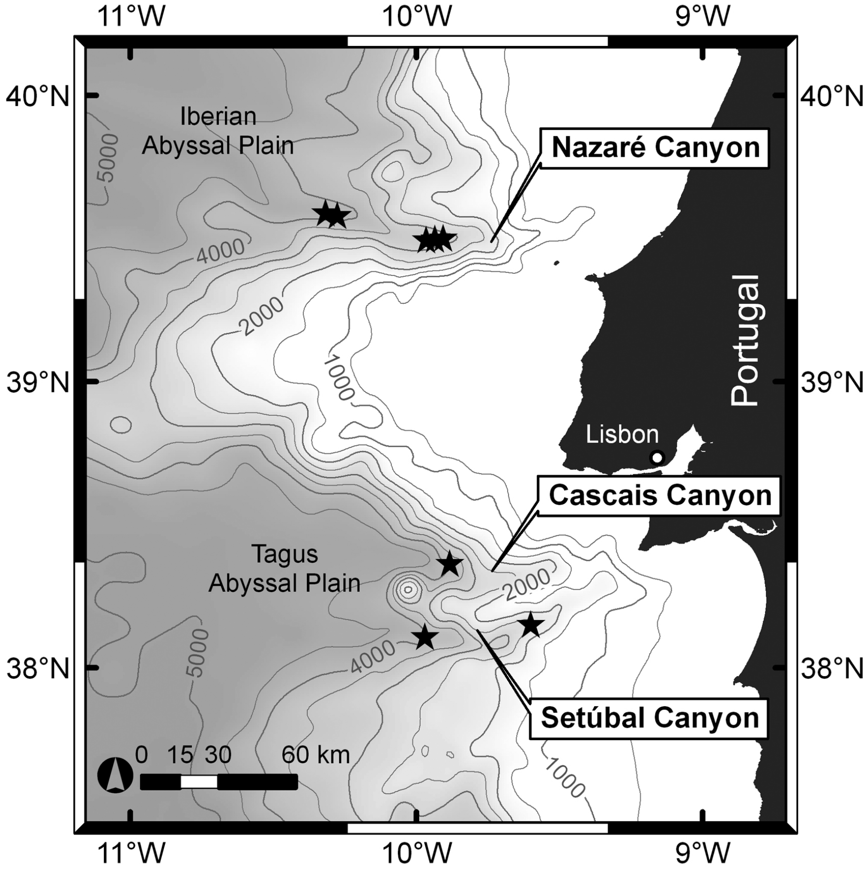


FIGURE 2.1: Map of Iberian Peninsula submarine canyon trap deployments as part of research expeditions RRS *Discovery* 297, RRS *Charles Darwin* 179, and RRS *James Cook* 010.

2.2.1.1 Nazaré Canyon

As one of the main target areas of the HERMES project, Nazaré is the most studied of all the candidate canyons, . Often referred to as the 'Grand Canyon' of the deep sea, the Nazaré Canyon is a huge submarine canyon approximately 210 km from head to mouth. The canyon extends westward away from the Portuguese Continental Margin (Tyler et al., 2009) toward the Iberian Abyssal Plain.

Nazaré Canyon is characterised by strong currents and a high degree of turbidity, especially towards the upper region of the canyon. Morphologically the canyon is composed of steep slopes, scarps, terraces, and overhangs. The substratum is a mix of rocks and sediments, ranging from sand to fine mud, in varying proportions (Tyler et al., 2009).

The upper canyon deeply incises the continental shelf to a depth of roughly 1000 m and continues away from the coast following an east-northeast to west-southwest direction (Arzola et al., 2008), while the middle and lower regions of the canyon follow an east to west path along the Hercynian Fault Zone (Tyler et al., 2009). The upper and lower regions are distinctly different to one another with the middle section sharing characteristics with both the upper and lower regions.

Both the upper and middle sections of the canyon have V-shaped profiles with a water depth that is less than 4000 m (de Stigter et al., 2007). The thalweg, an axial channel incised into the canyon floor, in these sections is relatively narrow at less than 100 m wide (Arzola et al., 2008). The topography of the upper and middle regions is rugged, gullies are common, and numerous semi-erosional scarps characteristic of submarine landslides are visible (Tyler et al., 2009). These landslides are most probably the result of external forcing such as earthquakes (Thomson & Weaver, 1994; Weaver et al., 2000), sea level rise, and increased sediment flux (Figure 2.2; Arzola et al., 2008).

Approximately 120 km from the canyon head, the main channel opens out to form a more U-shaped profile roughly 7.5 km wide and with an incline of 0.5°, this indicates the beginning of the lower region of the canyon, which is bordered by the Gil Vicente and Duarte Pacheco ridges. In this region the thalweg widens out to 500 m and the floor is covered in coarse gravel interspersed with large boulders. The main canyon channel is flanked by terraces sitting parallel to the canyon axis, these terraces form a depocentre, with sediment carried down the channel becoming deposited here (Tyler et al., 2009).

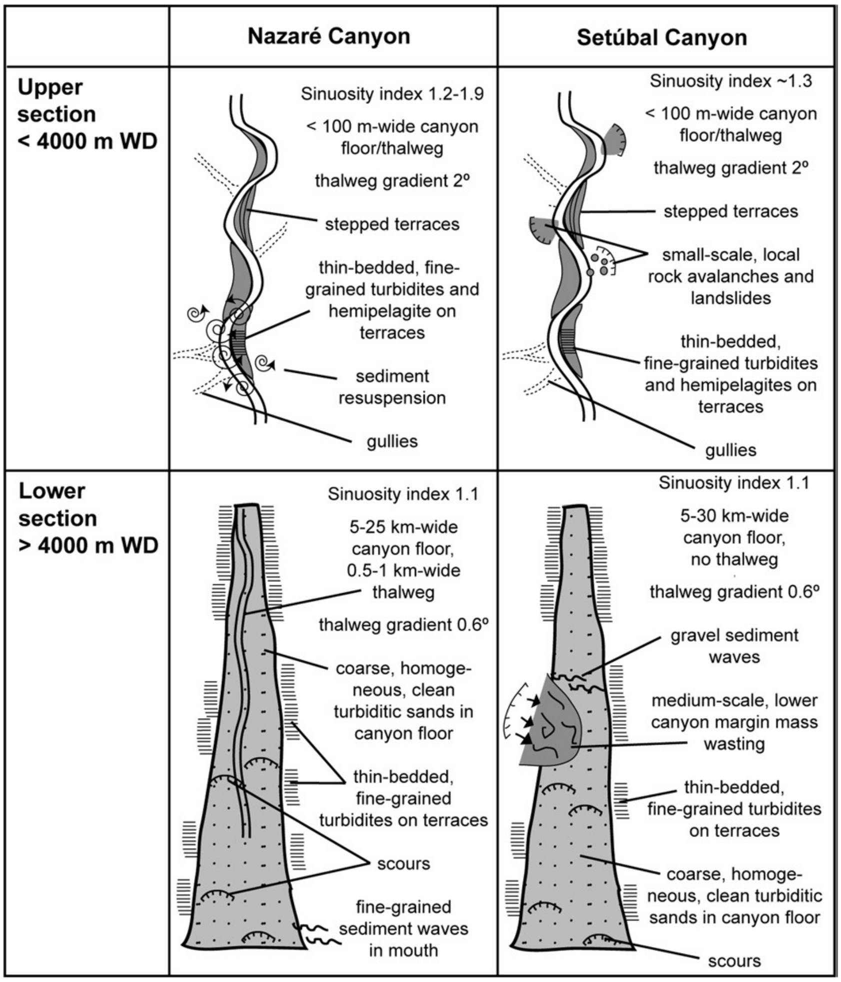


Figure 2.2: Cartoon summarising the main sedimentary features and processes that are observed in the upper and lower sections of Nazaré and Setbal Canyons. From Arzola et al., 2008.

Little sediment travels further down the canyon, creating a lower energy environment after these terraces (de Stigter et al., 2007).

2.2.1.2 Setúbal Canyon

The Setúbal-Lisbon Canyon is morphologically similar to the Nazaré Canyon with a main valley extending 175 km from the shelf toward the Tagus Abyssal Plain (Figure 2.2; Arzola et al., 2008). As the second largest canyon system on the Western Iberian Margin, the Setúbal-Lisbon Canyon is comprised of two canyons that converge at approximately 2000 m deep, the Lisbon Canyon being a major tributary of the Setúbal Canyon (Garcia et al., 2010).

Both canyons are fed by large river systems. The Sado River feeds directly into the Lisbon Canyon with the Tagus River feeding into the Setúbal Canyon. The upper regions of both canyons and the middle region of the Setúbal Canyon (less than 4000 m water depth) are characterised by steep, heavily gullied walls and narrow V-shaped channels (Garcia et al., 2010). A deep thalweg approximately 100 m wide incises the upper canyon-bed. Downstream, the lower Setúbal Canyon widens out to greater than 10 km with less steep walls and a U-shaped channel with no clear thalweg (Arzola et al., 2008).

2.2.1.3 Cascais Canyon

Cascais Canyon is one of the smaller submarine canyons on the Portuguese Margin and at 62 km from head to mouth it is the smallest target canyon of this study. There are three separate tributaries of the canyon, starting at approximately 175m water depth and eventually converging to form one main channel. The upper and middle sections of the canyon have a V-shaped valley with steep walls up to 1800 m high, the deeply incised thalweg is less than 100 m wide. As in the Setúbal-Lisbon and Nazaré Canyons the lower region widens out into a U-shaped channel with a flatter more rounded bottom (Arzola, 2008).

2.2.2 Sample collection

A total of eight baited trap deployments were made, five in Nazaré Canyon, two in Setúbal, and one in Cascais. Sampling occurred on three scientific research expeditions (RRS *Discovery* 297, RRS *Charles Darwin* 179, RRS *James Cook* 010) between August 2005 and June 2007 as part of the European HERMES (Hotspot Ecosystem Research on the Margins of European Seas) Project (Table 2.1). Samples were collected using a basic trap design comprising of a funnelled entrance leading into a container with bait attached inside. All deployments during D297 and CD179 utilised a free-fall lander frame with one trap at the base and one a metre above (Figure 2.3). Recovery was via an iXSea acoustic release attached to the frame alongside the trap. The JC010/094 deployment used two bottle traps placed on the seafloor and recovered using the remotely operated vehicle (ROV) *Isis*. All but one of the traps were baited with a single raw mackerel (*Scomber scombrus*) of approximately equal size. Trap CD179/56817 was baited with

Table 2.1: Trap deployments made within the Iberian Margin submarine canyons during research expeditions RRS *Discovery* 297, RRS *Charles Darwin* 179, and RRS *James Cook* 010. [1]Data from CTD casts deployed in the vicinity (< 2.5 km radius) of each baited trap; [2]averaged data from Cunha et al., 2011.

Canyon	Deployment	Duration hh:mm	Depth m	Latitude	Longitude	Temp.[1] °C	$[O_2]^1$ μmol l^{-1}	Sal.[1]	TOC[2] mg $g^{-}1$
Nazaré	JC010/094	43:16	3400	39.4983	-09.9367	2.63	252.20	34.93	18.3
	CD179/56855	23:02	3499	39.5027	-09.9050	2.63	252.20	34.93	18.3
	D297/15734	21:28	3600	39.4963	-09.9648	2.63	252.20	34.93	18.3
	D297/15741	24:22	4286	39.5825	-10.2750	2.49	258.20	34.90	18.2
	CD179/56847	24:34	4403	39.5917	-10.3167	2.49	258.20	34.90	18.2
Setúbal	CD179/56817	31:14	3194	38.1528	-09.6000	2.79	-	34.95	13.0
	CD179/56839	24:12	4445	38.1095	-09.9697	2.50	-	34.90	10.6
Cascais	CD179/56837	30:17	4230	38.3662	-09.8834	2.46	-	34.90	11.2

smoked fish fillets. Bait was wrapped in muslin cloth to limit incursion into the bait and facilitate recovery of amphipod specimens. Upon recovery, the contents of all traps were fixed in 4 % buffered formaldehyde-saline solution and subsequently preserved in 80 % industrial methylated spirits. Trap deployment and recovery was performed by Benjamin Boorman. Teresa Amaro and Teresa Madurell preserved unsorted samples upon trap recovery.

2.2.3 Sample analysis

All amphipods were identified to species level by the author using morphological characteristics viewed under a stereo dissecting microscope. Assistance with taxonomy and species identification was provided by Tammy Horton and Michael H. Thurston. Following sorting, counts of each species were taken. For the purposes of this study the contents of the two traps used in each deployment were analysed as a whole.

Statistical analyses were performed by the author. Abundance data were converted to percentage composition and square-root transformed. Standardisation using percentage composition allowed for comparison of different sized samples while square-root transformation reduced the skewing effect of highly dominant species. Bray-Curtis Similarity matrices (Bray & Curtis, 1957) were subsequently produced. A one-way analysis of similarities (ANOSIM; Clarke, 1993) was performed using PRIMER 6 (Plymouth Routines In Multivariate Ecological Research; Clarke & Gorley, 2006) statistical software to determine if community composition varied significantly between samples. A SIMPER

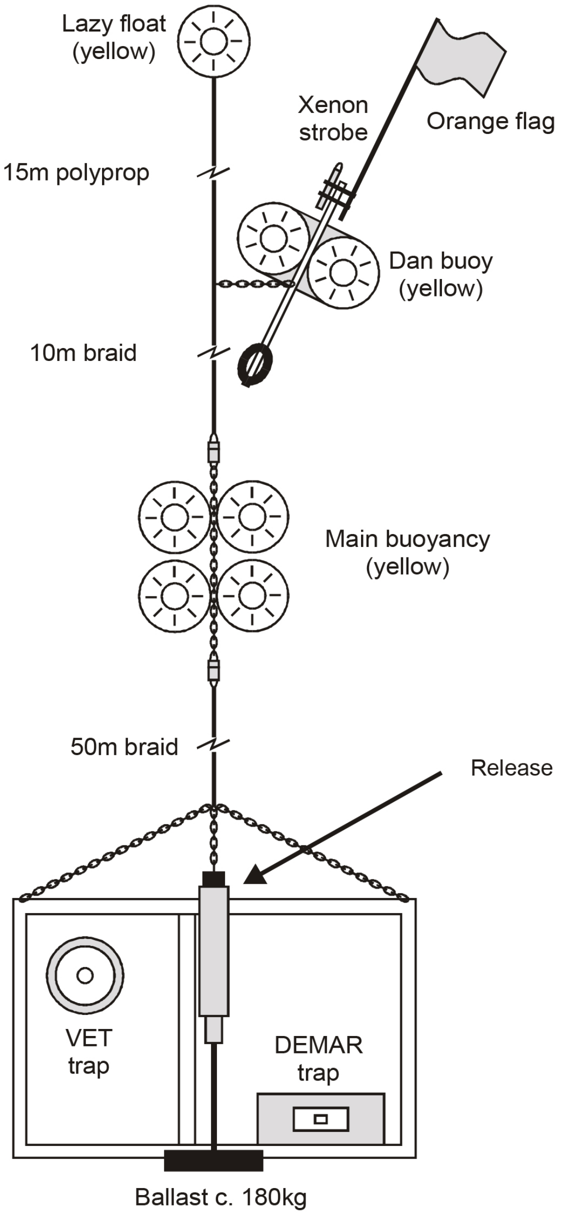


Figure 2.3: DEMAR/VET configuration amphipod trap (National Oceanography Centre, Southampton, UK) and mooring arrangement as used for all deployments except JC010/094. The Vertical Eurythenes Trap (VET) was suspended 1 m above the bottom. It was comprised of a 725 mm long cylinder of 300 mm diameter. A mesh funnel entrance of 45 mm aperture was situated at either end with bait attached in the centre of the trap. The De-rated Mark and Recapture (DEMAR) trap was a 500 mm by 500 mm by 200 mm box. Each of the four sides had a 40 mm square aperture funnelled entrance. Bait was attached in the centre of the trap, equidistant from all four trap openings. From Bett et al., 2003.

analysis (Clarke, 1993) was used to identify which components of the community were responsible for any variability detected.

Study areas were grouped into megahabitats (e.g., canyon, abyssal plain) and macrohabitats (e.g., lower canyon, middle canyon; de Stigter et al., 2007) to facilitate comparative analyses between locales (Greene et al., 1999). Samples from the Iberian submarine canyons were compared using canyon and depth as factors to test for dissimilarity between macrohabitats within submarine canyons. Canyon samples were compared to published records of scavenging amphipod community composition from traps deployed in the Iberian Abyssal Plain as part of the 1981 ABYPLANE expedition (Thurston, 1990). Where possible, data on environmental variables were obtained from CTD casts deployed in the vicinity (< 2.5 km radius) and from UKORS megacores and UNSEL box cores (Table 2.1; Cunha et al., 2011). Temperature and total organic carbon (TOC) measurements were grouped into discrete categorical bins (temperature, ≤ 2.5 °C, > 2.5 °C; TOC, ≤ 15 mg g^{-1}, > 15 mg g^{-1}) to facilitate subsequent factorial analysis.

The diversity of each site was measured using Simpson's Index of Diversity (D; Simpson, 1949):

$$D = 1 - \sum_{i=1}^{S} \left(\frac{n_i(n_i - 1)}{N(N-1)} \right)$$

where S is the total number of species, n_i the number of individuals of the i^{th} species, and N the total number of individuals in the sample. The calculated indices were compared with those calculated for the adjacent abyssal plain using published data (Table 2.2; Thurston, 1990) with a Mann-Whitney U test. Evenness was measured using Pielou's evenness index (J'; Pielou, 1966):

$$J' = \frac{-\sum_{i=1}^{S} \frac{n_i}{N} \ln \frac{n_i}{N}}{\ln(S)}$$

and compared with a Mann-Whitney U test.

Table 2.2: Species composition and abundance for scavenging amphipod samples collected from baited trap deployments made on the abyssal plains adjacent to the Iberian Margin submarine canyons as part of the 1981 ABYPLANE research expedition. Taken from Thurston, 1990. Species richness (S), Pielous's Eveness (J'), and Simpson's Index of Diversity (D) shown.

Station	na09	na10	na11	na12	na13	na14	na15
Latitude	39.9300	39.9300	42.8617	42.8617	42.9933	42.9933	42.9967
Longitude	-15.1083	-15.1083	-15.9117	-15.9117	-14.1417	-14.1417	-14.1033
Date deployed	08/06/1981	08/06/1981	10/06/1981	10/06/1981	12/06/1981	12/06/1981	13/06/1981
Depth (m)	3400	3499	3600	4286	4403	3194	4445
Species richness (S)	3	6	3	5	5	6	1
Simpon's Index (D)	0.61	0.73	0.59	0.67	0.58	0.65	–
Pielou's Eveness (J')	0.82	0.82	0.84	0.75	0.68	0.71	–
Paralicella caperesca	–	26	5	11	36	58	–
Paralicella tenuipes	1	7	2	1	16	20	–
Eurythenes gryllus	5	20	10	13	4	15	1
Orchomenella gerulicorbis	2	6	–	2	4	11	–
Cyclocaris sp. nov.	–	2	–	–	–	–	–
Valettietta gracilis	–	4	–	–	–	1	–
Abyssorchomene chevreuxi	–	–	–	2	1	2	–
Total	8	65	17	29	61	107	1

2.3 Results

Large catches of scavenging amphipods were obtained from all but three of the deployments. During deployment D297/15734 the trap was damaged while in situ, possibly by strong currents in the canyon as recorded on the seabed lander system ROBIO (RObust BIOdiversity; OceanLab, Aberdeenshire, UK) deployed at the same time nearby (Weaver, 2005). Smoked fish was used instead of raw mackerel for deployment CD179/56817. Deployment JC010/094 was made using small bottle traps with funnelled entrances, deployed by ROV. Despite these three deployments returning smaller catches, the overall composition of the catches appeared to be unaffected, clustering with standard deployments in ordination plots (Figure 2.4). Therefore these samples were included in analysis of community structure following standardisation for sample size.

Ten species of lysianassoid amphipod were identified, representing six scavenging amphipod families (Table 2.3; Figure 2.5). Eight of the species have been recorded previously on the abyssal plains of the North-East Atlantic (Christiansen, 1996; Thurston, 1990, unpublished data). Four species are as yet undescribed; *Cyclocaris* sp. nov., *Valettietta* sp. nov., and two species of *Paracallisoma*.

Paralicella caperesca Shulenberger & Barnard, 1976 was the dominant species in all but one sample. *Paralicella caperesca* and *P. tenuipes* Chevreux, 1908 accounted for between

Table 2.3: Species composition and abundance (percentage contribution in parentheses) for scavenging amphipod component of samples collected from baited trap deployments in Iberian Margin submarine canyons (NC: Nazaré Canyon, SC: Setúbal Canyon; CC: Cascais Canyon). Species richness (S), Pielou's Eveness (J'), and Simpson's Index of Diversity (D) shown.

Expedition	JC010	CD179	D297	D297	CD179	CD179	CD179	CD179
Station	#094	#56855	#15734	#15741	#56847	#56817	#56839	#56837
Canyon	NC	NC	NC	NC	NC	SC	SC	CC
Depth (m)	3400	3499	3600	4286	4403	3194	4445	4230
Species richness (S)	3	6	5	10	9	4	8	6
Simpon's Index (D)	0.30	0.23	0.25	0.59	0.59	0.41	0.25	0.65
Pielou's Eveness (J')	0.48	0.27	0.30	0.47	0.49	0.52	0.29	0.66
Paralicella caperesca	38 (82.6)	889 (87.1)	259 (86.0)	1424 (40.7)	4217 (55.6)	66 (74.2)	825 (86.0)	558 (47.9)
Paralicella tenuipes	7 (15.2)	8 (0.8)	35 (11.6)	1716 (49.0)	2287 (30.1)	19 (21.3)	71 (7.4)	360 (30.9)
Eurythenes gryllus	–	18 (1.8)	–	77 (2.2)	23 (0.3)	2 (2.2)	14 (1.5)	10 (0.9)
Orchomenella gerulicorbis	–	99 (9.7)	2 (0.7)	191 (5.5)	845 (11.1)	2 (2.2)	22 (2.3)	197 (16.9)
Cyclocaris sp. nov.	–	–	1 (0.3)	40 (1.1)	3 (<0.1)	–	1 (0.1)	–
Valettietta gracilis	–	6 (0.6)	–	3 (0.1)	134 (1.8)	–	12 (1.3)	29 (0.9)
Valettietta lobata	–	1 (0.1)	–	1 (< 0.1)	1 (1.8)	–	–	–
Valettietta sp. nov.	–	–	–	6 (0.7)	–	–	–	–
Paracallisoma sp. nov. 1	1 (2.2)	–	4 (1.3)	42 (1.2)	75 (1.0)	–	12 (1.3)	10 (0.9)
Paracallisoma sp. nov. 2	–	–	–	1 (< 0.1)	5 (< 0.1)	–	2 (0.2)	–
Total	46	1021	301	3501	7590	89	959	1164

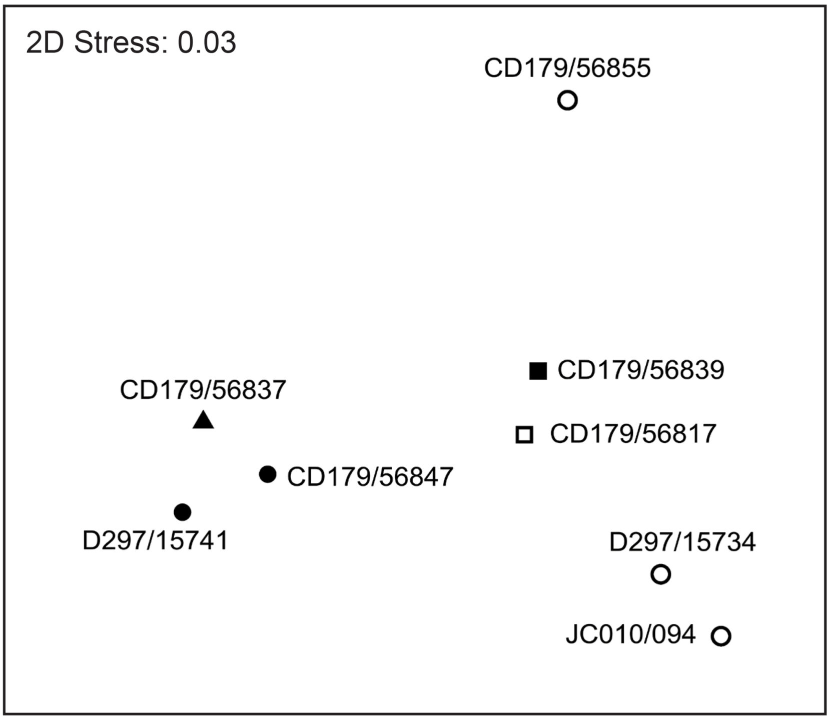


Figure 2.4: MDS plot of all canyon samples. Samples coded by canyon (circles, Nazaré Canyon; squares, Setúbal Canyon; triangles, Cascais Canyon) and depth (open symbols, middle canyon; filled symbols, lower canyon). Sample number shown next to each point.

77.7 % and 96.1 % of all scavenging amphipod specimens in each sample (Figure 2.5). The prevalence of *P. tenuipes* was reduced at shallower sites. This trend was particularly apparent in Nazaré Canyon where this species dominated at the lower canyon site but represented less than 1 % of the total scavenging amphipod component of the middle canyon sites.

No significant difference in scavenging amphipod communities was observed between submarine canyons (one-way ANOSIM: R = -0.269, p = 0.885). The limited number of replicates within each canyon may be undermining this analysis but ordination plots show little clustering of points by canyon (Figure 2.4). A significant difference was evident between sample sites in the middle and lower canyon (ANOSIM: $R = 0.494$, $p = 0.040$). There was no significant difference between communities based upon temperature (ANOSIM: $R = 0.124$, $p = 0.248$) or TOC of the sediments (ANOSIM: R = -0.333, $p = 0.971$).

The scavenging amphipod assemblages from canyons differed significantly from those of the adjacent Iberian Abyssal Plain (ANOSIM: $R = 0.219$, $p = 0.018$). SIMPER analysis

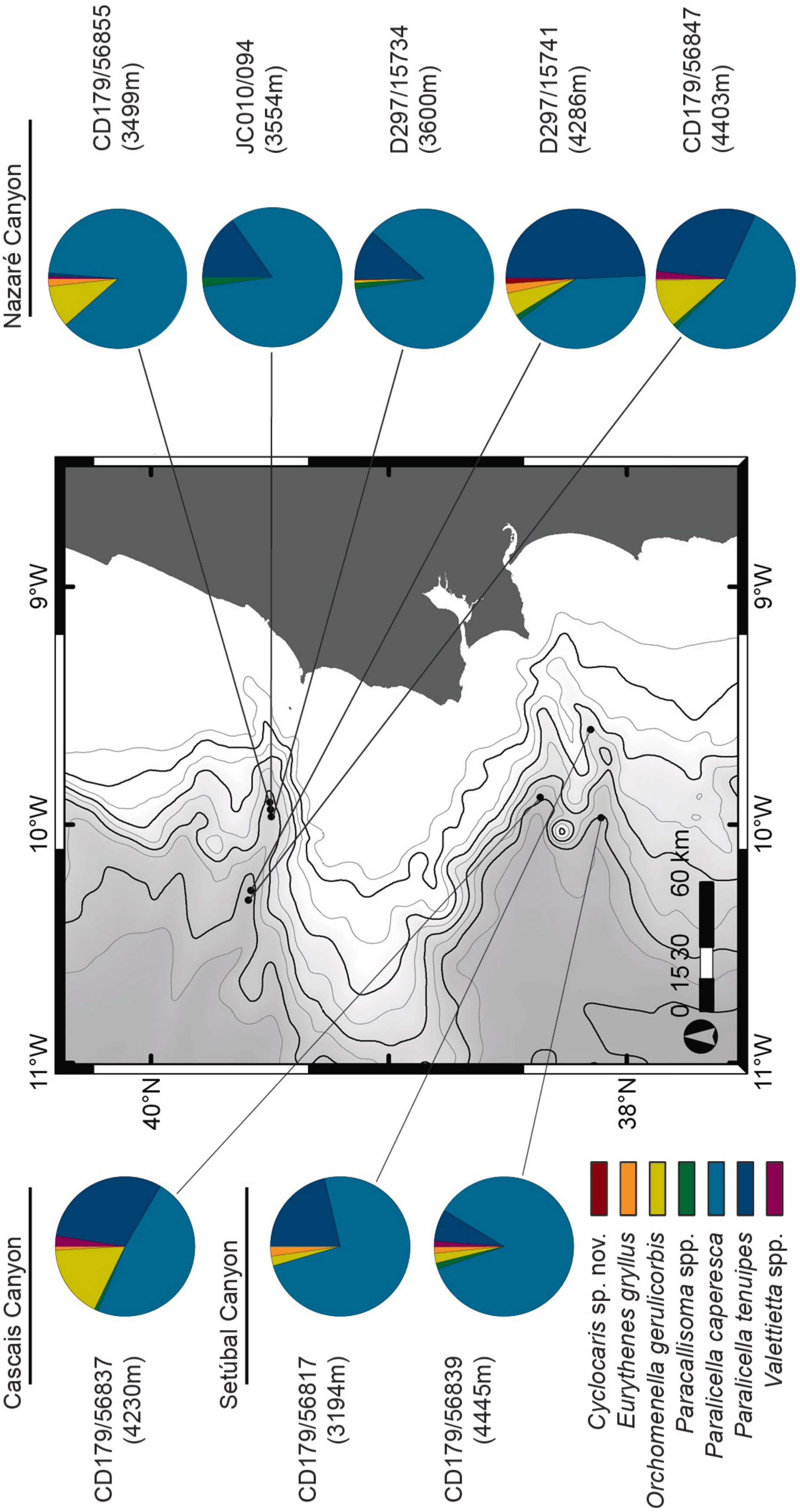


FIGURE 2.5: Species composition of samples collected from trap deployments in submarine canyons off the Iberian Peninsula.

showed that the majority (~72 %) of this dissimilarity was explained by differences in catches of *E. gryllus* (34.5 %), *P. caperesca* (24.8 %), and *P. tenuipes* (12.4 %).

Simpson's Index of Diversity values ranged from 0.23 to 0.65 (n = 9, median = 0.32, Q1 = 0.25, Q3 = 0.59) and were generally lower than values calculated for the abyssal plain (n = 6, median = 0.63, Q1= 0.59, Q3 = 0.68). This difference was significant (Mann-Whitney U test; $p = 0.013$). Pielou's Evenness Index showed the composition of abyssal plain samples was more even than canyon samples (Mann-Whitney U test; $p = 0.013$), with reduced dominance of *Paralicella* spp. in plain samples.

2.4 Discussion

2.4.1 Community composition

The similarity of communities between canyons demonstrates the wide distribution of deep-sea scavenging amphipods and confirms that canyons do not restrict the movement of motile scavenging fauna. A similar trend is evident in abyssal basins, with little community variation between adjoining abyssal plains in the North-East Atlantic (Thurston, 1990).

While the scavenging amphipod species identified in canyons are largely identical to those on the adjacent abyssal plains, there is a significant difference in the composition of the assemblages in these two habitats. This difference may be caused by temporal variability, plain samples were taken more than a decade before canyon samples (Thurston, 1990). Unpublished data from the Porcupine Abyssal Plain time series indicate that inter-annual and seasonal variability have little effect on community composition of scavenging amphipod assemblages. Therefore it is unlikely that differences seen between canyons and plains are due to temporal variation but this possibility cannot be completely ruled out. The results of the SIMPER analysis coupled with the significant difference in Pielous's Evenness Index suggest that the disparity in community composition is owing to the reduced importance of *Paralicella* spp. and increased evenness of community composition in abyssal plain settings, including a greater representation of *E. gryllus.* A more even distribution of species results in a higher diversity index when measured using indices, such as Simpson's, despite few differences in species richness.

A similar trend of high abundances of a few dominant species in submarine canyon communities has also been observed in scavenging fish (King et al., 2008; Stefanescu et al., 1994) and various macrofauna (Paterson et al., 2011). Cunha et al., 2011 identified a trend of high abundance of dominant species in macrofauna of Nazaré and Setúbal canyons but not in Cascais, demonstrating the complex and heterogenous nature of submarine canyons. The similarity of the assemblages in the different canyons together with the occurrence of species with global distributions, the mobility of amphipods (Boudrias, 2002), and the interconnectivity evident between canyons and abyssal plains (Vetter & Dayton, 1998) support the theory that the observed differences within canyons are mainly due to variation in environmental conditions rather than canyons acting as physical barriers to dispersal.

Although community composition does not vary significantly between canyons, there is a clear difference in community composition within canyons at different depths. Within the limitations of this study, it has not been possible to establish which of the many depth-correlated variables (e.g. hydrostatic pressure, temperature, salinity, oxygen concentration, POC flux) specifically leads to the community differences seen. Temperature, salinity, and oxygen concentration varied little between canyon sites and were not found to contribute significantly toward variability in community composition when tested as individual factors. Sediment TOC, although much more variable, also had no detectable effect on community composition. It may be that hydrostatic pressure alone is responsible for these differences. The polar emergence of *E. gryllus* (Ainley et al., 1986), a deep-sea scavenger primarily seen at abyssal depths at mid-latitudes (Ingram & Hessler, 1983; Smith & Baldwin, 1984), suggests that temperature also plays a role in the depth distribution limitations of deep-sea scavenging amphipods (Thurston et al., 2002). A more feasible explanation is that both of these depth-correlated variables, along with other variables that correlate to depth, such as oxygen concentration, each contribute a small amount toward the community-level differences. While their individual effects are not detectable, the cumulative and interacting influences of these factors are detectable. The synergistic effect of low temperature and high pressure upon respiration has been found during laboratory tests on the deep sea lysianassoid *Stephonyx biscayensis* Chevreux, 1908 (Brown & Thatje, 2011), but the physiological limits of the species in the current study remain unknown.

The dominance in all samples of *Paralicella*, a genus commonly identified in traps deployed on the abyssal plains of the North-East Atlantic (Thurston, 1990, unpublished data), indicates that members of this taxon are highly sucessful scavengers. Both *P. caperesca* and *P. tenuipes* have been identified as specialist scavengers with adaptations that allow them to monopolise food-falls (Thurston, 1979). The reduced prevalence of *P. tenuipes* at shallower sites, as particularly apparent in Nazaré Canyon, indicates that the upper depth limit of this species is shallower than that of its congener.

Very little is known about the other scavenging amphipod species identified. *Cyclocaris* sp. nov. was morphologically similar to that identified by Thurston (1990) as being distinctly different to *Cyclocaris tahitensis* Stebbing, 1888 and *C. guilelmi* Chevreux, 1899. *Orchomenella gerulicorbis* has been previously found at abyssal depths in the North Atlantic (Thurston, 1990) and North Pacific (Ingram & Hessler, 1983; Shulenberger & Barnard, 1976). *Valettietta gracilis*, *V. lobata*, and *Valettietta* sp. nov. are relatively primitive species with a lack of modified mandibular molars distinguishing them from the other scavenging amphipods collected in this study (Thurston, 1990). It has been previously observed that *Valettietta* spp. are more commonly found in traps deployed for extended periods of time (Rice & Herring, 1993). This suggests the potential for succession of scavenging amphipods at food falls with community composition change over time. The effect of deployment duration is an area that requires further investigation but is not expected to alter the results presented here as deployment durations did not differ substantially.

2.4.2 Relative abundance

Estimating background population size based on catches from baited traps, as performed previously for scavenging fishes using baited camera data (Priede & Merrett, 1998; Sainte-Marie & Hargrave, 1987), is not possible for deep-sea scavenging amphipods, which can rarely be identified in photographs and have unknown maximum swim speeds. Despite this, the large catches found in this study can be qualitatively linked to the size of the background populations (Blankenship et al., 2006). Compared to catches from similar traps deployed on the abyssal plains of the North-Eastern Atlantic (Table 2.2; Thurston, 1990), submarine canyons house very large assemblages of scavenging amphipods.

The large background populations of deep-sea scavenging amphipods, indicated by catches from canyons sampled, can be linked to high levels of sedimentation and enhanced concentrations of associated organic matter found (Epping et al., 2002; Garcia et al., 2010; Masson et al., 2010; Vetter & Dayton, 1998). Setúbal and Cascais Canyons are fed by large river systems (Sado and Tagus Rivers, respectively; Arzola et al., 2008). The mouths of these rivers flow directly into the canyon heads. Estuarine input results in large quantities of terrigenous organic matter entering the canyon system (Cúrdia et al., 2004). The extent to which this material travels down these two canyons is thought to be limited, in comparison to Nazaré, owing to the rarity of large-scale episodic events, which are a particular feature of down-canyon sediment transport (de Stigter et al., 2011).

Nazaré Canyon has no direct link to any large river systems, yet it has been estimated to have the highest levels of organic carbon and sediment input (Garcia et al., 2010; Masson et al., 2010). Heavy metal contamination of sediments in the canyon suggests output from a number of small river systems enters the canyon (Oliveira et al., 2011), however, inputs from shelf sediments are the most likely source of organic matter input. This provides an explanation for why the catches from this canyon are particularly large compared to catches from Setúbal and Cascais canyons, with Nazaré Canyon supporting larger background populations of scavenging amphipods.

The largest catches of all canyon deployments were seen in the deepest sites of the Nazaré Canyon. The location of these sites correlates with flat terraces observed during a video survey of the canyon using the ROV *Isis* (Tyler et al., 2009). These terraces experience relatively weak currents, acting as depocentres for sediment and larger material. As such, these depocentres could experience more frequent settling of large food-falls, in turn supporting larger populations of scavengers. An increased settling rate of large food-falls provides a possible explanation for the abundant catches of the baited traps deployed in submarine canyons. The idea that these terraces are nutrient rich and high in organic matter is supported by the existence of large communities of xenophyophores (Gooday et al., 2011), single-celled protists whose presence is associated with high nutrient environments (Levin, 1991).

Input from rivers and coastal waters will undoubtedly include carcasses of large terrestrial, freshwater, and marine organisms, a food source that will be readily exploited by deep-sea scavenging amphipods. The productive waters associated with submarine canyons also make them ideal grounds for fishing (Figueiredo et al., 2001; Puig et al., 2012). An increase in food-falls, via the discard of bycatch from fisheries, has a positive effect on marine scavenger abundances (Kaiser & Hiddink, 2007), increasing secondary production (Bozzano & Sardà, 2002; Furness et al., 2007). Indeed some facultative scavengers switch from a predatory foraging strategy to a scavenging one in the presence of fisheries discard (Laptikhovsky & Fetisov, 1999). Carrion from overlying surface waters is believed to influence benthic abyssal communities (Drazen et al., 2012) but the depth penetration of large carrion into the deep sea remains largely unknown. This is primarily due to very few naturally occurring food-falls having been found at abyssal depths (e.g., Klages et al., 2001; Smith & Hessler, 1987; Soltwedel et al., 2003; Stockton & DeLaca, 1982), as such, there is currently no evidence of increased large food-fall input into the canyons studied. It is, however, presumed that a sufficient number of large carcasses do reach abyssal depths regularly enough to support a diverse and abundant scavenging fauna.

2.5 Conclusions

Scavenging amphipod assemblages in submarine canyons are dominated by a few common abyssal species occurring in large numbers with no evidence for endemic canyon species. This is in direct contrast to the initial hypotheses. Evidence suggests that scavenging amphipods can maintain larger populations in submarine canyons than they do on the open slope or abyssal plains at similar depths. This study shows that depth-correlated variables are an important control on scavenging amphipod distributions with a discernible difference observed between communities at different depths within submarine canyons.

Chapter 3

A tale of two species:

Population studies on *Abyssorchomene abyssorum* and *Paralicella caperesca*

3.1 Introduction

Through their role in recycling organic carbon from large food-falls, scavenging organisms, and in particular scavenging amphipods, are a vital component of secondary production cycles that support numerous deep-sea ecosystems (Britton & Morton, 1994; Christiansen & Diel-Christiansen, 1993; Payne & Moore, 2006; Stockton & DeLaca, 1982). In spite of this, our understanding of the ecology of these organisms remains poor. A concerted effort in the field has furthered our understanding of deep-sea scavenging amphipods and their distribution at the community level (e.g. Duffy et al., 2012; Horton et al., 2013; Jamieson et al., 2011; Thurston, 1990), but few studies have examined the factors affecting population structure and distribution of deep-sea scavenging amphipods.

Numerous population studies have been carried out on shallow water amphipods (see Sainte-Marie, 1991 for a comprehensive review of pre-1990 literature; Arndt & Beuchel, 2006; Nygård et al., 2009). The study of deep-sea populations is, however, largely limited to the giant amphipods *Eurythenes gryllus* Lichtenstein, 1822 (Ingram & Hessler, 1987; Premke et al., 2006; Thurston et al., 2002) and *Alicella gigantea* Chevreux, 1899 (Barnard & Ingram, 1986), and species found in vent (Sheader & Van Dover, 2007;

Sheader et al., 2000, 2004), canyon (Kaïm-Malka, 2003, 2004, 2005), and trench environments (Blankenship et al., 2006; Thurston et al., 2002).

Characterisation of amphipod populations focuses on the identification of discrete size-classes, or growth stages, representing successive moults. Identification of size-classes is possible by identifying normal distributions from polymodal length frequency distribution data. Identification of distinct size-classes is not always possible. While both Ingram & Hessler (1987) and Premke et al. (2006) were able to confidently identify size-classes of *E. gryllus*, Thurston et al. (2002) was unable to separate out size classes for this species from a population in the Atacama trench.

Without detracting from the importance of previous studies, *E. gryllus* is rarely the most abundant species in deep-sea scavenging communities, and vent, canyon, and trench environments account for a very small part of the deep-sea by area. Mid-ocean ridges, on the other hand, represent a large area of the deep-sea benthic habitat, yet they have been poorly studied beyond their hydrothermal vent systems. The Mid-Atlantic Ridge (MAR) bisects the Atlantic Ocean and accounts for 45.7% (3 704 404 km^2) of seabed in lower bathyal (800 – 3500 m) depths in the North Atlantic (Niedzielski et al., in press; Priede et al., 2013, in press). Prior to the commencement of the MARECO and ECOMAR projects very little was known of the ecosystems of this environment. Following 19 research expeditions, involving partners from 17 countries, our understanding has progressed substantially.

The region of the MAR at the Charlie Gibbs Fracture Zone (CGFZ) is particularly interesting due to the complex topography and its effect on the North Atlantic Current (Bower & von Appen, 2008), and subsequent bounding of the sub-polar front (Soiland et al., 2008). The water circulation through the CGFZ and presence of the front has been suggested as a barrier to movement of fauna, eggs, and larvae either side of the CGFZ (McManus & Woodson, 2012; Woodson et al., 2012). The frontal region has been identified as an area with distinct patterns of primary productivity (Miller et al., 2013; Taylor & Ferrari, 2011). Owing to these oceanographic conditions, the four study areas identified for study by the ECOMAR project experience distinctly different conditions, particularly with regard to productivity north and south of the CGFZ (Tilstone et al., 2009). Northern stations are under cooler surface waters, lying north of the sub-polar front while southern stations lie under surface waters within the frontal zone (Miller et al., 2013).

The ECOMAR project provided a unique opportunity to study deep-sea scavenging amphipod communities at a single depth ($\sim$ 2500 m) across four geographically separated sampling areas at the MAR over a four-year period. Distinct scavenging amphipod assemblages were found at each sampling area with significant differences north and south of the Charlie-Gibbs Fracture Zone (CGFZ; Horton et al., 2013). All samples were dominated by the lysianassoid amphipod *Abyssorchomene abyssorum* Stebbing, 1888. The presence of this species in high abundances at all sampling areas provided the opportunity to study these organisms at the population level.

Relative to the MAR, submarine canyons account for only a small area of the deep-sea environment. However, their role as secondary production hotspots (De Leo et al., 2010; Gage & Tyler, 1991; Jannasch & Taylor, 1984; Soliman & Rowe, 2008; Van Oevelen et al., 2011; Vetter, 1995) makes them interesting study sites for population analysis. The finding of large numbers of *Paralicella caperesca* in submarine canyons (Duffy et al., 2012) allows for canyon populations of this species to be compared with their counterparts inhabiting abyssal plains. Comparing canyon populations to those of the abyssal plain allows further examination of how the heightened production of canyon environments is affecting growth and reproduction in scavenging amphipod species.

Like all other scavenging amphipods, *Abyssorchomene abyssorum* and *Paralicella caperesca* have limited dispersive ability, obligate brooding, and direct development; yet evidence suggests both species have wide-ranging, cosmopolitan distributions (Barnard & Karaman, 1991; Thurston, 1990). Both species have been found to dominate baited trap samples in their respective study areas (Duffy et al., 2012; Horton et al., 2013). Very little is known about the life histories of these two species. Both possess mandibular molars indicative of a scavenging lifestyle (Thurston, 1990) and have modified digestive tracts to facilitate ingestion and assimilation of large quantities of food (Dahl, 1979). *Paralicella caperesca* is able to distend its pereon to a far greater extent than *A. abyssorum*, suggesting *P. caperesca* is a more specialist scavenger while *A. abyssorum* follows a more generalist feeding strategy (Shulenberger & Barnard, 1976; Thurston, 1979).

An in-depth analysis of the populations of *A. abyssorum* inhabiting the MAR and *P.*

caperesca populations from submarine canyons, will provide vital information concerning the life history of these species and will help us to understand their apparent success in the deep sea. Analysing how populations vary between sampling areas may facilitate the identification of the environmental factors responsible for population-level variation amongst sampling areas and help identify how these two species have become so successful in their respective, but very different, habitats. It is hypothesised that populations of *Abyssorchomene abyssorum* will differ in their composition north and south of the Charlie Gibbs Fracture Zone, owing to differences in productivity in overlying surface waters. Populations of *Paralicella caperesca* from submarine canyons are hypothesised to be distinctly different to their counterparts from non-canyon environments.

3.2 Methods

3.2.1 Sample collection

3.2.1.1 *Abyssorchomene abyssorum*

Four ECOMAR sampling areas were studied (Figure 3.2) during research expeditions in the boreal summers of 2007, 2009, and 2010 (RRS *James Cook* expeditions JC011, JC037, and JC048 respectively). Amphipods were collected using baited traps attached to free-fall landers by Benjamin Boorman, Jessica Craig, Claudia Alt, and the author. The lander design and trap arrangement varied across years however the basic trap design was consistent (Horton et al., 2013). The DEMAR/VET trap configuration (Figure 2.3) was used for all JC011 deployments. JC037 deployments used two baited core tubes resulting from the loss of the DEMAR/VET lander. JC048 deployments used the new Amphitrap setup (Figure 3.1). All traps were baited with a whole mackerel (*Scomber scombrus*), either in a meshed off section of the trap (DEMAR/VET) or wrapped in muslin cloth (Amphitrap and core tube traps). Soak time varied (13–101 hours) as a result of weather conditions and operational constraints. For this reason samples were selected such that the effects of variable soak time were minimised with particularly long deployments excluded in favour of shorter deployments at the same sampling area where possible (Table 3.1).

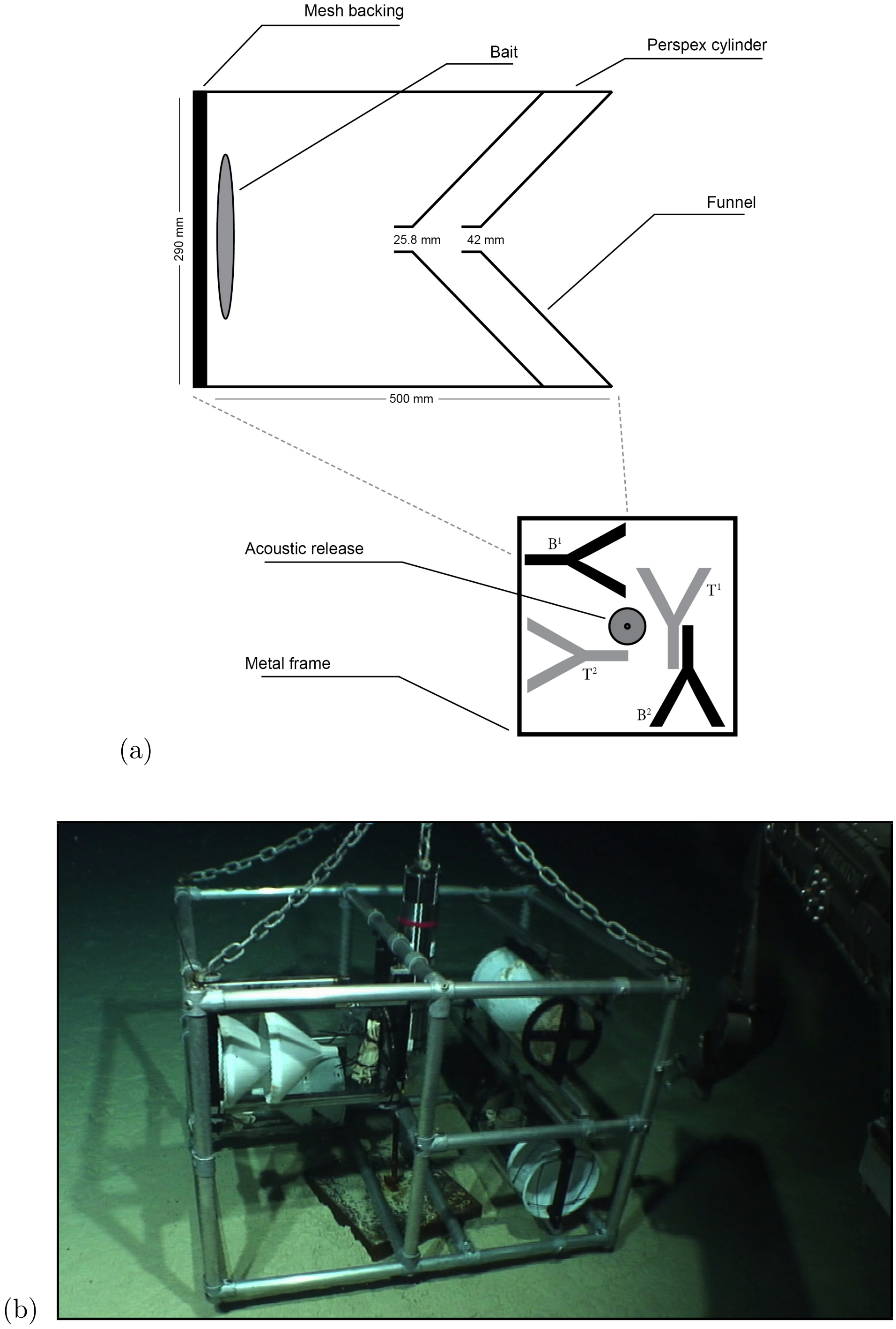


FIGURE 3.1: Amphitrap trap configuration as used for all JC048 deployments. 3.1(a). Drawing of Amphitrap trap configuration (National Oceanography Centre, Southampton, UK), as viewed from above. B^1, bottom trap #1; B^2, bottom trap #2; T^1, top trap #1; T^2, top trap #2. Enlarged section shows a diagrammatic representation of one double-funnelled trap used in all four trap bays. 3.1(b) Photograph of deployed Amphitrap at station #JC048/008, Mid-Atlantic Ridge (53.9886, -36.1345, 2628 m deep) taken on 07/06/2010 using ROV *Isis*.

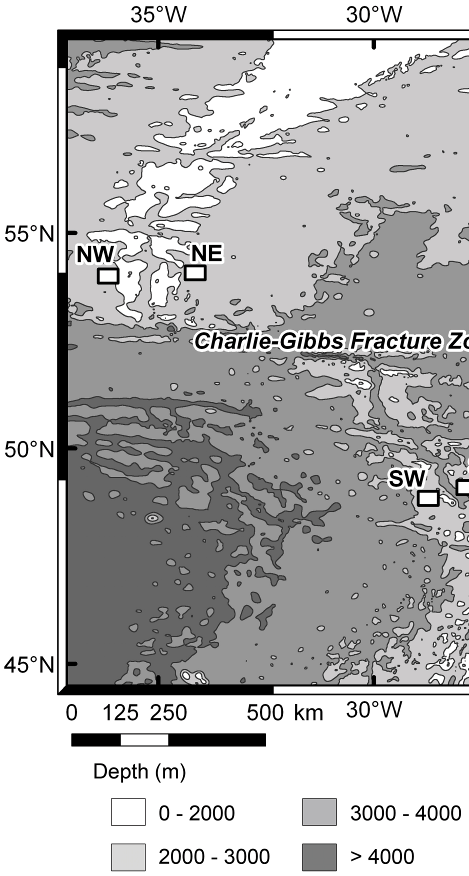


Figure 3.2: Bathymetric map of ECOMAR study area coloured by water depth. Sampling areas highlighted by white boxes.

Due to operational constraints the southwest sampling area was only sampled in 2010 and the southeast area was sampled during two years (2009, 2010). Both northern areas were sampled successfully on all three expeditions. The contents of the traps were fixed in either 100% ethanol or 4% buffered formaldehyde-saline solution. Formaldehyde-fixed material was subsequently transferred to 80% industrial methylated spirit. Samples were sorted to species level by Tammy Horton with assistance from the author (Horton et al., 2013) with the *A. abyssorum* component of selected samples used for population analysis in this study. Every individual was assigned a unique identification number and 200 individuals were randomly selected from each sample using a random number generator.

Table 3.1: Baited trap deployments, made as part of the ECOMAR project (Horton et al., 2013), whose *Abyssorchomene abyssorum* component was used for population analysis.

Area	Deployment	Latitude	Longitude	Depth m	Date deployed dd/mm/yyyy	Duration hh:mm
NE	JC011/098	54.0680	-34.1590	2500	09/07/2007	46:58
	JC037/083	54.0385	-34.1590	2452	02/09/2009	32:21
	JC048/020	54.0658	-34.1520	2505	08/06/2010	24:09
NW	JC011/079	53.9406	-36.1876	2564	05/05/2007	42:09
	JC037/052	53.9886	-36.1353	2570	25/07/2009	35:13
	JC048/008	53.9886	-36.1345	2628	02/06/2010	101:20
SE	JC037/013	49.0333	-27.7240	2501	08/07/2009	41:45
	JC048/046	49.0335	-27.7240	2507	23/06/2010	75:28
SW	JC048/032	48.7890	-28.6408	2448	16/06/2010	75:28

3.2.1.2 *Paralicella caperesca*

Paralicella caperesca specimens from seven of the eight samples used for canyon community analysis (Chapter 2; Duffy et al., 2012) were used for population analysis (Figure 2.1; Table 3.2). The sample from the JC010/094 deployment was not used for population analysis because of the small number of *P. caperesca* found and the fact that this sample was obtained using a different trap setup. As such, four samples from deployments in Nazaré Canyon, two from Setúbal, and one from Cascais, were used to represent submarine canyon populations. For large samples (> 600 individuals) a random subsample of 200 individuals was taken. To allow comparison between populations in submarine canyons and those of non-canyon environments, comparable samples were identified from the Discovery Collections (National Oceanography Centre, Southampton, UK). Plain samples chosen contained sufficient numbers of *P. caperesca* and were sampled during the same year or at a similar time of year as the HERMES canyon samples (Table 3.3; Figure 3.3). Four of these samples were from abyssal plains in the NE Atlantic (Porcupine, Madeira, and Cape Verde Abyssal Plains), and one from the Porcupine Seabight. The Porcupine Seabight sample provided a sample from a shallower water depth to make the comparison with submarine canyons more balanced. The identification of species was confirmed and samples were analysed in full as outlined below.

Table 3.2: Trap deployments made within the Iberian Margin submarine canyons whose *Paralicella caperesca* component was used for population analysis. Samples collected during research expeditions RRS *Discovery* 297, RRS *Charles Darwin* 179, and RRS *James Cook* 010.

Canyon	Deployment	Latitude	Longitude	Depth m	Date deployed dd/mm/yyyy	Duration hh:mm
Nazaré	CD179/56855	39.5027	-09.9050	3499	11/05/2006	23:02
	D297/15734	39.4963	-09.9648	3600	01/08/2005	21:28
	D297/15741	39.5825	-10.2750	4286	04/08/2005	24:22
	CD179/56847	39.5917	-10.3167	4403	07/05/2006	24:34
Setúbal	CD179/56817	38.1528	-09.6000	3194	25/04/2006	31:14
	CD179/56839	38.1095	-09.9697	4445	04/05/2006	24:12
Cascais	CD179/56837	38.3662	-09.8834	4230	02/05/2006	30:17

3.2.2 Data collection

All selected individuals were dissected and measured under a stereo-dissecting microscope by the author. Specimens were preserved in a variety of postures and many were

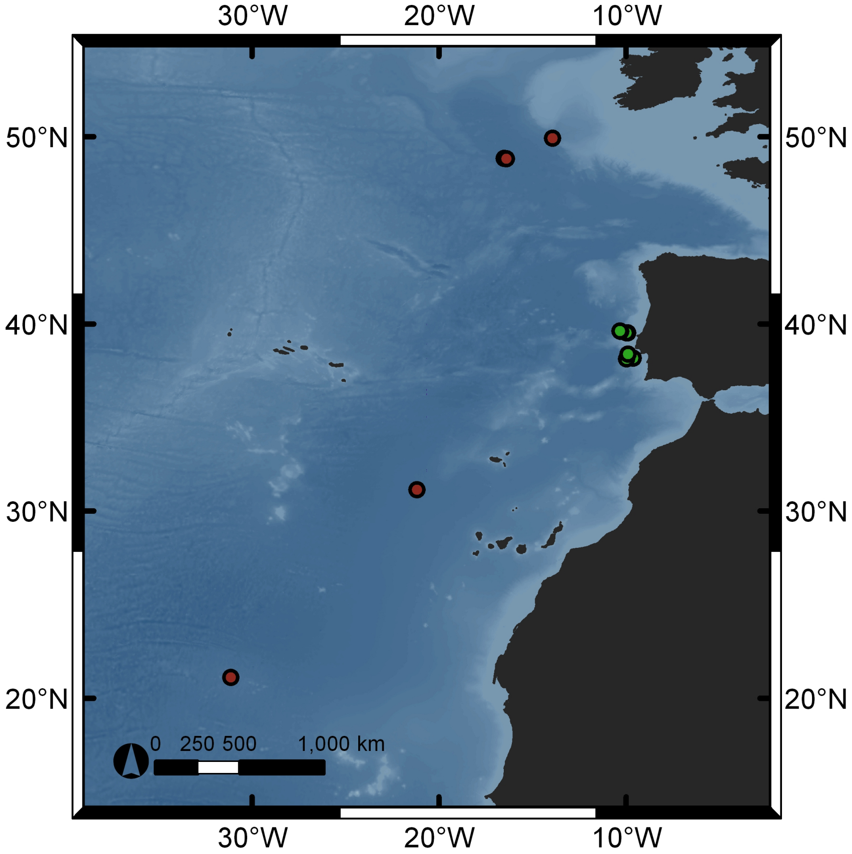


Figure 3.3: Map of sampling sites used for *Paralicella caperesca* population analysis. Canyon sites indicated by green marks (see figure 2.1 for higher resolution map). Non-canyon sites indicated by red marks.

Table 3.3: Samples from the Discovery Collections whose *Paralicella caperesca* component was used for comparison against canyon samples for population analysis. Samples from Porcupine Abyssal Plain (PAP), Cape Verde Abyssal Plain (CVP), Madeira Abyssal Plain (MAP), and Porcupine Seabight (PSB).

Area	Deployment	Latitude	Longitude	Depth m	Date deployed dd/mm/yyyy	Duration hh:mm
PAP	C085/52216/005	48.8337	-16.5070	4542	23/06/1985	11:05
	D229/13200/031	48.8132	-16.3905	4842	11/07/1997	05:22
MAP	D194/12174/020	31.1267	-21.1667	4941	18/08/1990	15:17
CVP	D204/12600/044	21.0867	-31.1100	4540	09/10/1993	10:45
PSB	D092/9756/008	49.8933	-13.9117	3852	13/04/1979	04:15

damaged, making it difficult or impossible to accurately measure total body length for all individuals. Past studies have resolved this problem by measuring an individual body-part as a proxy for total body length. A range of proxies have been used previously, including coxal plate 4 diagonal length (Blankenship et al., 2006; Chapelle, 1995), pereonite 1 dorsal length, (Nygård et al., 2009; Thurston et al., 2002), the length of the dorsal margin of pleonite 1 (Sheader & Van Dover, 2007; Sheader et al., 2004), dorsal margin length of pleonite 3 (Sheader et al., 2000). In this study coxal plate 4 was used as a proxy for total body length.

The total body length (distance along the dorsal margin between the anterior margin of the head and the tip of the telson) of all intact *A. abyssorum* from sample JC048/032 and 50 randomly selected *P. caperesca* from sample D297/15734 was measured. This was performed using a digital graphics tablet and HTML-assisted Measuring System (HaMS; Rocket Commerce) calibrated using a stage graticule of known length. The HaMS software measured the number of pixels travelled along a drawn line and converted this to an actual measurement using the calculated calibration. Use of HaMS permitted accurate and precise measurement of a curved line. These data were subsequently correlated to the diagonal linear measure of coxal plate 4 (as in Chapelle, 1995), which were made using a stage graticule. Estimation of total body length for all remaining specimens was possible using the coxal plate 4 measurement as a proxy.

Identification of primary and secondary sexual characteristics allowed for accurate sexing of all but the smallest individuals, which were classified as unsexed juveniles. Along with coxal plate 4, antenna 1 (length, number of articles, accessory flagellum length), antenna 2 (length, number of articles), and secondary sexual characteristics (oostegite length and presence of oostegite setae in females, presence of genital papillae in males) were also measured. Oocytes of females at varying stages of sexual maturity were measured and counted. The half-range of mature female body length (HMFBL) ratio (Sainte-Marie, 1991) for *A. abyssorum* was calculated from the maximum and mean mature female body length. HMFBL ratio is a proposed means to determine between iteroparous (HMFBL > 0.3478) and semelparous (HMFBL < 0.1304) species.

3.2.3 Population characterisation

All data analyses were performed exclusively by the author. Identification of size-classes of amphipods is possible using measurements of total body length or a correlated proxy (Blankenship et al., 2006; Kaïm-Malka, 2003, 2004, 2005; Premke et al., 2006; Sheader & Van Dover, 2007; Sheader et al., 2000, 2004; Thurston et al., 2002). Oostegite measurements for females and coxal plate 4 measurements for each sex, including a separate histogram for unsexed juveniles, were plotted as probability density histograms. The identification of normal distributions, each representing an oostegite stage or size-class, was initially performed by eye. The presence and parameters of each of these distributions were confirmed using the probability paper method (Cassie, 1954; Harding, 1949) and the 'mixdist' package (Macdonald & Du, 2011; Macdonald & Pitcher, 1979) in R statistical software (R Development Core Team, 2012). The goodness of fit of each of the modelled distributions was confirmed using the ANOVA function included in the 'mixdist' package.

3.2.4 Comparison of populations

3.2.4.1 *Abyssorchomene abyssorum*

Non-parametric statistical tests were used to compare male:female, mature:immature female, and juvenile:non-juvenile ratios amongst sampling areas (Kruskal-Wallis test) and either side of the MAR and CGFZ (Mann-Whitney U test). Once parameters for size-classes were accurately determined, all 200 individuals from each sample were assigned to the appropriate size-class based on 95% confidence limits (2 standard deviations from the mean). Where overlap of these limits occurred individuals were assigned to size-classes based on the relative proportions of each size-class. Once classified, data were analysed using PRIMER 6 statistical software (Clarke & Gorley, 2006). Each size-class was treated as a 'species' in each sample in order to perform multivariate analyses to compare the size-class composition of populations at each sampling area.

Data were root transformed to minimise the skewing effect of highly dominant size-classes. A similarity matrix was created based on Bray-Curtis similarities (Bray & Curtis, 1957) and a multidimensional scaling (MDS) plot was created to visualise population similarity. Cluster analysis was used to group stations based on similarity. Populations were compared using ANOSIM tests with sampling area (NE, NW, SE, SW) and sampling year as factors. Stations north and south of the CGFZ and east and west of the MAR were grouped and compared using ANOSIM tests (N/S, E/W). A SIMPER analysis was used to identify which components of the population were contributing most to variability seen (Clarke, 1993).

3.2.4.2 ***Paralicella caperesca***

Non-parametric statistical tests were used to compare male:female and juvenile:non-juvenile ratios between canyon samples and non-canyon samples (Mann-Whitney U test). Once parameters for size-classes were accurately determined, individuals from each sample were assigned to the appropriate size-class based on 95% confidence limits (2 standard deviations from the mean). Where overlap of these limits occurred individuals were assigned to size-classes based on the relative proportions of each size-class. Following classification, data were analysed using multivariate tests as part PRIMER 6 statistical software (Clarke & Gorley, 2006).

Data were root transformed to reduce skewing and standardised to account for different sample sizes. Following creation of a Bray-Curtis similarity matrix an MDS plot was created and cluster analysis was used to group samples. Populations were compared using ANOSIM tests with sampling area (canyon, non-canyon) as the lone factor. A SIMPER analysis was used to identify which components of the population were contributing to observed dissimilarity between sample groups (Clarke, 1993).

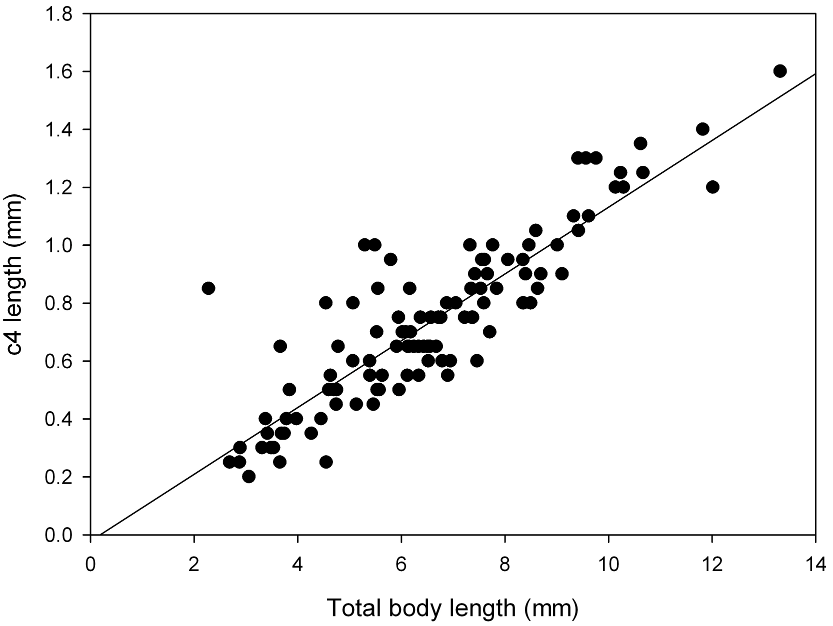


FIGURE 3.4: Linear correlation between total body length and coxal plate 4 length for *Abyssorchomene abyssorum*. n = 110, y = 0.1153x - 0.0215, R^2 = 0.7700. Measurements of all intact individuals from sample JC048/032.

3.3 Results

3.3.1 *Abyssorchomene abyssorum*

In total, 1 800 *Abyssorchomene abyssorum* were dissected and measured from the collected samples. Males, females, and juveniles were identified in all samples. Mature females bearing setose oostegites were frequently observed but no ovigerous females were identified. There was a strong positive correlation between total body length and coxal plate 4 length (Figure 3.4; n = 110, y = 0.1153x - 0.0215, R^2 = 0.7700). This relationship permitted the use of coxal plate 4 measurements as a proxy for total body length using the equation:

$$L = \frac{C + 0.0215}{0.1153}$$

where L is the estimated total body length and C is the linear measure of coxal plate 4. Estimated total body length ranged from 1.92 mm to 16.67 mm. No individuals smaller than 4.09 mm showed primary or secondary sexual characteristics and were identified as juveniles. With few exceptions individuals larger than this exhibited both primary and secondary sexual characteristics.

Table 3.4: Mean body length (mm) for all *Abyssorchomene abyssorum* size-classes identified from combined data for juveniles and males, and split data for females north (N) and south (S) of the Charlie-Gibbs Fracture Zone. Linear growth factor between successive size-classes in parentheses.

Size-class	Males	**Size-class**	Females (N)	Females (S)
J1	2.61	**J1**	2.61	2.61
	(1.51)		(1.51)	(1.51)
J2	3.89	**J2**	3.89	3.89
	(1.42)		(1.38)	(1.50)
M2	5.45	**F2**	5.30	5.74
	(1.37)		(1.19)	(1.19)
M3	7.40	**F3**	6.26	6.78
	(1.44)		(1.26)	(1.24)
M4	10.60	**F4**	7.82	8.43
			(1.35)	(1.33)
		F5	10.51	11.20
			(1.20)	(1.22)
		F6	12.59	13.72
			(1.11)	
		F7	13.98	–
			(1.18)	
		F8	16.41	–

3.3.1.1 Sexual dimorphism

The estimated total body lengths of males were significantly smaller than those of females (Table 3.4; Figure 3.5a; Mann-Whitney U: $n = 997$, $U = 72\,416$, $p < 0.001$). Males ranged in total body length from 4.09 mm to 11.90 mm (Median = 7.12 mm, IQ range = 5.82 mm to 7.99 mm). Females ranged in body size from 5.39 mm to 16.67 mm (Median = 8.43, IQ range = 6.69 mm to 11.03 mm). The largest individuals (> 12 mm total body length) were exclusively female. Males possessed significantly longer antenna 1 and antenna 2, relative to total body length, than those of the females (Figure 3.5b; MWU: $n = 990$, $U = 231\,997$, p < 0.001; n = 980, U = 222 405, p < 0.001 respectively) with differences becoming more pronounced with increasing body size (Figure 3.6). As a function of antenna length (articles mm^{-1}), males possessed significantly more articles on antenna 1 and antenna 2 than females (MWU: $n = 990$, $U = 176\,935$, $p < 0.001$; $n = 979$, $U = 13\,049$, $p = 0.001$ respectively).

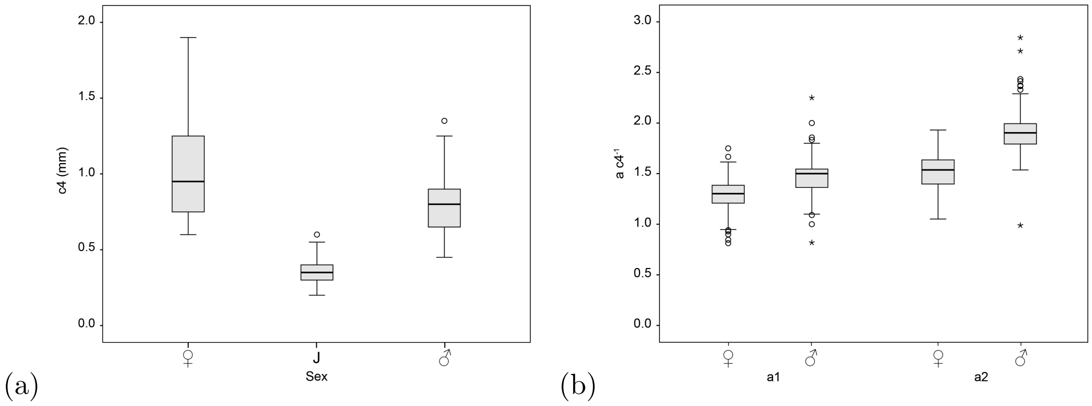


Figure 3.5: Comparison between sexes for *Abyssorchomene abyssorum* from all stations at all sampling areas. 3.5(a) Length of coxal plate 4, a proxy for total body length, for males, juveniles, and females. 3.5(b) Length of antennae as a function of coxal plate 4 length for antenna 1 and antenna 2 in male and female *A. abyssorum.* Median and interquartile ranges shown, ○ = data points outside the interquartile range, ∗ = statistical outliers.

3.3.1.2 Sexual development

Two ovaries, lying dorso-laterally either side of the gut, could be identified between pereonites 3 and 7 in females as small as 5.39 mm. Complete ovaries were recoverable from only 40 individuals due to the poor condition of specimens. Both ovaries contained similar numbers of ellipsoid oocytes of approximately equal size in a linear arrangement (Figure 3.7). Ooctye size, calculated as the area of an ellipse ($\pi r1r2$), generally increased with body size but was not closely correlated (Figure 3.8a; R^2 =0.0189). Some large females had relatively small oocytes and some small females possessed large oocytes. The total number of oocytes within each ovary ranged from 18 to 39 and had a weak, inverse correlation to oocyte size (R^2 =0.0011). There was no apparent relationship between oocyte number and total body length (Figure 3.8b).

Oostegite buds were visible on females as small as 5.82 mm in length but the majority (94.5%) of females of this size lacked any trace of oostegites (Figure 3.9). Larger females possessed oostegites of varying size. A probability density histogram of oostegite length as a ratio of gill length (Figure 3.10) identified three distinct oostegite stages (OS1 – OS3; Table 3.5) with limited overlap. The presence and parameters of these stages were confirmed using the probability paper method.

Setose oostegites, an indicator of female maturity, were observed in individuals from all three oostegite stages in differing frequencies. Of 73 individuals of OS3, 61 (83.6%)

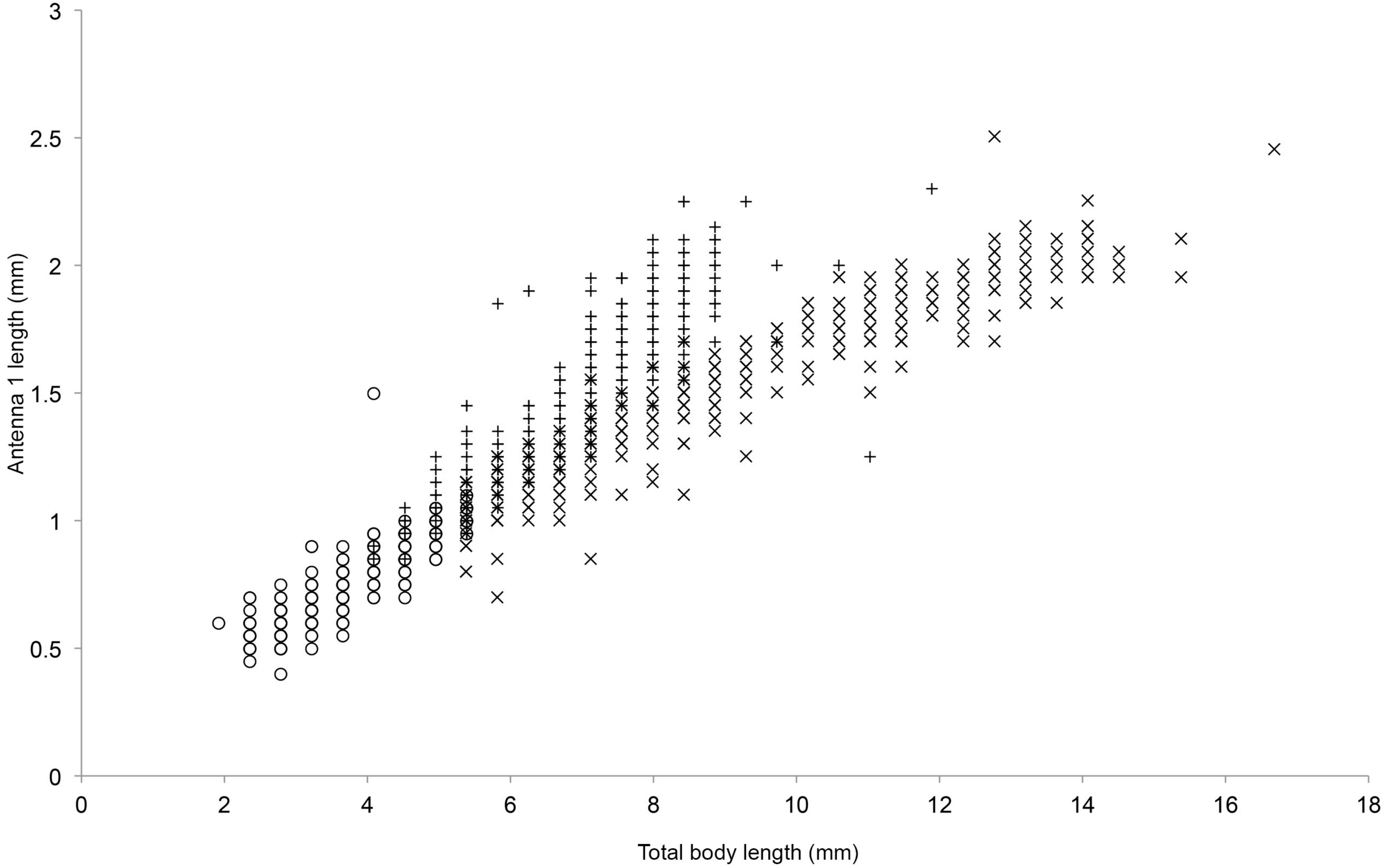


FIGURE 3.6: Relationship between antenna 1 and coxal plate 4 lengths for all individuals of *Abyssorchomene abyssorum* with intact antennae from all samples, points plotted by sex. + = males; × = females; ○ = juveniles.

TABLE 3.5: Counts of oostegite stage (OS), identified from oostegite:gill ratios, for each female size-class of *Abyssorchomene abyssorum*.

OS	Mean oos:gill ratio	F2	F3	F4	F5	F6	F7	F8
OS0	–	69	50	45	3	1	0	0
OS1	0.20	4	16	102	17	1	1	0
OS2	0.60	1	0	2	64	2	0	0
OS3	1.20	0	0	0	29	37	6	1
(setose)		(-)	(-)	(-)	(23)	(33)	(6)	(1)

possessed setose oostegites. Only 2 out of 69 individuals (2.9%) of OS2 and a single specimen of the 141 OS1 individuals (0.7%) bore setae on their oostegites.

Testes were identifiable in the majority of males identified by penile papillae presence but they were in generally poor condition making developmental classification impossible. Penile papillae in this species were relatively large, extending to the mid-point of the ventral surface and producing marked downward protrusions that were easily identified on examination of pereonite 7.

3.3.1.3 Population characterisation

Individuals that could not be sexed were assigned to two juvenile stages (Figure 3.11a). The smaller individuals met the conditions of a normal distribution and could confidently be grouped as such (J1). Unsexed individuals that could not be sexed but were more than 2σ larger than J1μ were grouped as J2 juveniles. The distribution of J2 overlapped with the smallest sexed individuals (M2, F2; Figure 3.11a) and size-class numbering was used as to reflect this. Males from all sampling areas were found to fall into three distinct size-classes (M2, M3, M4; Figure 3.11b). The presence and number of these size-classes were confirmed using the probability paper method. The boundaries, mean, standard deviation, and relative proportion of each of these size-classes (Table 3.4) were

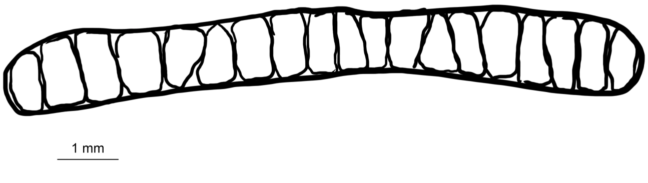
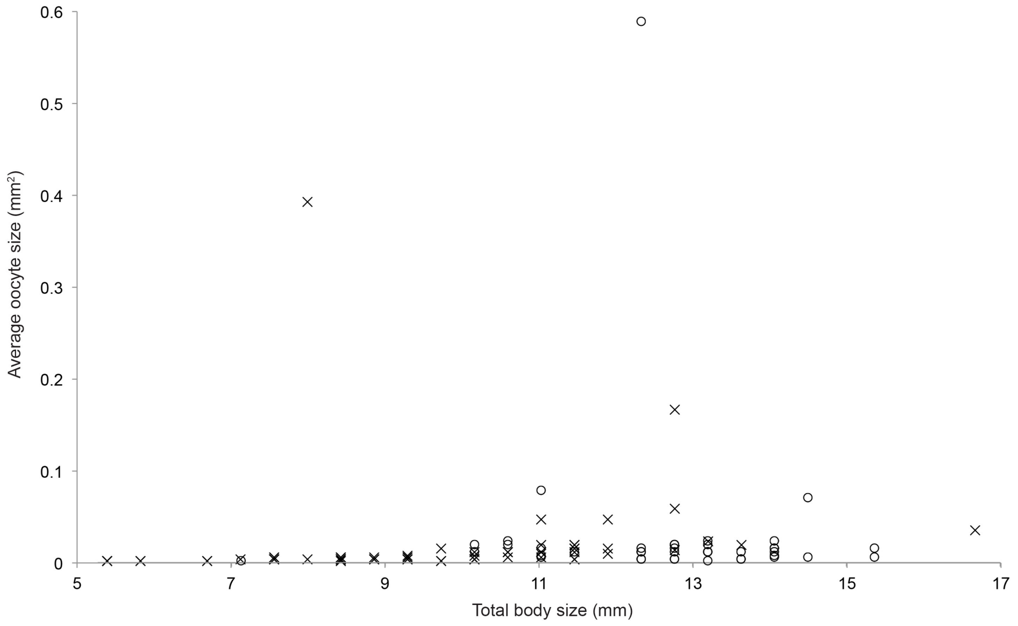
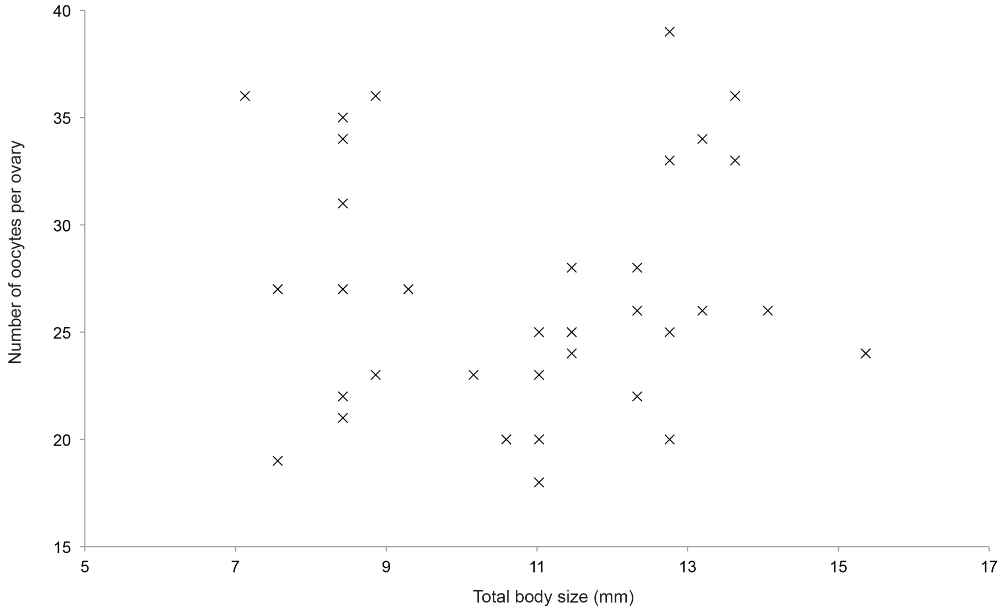


FIGURE 3.7: Cartoon representation of a typical full *Abyssorchomene abyssorum* ovary demonstrating linear arrangement of ellipsoid oocyctes.



(a)



(b)

Figure 3.8: Oocyte size and number relative to body length for *Abyssorchomene abyssorum.* 3.8(a) Average oocyte size relative to body length for all females from all samples where ovaries or partial ovaries could be identified. × = immature females, ○ = mature females with setose oostegites. 3.8(b) Total oocyte count for all complete ovaries identified compared to total female body length.

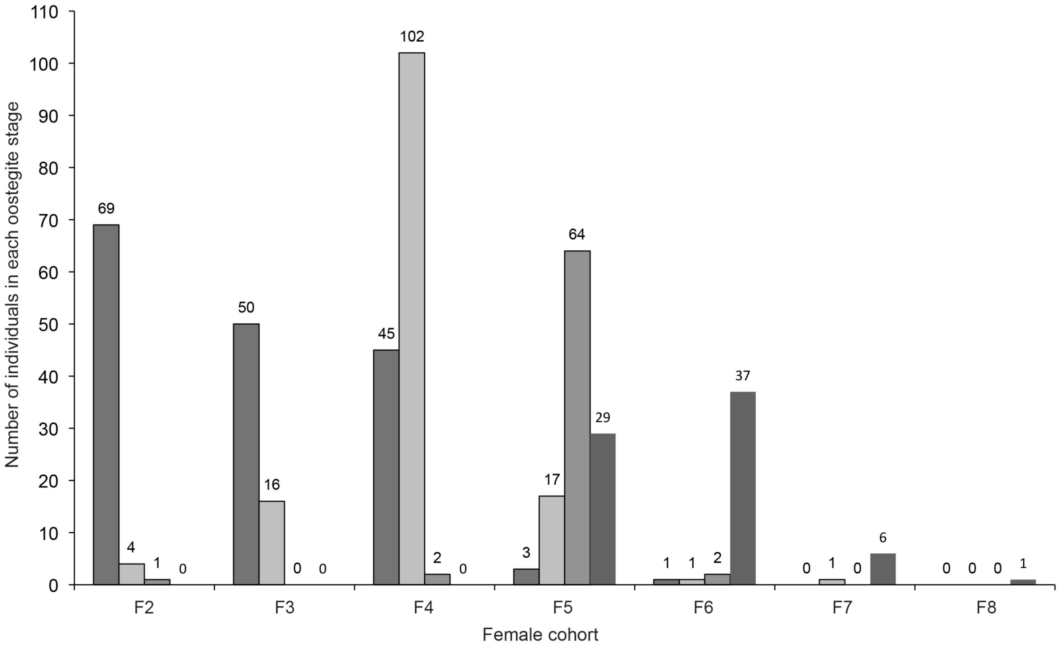


FIGURE 3.9: Counts of each oostegite stage for all female size-classes of *Abyssorchomene abyssorum* in all samples. Bars for each size-class left to right from OS0, no oostegites, to OS3, large oostegites relative to body size.

further refined using a 'mixdist' model, which satisfactorily fitted the data (ANOVA: $d.f. = 6$, $\chi^2 = 17.00$, $p = 0.2562$). A total of 7 size-classes were identified for females (F2 – F8). The five smallest size-classes (F2 – F5) were observed in samples from north and south of the CGFZ but the parameters of these size-classes varied north and south of the CGFZ. Size-classes of females from north of the CGFZ (Figure 3.11c) were consistently smaller than those at southern areas (Figure 3.11d). The occurrence and parameters of these size-classes were confirmed using the probability paper method and a 'mixdist' model fitted to the data (ANOVA: north, $d.f. = 9$, $\chi^2 = 8.42$, $p = 0.4925$; south, $d.f. = 12$, $\chi^2 = 12.37$, $p = 0.4165$). Size-classes F7 and F8 were represented by a handful of individuals at the northern sampling areas only. Linear growth factors between size-classes J1 and J2, and J2 and F2/M2 were high (Table 3.4). Increments between size-classes of females from the northern sampling areas fell in the range of 1.11 – 1.35 and those from the southern sampling areas in the range of 1.19 – 1.33.

Oostegite stages were distributed across female size-classes (Figure 3.10). Individuals with ovaries but no visible oostegites (OS0) were found in all but the two largest female size-classes (F7, F8). The smallest oostegites (OS1) were found in all size-classes apart from F8, which was represented by one large individual with setose OS3 oostegites. The sole amphipod with OS1 oostegites in the F7 size-class possessed setose oostegites

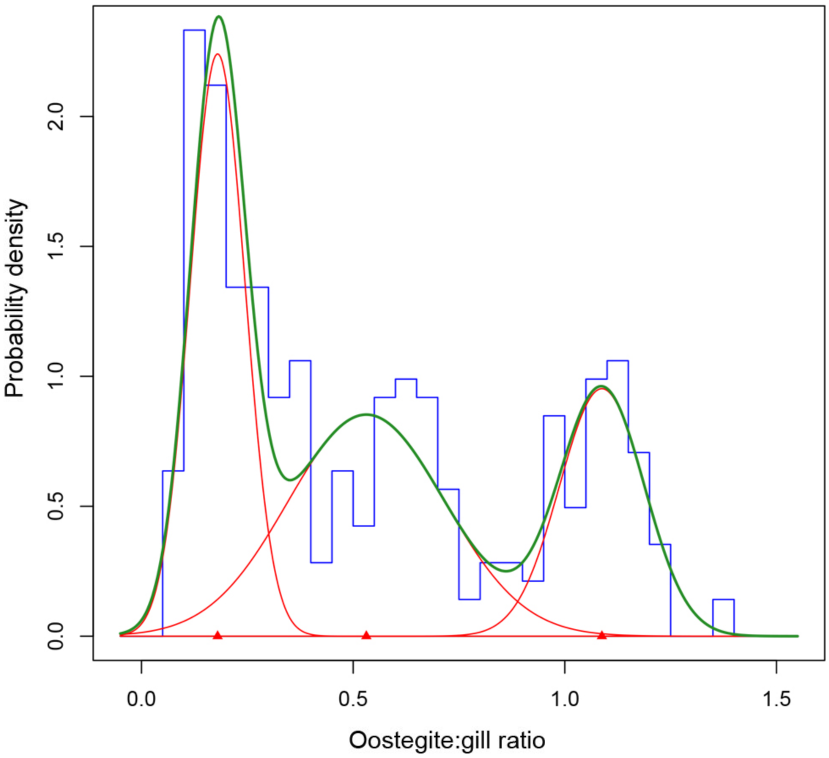


FIGURE 3.10: Probability density histogram for oostegite:gill ratios for all female *Abyssorchomene abyssorum* possessing oostegites from all samples. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Red lines represent the distribution of each oostegite stage, green line represents entire population.

in spite of their small size. Setose OS3 oostegites were found in individuals from size-classes F5 – F8. The HMFBL ratio (Sainte-Marie, 1991) was calculated as 0.2297, placing A. abyssorum between the expected ratios for iteroparous (> 0.3478) and semelparous (< 0.1304) species.

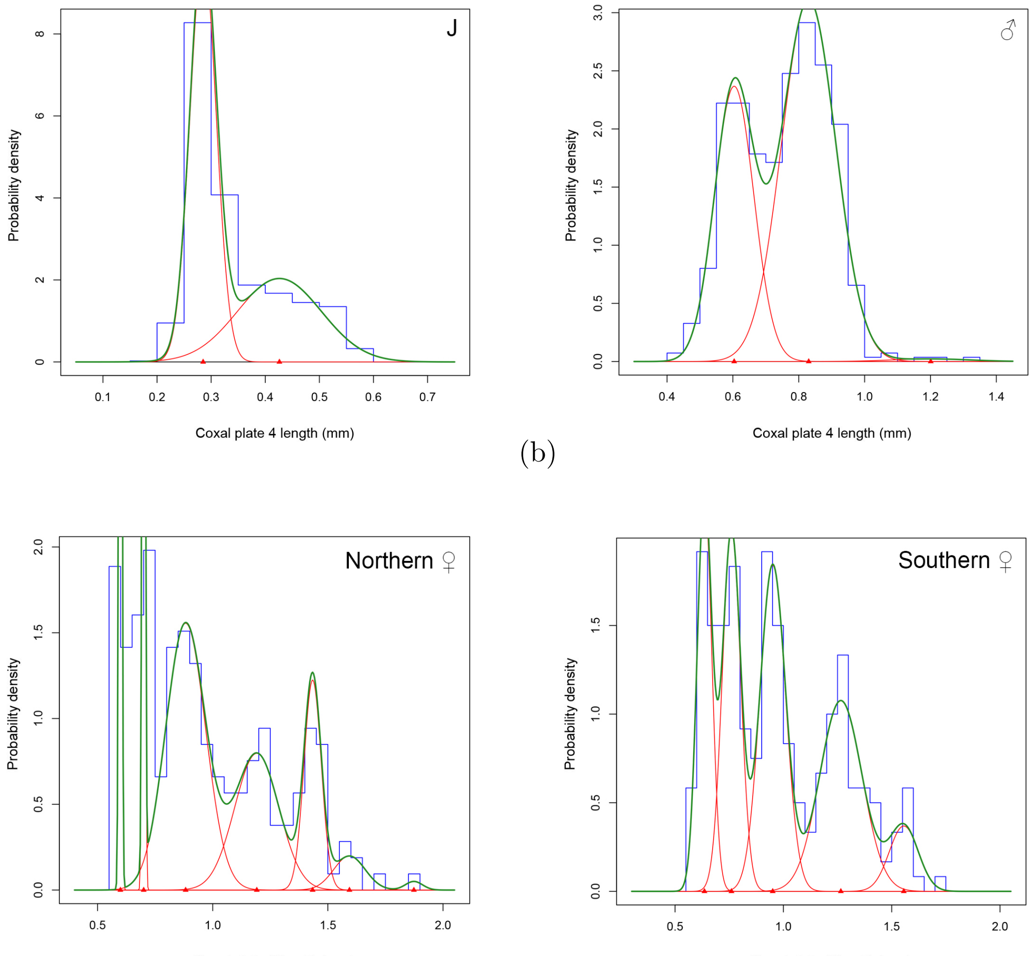
3.3.1.4 Population comparison

The male:female and mature:immature female ratios did not differ significantly amongst sampling areas (Table 3.6; Kruskal-Wallis: $n = 9$, $d.f. = 3$, $H = 3.489$, $p = 0.322$; $n = 9$, $d.f. = 3$, $H = 0.178$, $p = 0.981$ respectively). The juvenile:non-juvenile ratio did not differ significantly amongst sampling areas (KW: $n = 9$, $d.f. = 3$, $H = 5.622$, $p = 0.132$) but was significantly different north and south of the CGFZ (MWU: $n = 9$, $U = 17$, $p = 0.048$) with significantly more juveniles north of the fracture zone.

TABLE 3.6: Total counts of males (M), females (F), and juveniles (J) of *Abyssorchomene abyssorum* from all samples. Population composition ratios used for univariate comparison shown.

Area	Deployment	M	F	Mature F	J	M:F	% mature F	M&F:J
NE	JC011/098	15	14	3	171	1.07	0.21	0.17
	JC037/083	20	5	0	175	4.00	0.00	0.14
	JC048/020	84	44	14	74	1.91	0.32	1.73
NW	JC011/079	53	95	3	102	0.56	0.03	1.45
	JC037/052	78	61	16	61	1.28	0.26	2.28
	JC048/008	62	43	5	95	1.44	0.12	1.11
SE	JC037/013	120	55	14	25	2.18	0.25	7.00
	JC048/046	88	83	3	28	1.06	0.04	6.11
SW	JC048/032	28	102	5	70	0.27	0.05	1.86

Multivariate analysis showed populations varied significantly based on sampling area (ANOSIM: $R = 0.379$, $p = 0.045$). Differences were not significant when stations were grouped based on their position relative to the MAR and CGFZ (ANOSIM: north/south, $R = 0.198$, $p = 0.143$; east/west, $R = 0.006$, $p = 0.373$) rather than by sampling area. There was no significant difference amongst stations based on year sampled (ANOSIM: $R = 0.100$, $p = 0.265$). Cluster analysis showed pre-2010 samples from the NE sampling area (JC011/098 and JC037/083) to be least similar to other samples (Figure 3.12). Both of these samples contained large numbers of juvenile size-classes (J1 and J2). SIMPER analysis showed dissimilarity was greatest between NE and SE sampling areas with 24.88% of this dissimilarity attributed to differences in J1 counts. Analysis of grouped stations showed 20.52% of north/south and 18.24% of east/west dissimilarity was also the result of J1 count variation.



(a) (b)

(c) (d)

FIGURE 3.11: Probability density histograms of coxal plate 4, a proxy for total body length, measures for *Abyssorchomene abyssorum*. 3.11(a) Combined data for juveniles from all samples. 3.11(b) Combined data for all males. 3.11(c) Females from stations north of the CGFZ. 3.11(d) Females from stations south of the CGFZ. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Red lines represent distribution of each identified size-class, green line represents entire population.

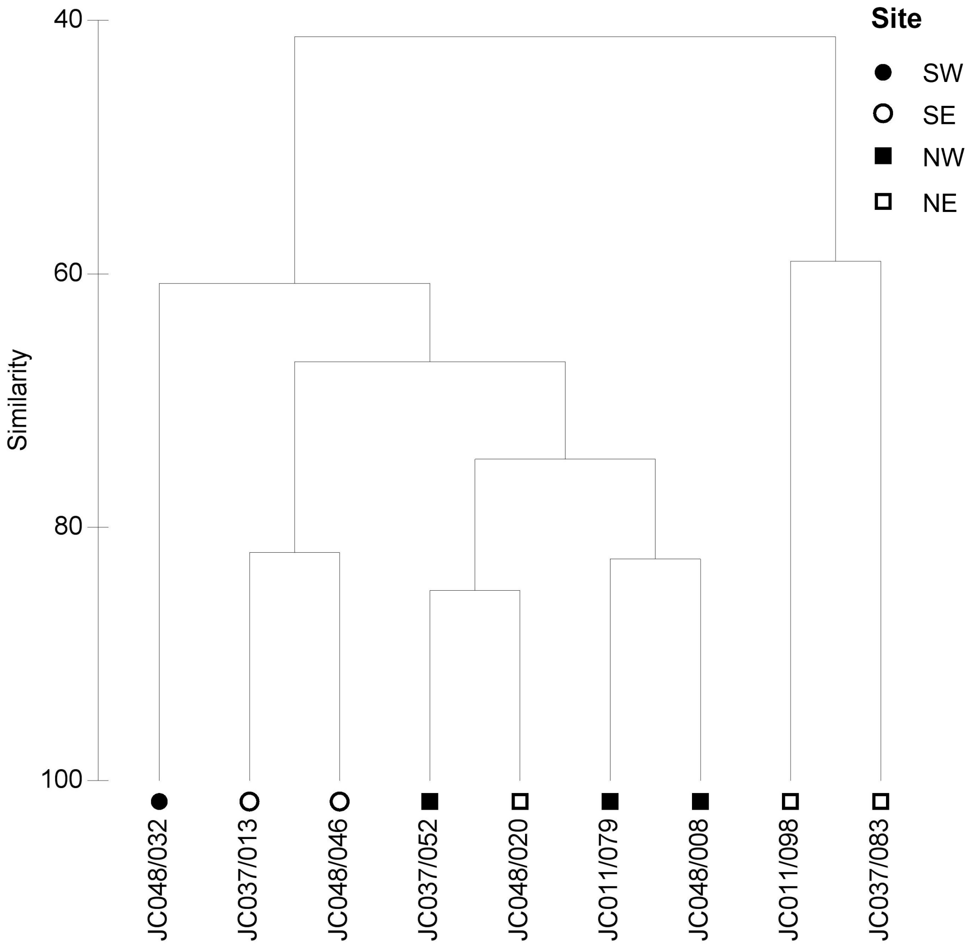


FIGURE 3.12: Dendrogram demonstrating similarity in population composition of *Abyssorchomene abyssorum* amongst all stations. Stations south of the CGFZ indicated by circles and northern stations indicated by squares. Filled symbols represent stations west of the MAR (●, ■) and open symbols represent stations east of the MAR (○, □).

3.3.2 *Paralicella caperesca*

In total, 1 422 *Paralicella caperesca* were dissected and measured from canyon samples, and 777 individuals were dissected and measured from non-canyon samples. Males, females, and juveniles were identified in all samples. No mature or ovigerous females were observed. There was a positive correlation between total body length and coxal plate 4 length (Figure 3.13; $n = 50$, $y = 0.1187x + 0.0982$, $R^2 = 0.4157$). While this relationship was relatively poor it permitted the use of coxal plate 4 measurements as a proxy for total body length. This approximate estimation was made using the equation:

$$L = \frac{C - 0.0982}{0.1187}$$

where L is the estimated total body length and C is the linear measure of coxal plate 4. Estimated total body length ranged from 1.70 mm to 22.34 mm. No individuals smaller than 4.65 mm showed primary or secondary sexual characteristics and were identified as juveniles. A small number of individuals of this size from canyon samples could be sexed. Individuals of 8.00 mm in length and larger consistently exhibited primary and secondary sexual characteristics in both canyon and non-canyon samples.

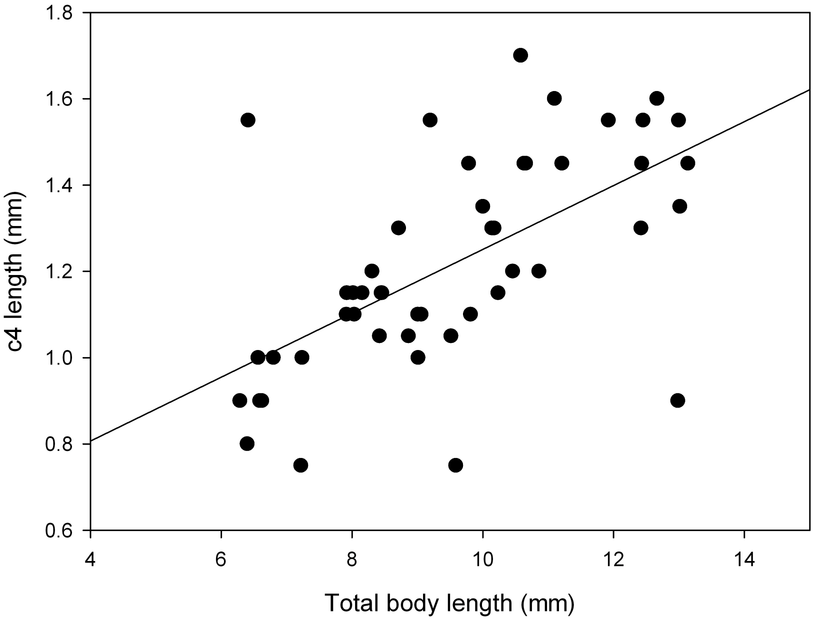


FIGURE 3.13: Linear correlation between total body length and coxal plate 4 length for *Paralicella caperesca*. $n = 50$, $y = 0.1187x + 0.0982$, $R^2 = 0.4157$. Measurements of 50 intact individuals from sample D297/15734.

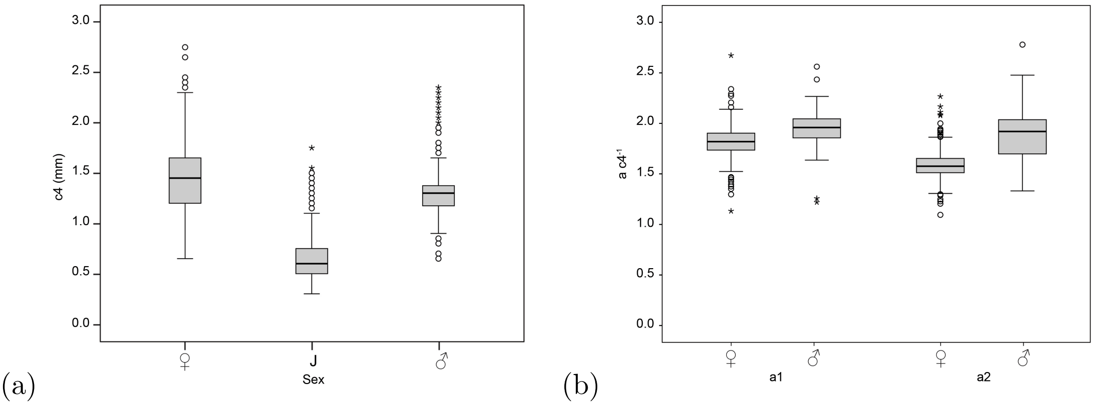


FIGURE 3.14: Comparison between sexes for *Paralicella caperesca* from all stations at all sampling areas. 3.14(a) Length of coxal plate 4, a proxy for total body length, for males, juveniles, and females. 3.14(b) Length of antennae as a function of coxal plate 4 length for antenna 1 and antenna 2 in male and female P. caperesca. Median and interquartile ranges shown, ○ = data points outside the interquartile range, $*$ = statistical outliers.

3.3.2.1 Sexual dimorphism

There was a significant difference between the size distributions of males and females (Figure 3.14a; Mann-Whitney U: $n = 759$, $U = 47\,884$, $p < 0.001$). Males ranged in total body length from 4.65 mm to 18.97 mm (Median = 10.12 mm, IQ range = 8.86 mm to 10.97mm). Females ranged in size from 4.65 mm to 22.34 mm long (Median = 11.39 mm, IQ range = 10.97 mm to 13.07 mm). Males possessed significantly longer antenna 1 and antenna 2, relative to total body length, than those of the females (Figure 3.14b; MWU: $n = 753$, $U = 95\,557$, p < 0.001; n = 754, U = 106 579, p < 0.001 respectively). The antennal differences between the sexes was most pronounced in antenna 2, with the antenna 1 to antenna 2 ratio significantly lower for males than females (MWU: $n = 750$, $U = 27\,681$, p < 0.001) with males more commonly possessing second antennae of equal length or longer than their first antennae. As a function of antenna length (articles mm^{-1}), males possessed significantly more articles on antenna 1 and antenna 2 than females (MWU: $n = 753$, $U = 68\,733$, $p = 0.015$; $n = 755$, $U = 84\,405$, $p = 0.001$ respectively).

3.3.2.2 Sexual development

A pair of ovaries could be identified between pereonites 3 and 7 either side of the gut in females as small as 4.65 mm. Complete ovaries were recoverable from 59 individuals.

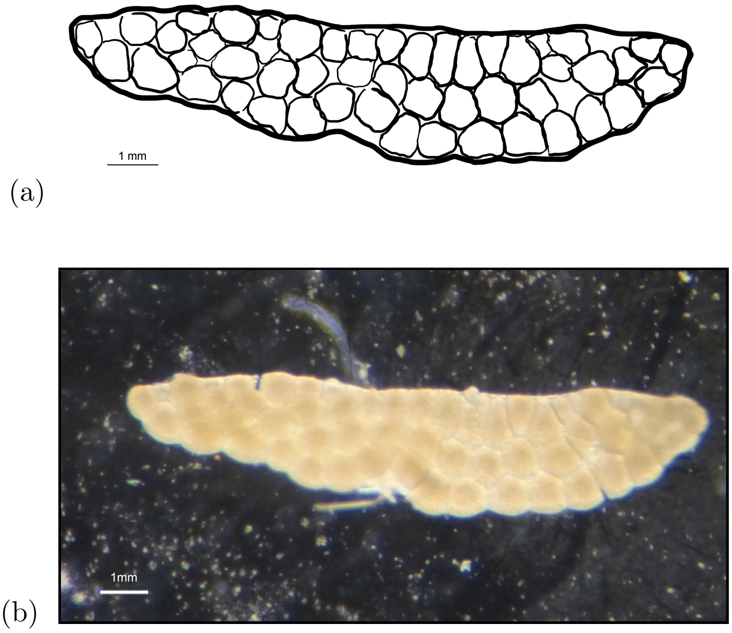
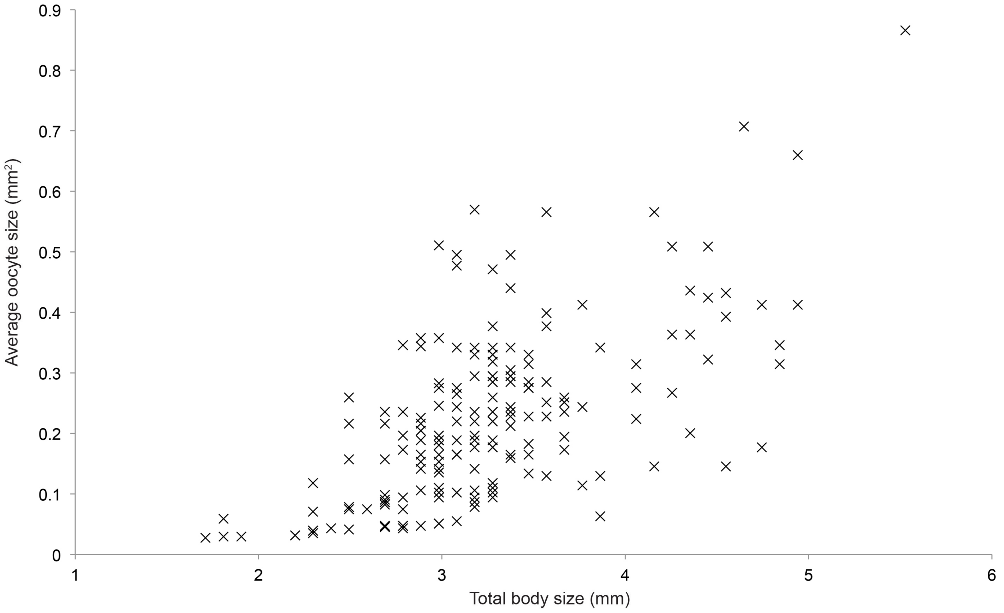


FIGURE 3.15: Cartoon representation (3.15a) and photograph (3.15b) of a typical full ovary, exhibiting three-tiered linear arrangement of oocytes, removed from a female *Paralicella caperesca*.

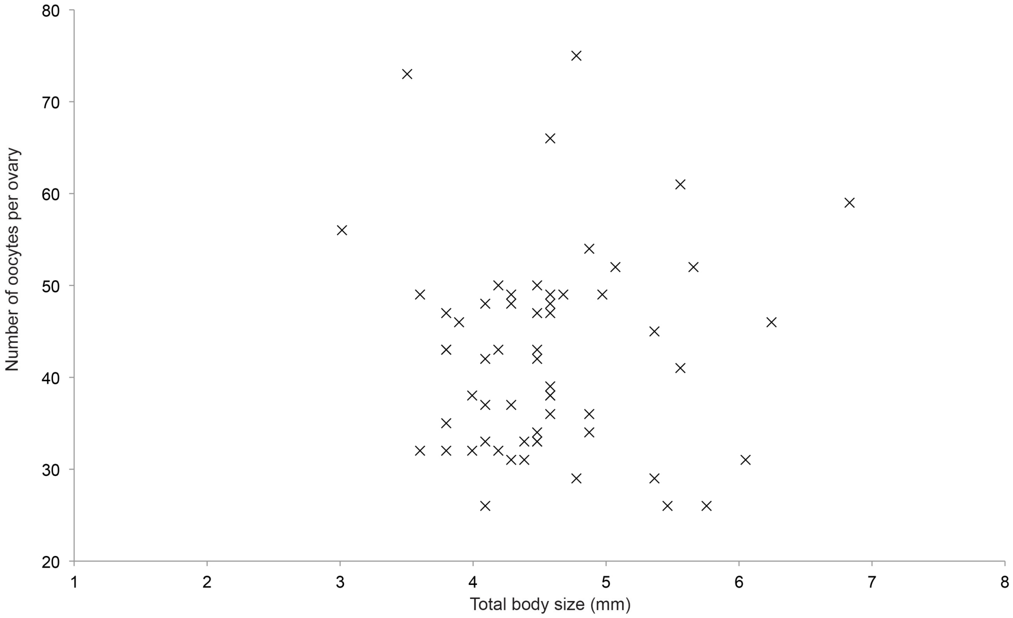
Both ovaries contained approximately equal numbers of spheroid oocytes of comparable size in a three-tiered linear arrangement (Figure 3.15). Ooctye size, calculated as the area of an ellipse, showed a positive correlation with estimated body size (Figure 3.16a; $R^2 = 0.3978$). There was no apparent relationship between oocyte number and estimated body size with the total number of oocytes per ovary varying little amongst females of varying size (Figure 3.16b). The total number of oocytes within each ovary ranged from 26 to 75 with an average of 42 oocytes per ovary.

The smallest female with visible oostegite buds was an estimated 4.65 mm in length but most females of this size had no detectable oostegites (Figure 3.17). Larger females possessed oostegites of varying size. A probability density histogram of oostegite length as a ratio of gill length (Figure 3.18) identified 4 oostegite stages (OS1 – OS4; Table 3.7) with minimal overlap. The presence and parameters of these stages were confirmed using the probability paper method.

Setose oostegites, were not seen on any individuals. Evidence of setal development was observed in individuals possessing particularly large oostegites but no setae had penetrated the oostegite margin. For this reason no females were deemed mature. Testes were identifiable in the majority of males seen however they were in generally poor



(a)



(b)

Figure 3.16: Oocyte size and number relative to body length for *Paralicella caperesca*. 3.8(a) Average oocyte size relative to body length for all females from all samples where ovaries or partial ovaries could be identified. 3.8(b) Total oocyte count for all complete ovaries identified compared to total female body length.

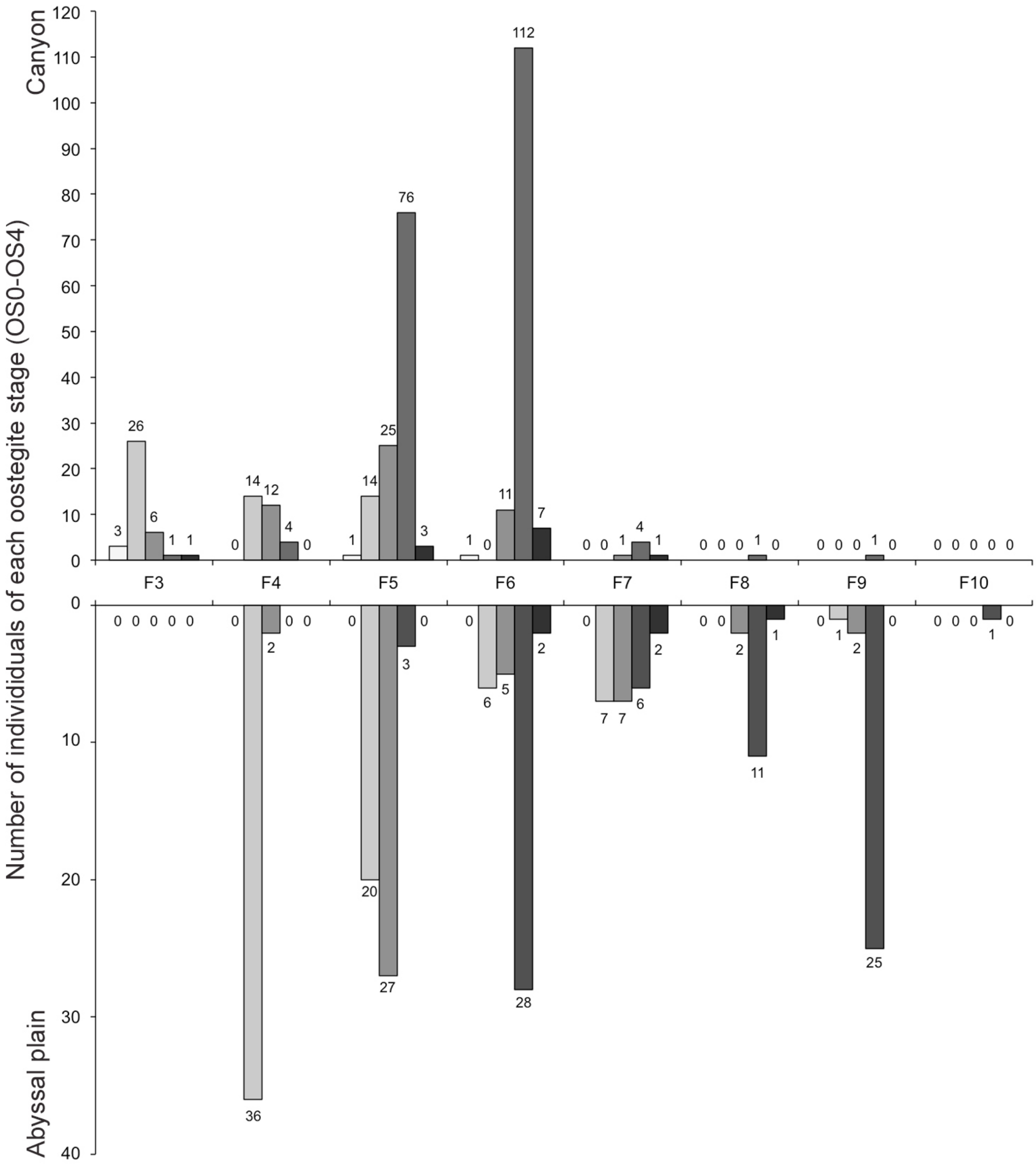


FIGURE 3.17: Counts of each oostegite stage for each female size-class of *Paralicella caperesca*. Grouped by sampling area, canyon samples on top and non-canyon samples below, note differing y axis scales. Bars for each size-class left to right from OS0, no oostegites, to OS4, large oostegites relative to body size.

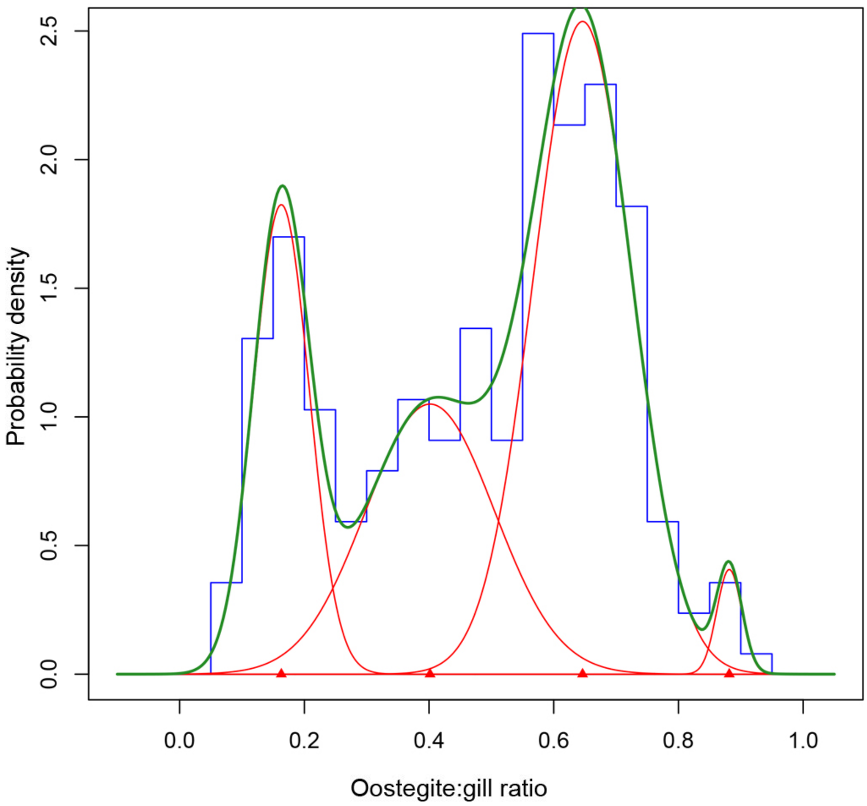


FIGURE 3.18: Probability density histogram for oostegite:gill ratios for all female *Paralicella caperesca* possessing oostegites from all samples. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Red lines represent the distribution of each oostegite stage, green line represents entire population.

TABLE 3.7: Counts of oostegite stage (OS), identified from oostegite:gill ratios, for each female size-class of *Paralicella caperesca*. Grouped by sampling area.

Area	OS	Mean oos:gill ratio	F3	F4	F5	F6	F7	F8	F9	F10
Non-Canyon	OS0	-	0	0	0	0	0	0	0	0
	OS1	0.16	0	36	20	6	7	0	1	0
	OS2	0.40	0	2	27	5	7	2	2	0
	OS3	0.65	0	0	3	28	6	11	25	1
	OS4	0.88	0	0	0	2	2	1	0	0
Canyon	OS0	-	3	0	1	1	0	0	0	0
	OS1	0.16	26	14	14	0	0	0	0	0
	OS2	0.40	6	12	25	11	1	0	0	0
	OS3	0.65	1	4	76	112	4	1	1	0
	OS4	0.88	1	0	3	7	1	0	0	0

condition making developmental classification impossible. Penile papillae in this species were small and could only be identified on close examination of the underside of pereonite 7. The smallest male possessing visible penile papillae was an estimated 4.65 mm in length.

3.3.2.3 Population characterisation

Size distributions differed between the canyon samples and non-canyon samples, therefore separate size-class analyses were performed. Individuals that could not be sexed were assigned to 4 identified juvenile stages (Figures 3.19a, 3.19b). The parameters for the identified size-classes are comparable for the smallest individuals (J1, J2) but the separation between canyon and non-canyon size-classes becomes more pronounced in larger size-classes (J3, J4). Canyon size-classes have consistently larger mean total body lengths than their non-canyon counterparts.

A total of 5 male (Figures 3.19c, 3.19d; M3 – M8) and 7 female (Figures 3.19e, 3.19f; F3 – F10) size-classes were identified (Table 3.8). The occurrence and parameters of these size-classes were confirmed using the probability paper method and a 'mixdist' model fitted to the data (ANOVA: Canyon males, $d.f. = 19$, $\chi^2 = 24.08$, $p = 0.1930$; canyon females, $d.f. = 25$, $\chi^2 = 51.88$, $p = 0.1243$; non-canyon males, $d.f. = 19$, $\chi^2 = 12.47$, $p = 0.8646$; non-canyon females, $d.f. = 20$, $\chi^2 = 25.53$, $p = 0.2634$). There was direct overlap between the largest juvenile (J3, J4) and smallest sexed (M3, M4, F3, F4) size-classes. Size-classes were numbered to reflect this.

Size-classes M3 and F3 were found exclusively in canyon samples with individuals of similar size from non-canyon environments showing no sexual characteristics and therefore classified as J3 juveniles. The largest size-class of males (M8) and females (F10) was not observed in canyon samples. Canyon size-classes possessed consistently larger mean total body lengths than their non-canyon counterparts (Table 3.8; Figure 3.19).

Linear growth factors between size-classes were comparable to those of *A. abyssorum* (Table 3.8). Increments between size-classes ranged from 1.10 – 1.84 with the largest growth increments between juvenile size-classes. Oostegite stages were distributed across female size-classes (Figure 3.17). More developed oostegites were more frequently observed in smaller individuals (F3 -F6) from canyons than from non-canyon environments.

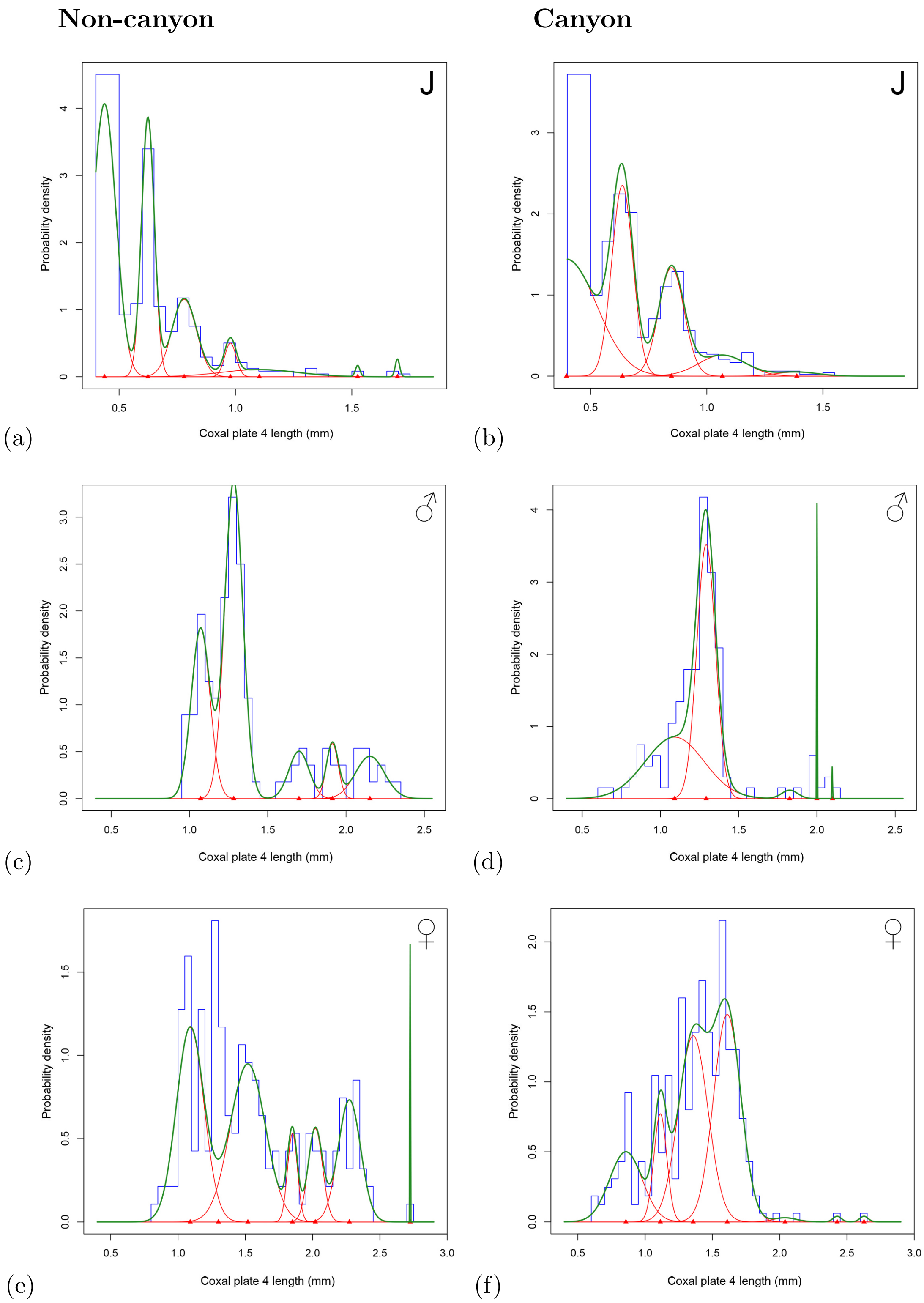


FIGURE 3.19: Probability density histograms of coxal plate 4, a proxy for total body length, measures for *Paralicella caperesca*. 3.19(a) Juveniles from all non-canyon samples. 3.19(b) Juveniles from all canyon samples. 3.19(c) Males from all non-canyon samples. 3.19(d) Males from all canyon samples. 3.19(e) Females from all non-canyon samples. 3.19(f) Females from all canyon samples. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Red lines represent distribution of each identified size-class, green line represents entire population.

Table 3.8: Mean body length (mm) for all *Paralicella caperesca* size-classes identified from split data for juveniles, males, and females from canyon and non-canyon environments. Linear growth factor between successive size-classes in parentheses.

Canyon									**Non-Canyon**								
Juv.			Male			Female			Juv.			Male			Female		
J1	2.51								**J1**	2.93							
		(1.84)									(1.52)						
J2	4.62								**J2**								
		(1.38)									(1.30)						
J3	6.39		**M3**	6.39		**F3**	6.39		**J3**	5.80		**M3**	5.80		**F3**	5.80	
		(1.29)			(1.29)			(1.29)			(1.29)			(1.29)			(1.29)
J4	8.24		**M4**	8.24		**F4**	8.24		**J4**	7.48		**M4**	7.48		**F4**	7.48	
					(1.27)			(1.30)						(1.34)			(1.36)
			M5	10.43		**F5**	10.68					**M5**	10.01		**F5**	10.18	
					(1.40)			(1.20)						(1.35)			(1.18)
			M6	14.56		**F6**	12.79					**M6**	13.55		**F6**	12.03	
					(1.10)			(1.28)						(1.13)			(1.23)
			M7	16.07		**F7**	16.41					**M7**	15.32		**F7**	14.81	
					(–)			(1.20)						(1.13)			(1.10)
			M8	–		**F8**	19.70					**M8**	17.34		**F8**	16.24	
								(1.09)									(1.13)
						F9	21.38								**F9**	18.35	
								(–)									(1.21)
						F10	–								**F10**	22.14	

Table 3.9: Total counts of males (M), females (F), and juveniles (J) of *Paralicella caperesca* from all samples. Population composition ratios used for univariate comparison shown.

Area	Deployment	M	F	J	M:F	M&F:J
Canyon	15734	81	4	81	0.05	0.95
	15741	8	12	180	1.50	9.00
	56817	22	13	28	0.59	0.80
	56837	80	33	400	0.41	3.54
	56839	69	86	95	1.25	0.61
	56847	38	19	143	0.50	2.51
	56855	27	18	35	0.67	0.78
Non-Canyon	12174	21	13	16	0.62	0.47
	12600	21	14	127	0.67	3.63
	13200	20	23	41	1.15	0.95
	52216	55	17	258	0.31	3.58
	9756	71	46	35	0.65	0.30

The HMFBL ratio (Sainte-Marie, 1991) could not be calculated as no mature females were identified.

3.3.2.4 Population comparison

The male:female and juvenile:non-juvenile ratios did not differ significantly between canyons and non-canyon environments (Table 3.9; Mann-Whitney U: $n = 12$, $U = 18.50$, $p = 0.876$; $n = 12$, $U = 16.00$, $p = 0.876$ respectively). Both ratios varied widely within test groups. Multivariate analysis showed population composition based on size-class abundance varied significantly between canyon and non-canyon samples (ANOSIM: $R = 0.497$, $p = 0.003$). Cluster analysis confirmed this difference (Figure 3.20) with distinct branches representing canyon and non-canyon samples. SIMPER analysis showed 30% of this dissimilarity was attributed to differences in the counts of the smallest juvenile size-classes (J1 – J3).

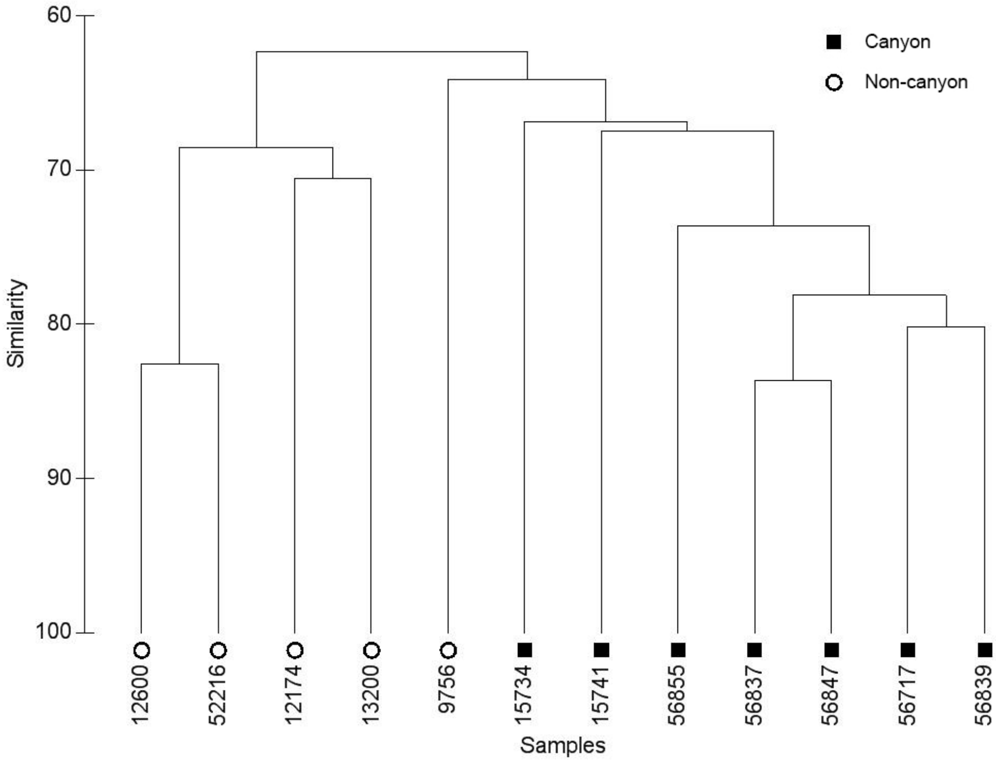


FIGURE 3.20: Dendrogram demonstrating similarity in population composition of *Paralicella caperesca* amongst all samples. Canyon samples indicated by ■, non-canyon samples indicated by ○.

3.4 Discussion

3.4.1 *Abyssorchomene abyssorum*

3.4.1.1 Sexual dimorphism

Females, on average, grew larger than males. The largest female measured had a body length greater than 16.5 mm whereas the largest male was less than 13 mm in length. This size disparity is in agreement with the pattern found by Sainte-Marie (1991) of larger females and smaller males amongst lysianassoids, and reflects the non-mate-guarding pre-copulatory behaviour characteristic of the superfamily (Conlan, 1991).

Relative to body size males had significantly longer antennae with significantly more articles per mm of antenna length. It is widely accepted that scavenging amphipods use chemoreception to detect food-falls (Bozzano & Sardà, 2002; Busdosh et al., 1982; Ide et al., 2006; Premke et al., 2003; Thurston, 1979) and it is possible that these chemosensing abilities extend to detecting any chemical cues given off by conspecifics.

The elongation of antennae, particularly antenna 2, is characteristic of amphipod species in which mating occurs freely in the water column without any form of amplexus or mate-guarding (Conlan, 1991). The effect of possessing longer antennae on chemosensory ability remains untested but it is hypothesised that longer, more articulate, antennae enhance chemosensing ability owing to an increase in chemoreceptor sites (Kauffman, 1994). Steele (1995) has advanced arguments that elongate antennae and associated organelles may enhance tactile detection of females by searching males prior to mating.

3.4.1.2 Sexual development

Each female had two ovaries of approximately equal size and number of oocytes. Based on this symmetry and the contents of complete ovaries recovered, the maximum possible brood size of an individual ranges from 36 – 78 offspring. There is no apparent relationship between oocyte number and body length in *A. abyssorum* (Figure 3.11b), as has also been recorded for immature *Paralicella caperesca* (Thurston, 1979) and *E. gryllus* (Ingram & Hessler, 1987). A reduction in the number of oocytes with ovarian maturation has been recorded for other lysianassoid species including *Hirondellea gigas* Birstein & Vinogradov, 1955 (Hessler et al., 1978), *P. caperesca* (Thurston, 1979), *Pseudorchomene rossi* Walker, 1903 (Thurston, 1979, as *Orchomene*), and *E. gryllus* (Ingram & Hessler, 1987). As such, actual brood size of A. abyssorum is most probably toward the lower end of this estimate. Brood size in lysianassoid species correlates with female body length but varies widely (Sainte-Marie, 1991). The estimated brood size of *A. abyssorum* is comparable to that of other lysianassoids of similar size (Figure 3.21).

In lysianassoid amphipods oostegites develop over a variable number of instars (Ingram & Hessler, 1987; Stockton & DeLaca, 1982), seven oostegite bearing size-classes have been identified in the case of *A. abyssorum.* Three oostegite size classes are apparent in *A. abyssorum* although the smallest oostegite stage (OS1) may be composed of multiple size-classes as size increases during early oostegite development are often small and potentially confound analyses. The frequency of the most developed oostegite stage (OS3) increased with increasing size-class number. The majority (84%) of oostegites belonging to the most developed stage (OS3) were setose. Setose OS3 oostegites were found in females from F5 onwards. The presence of long apical setae on oostegites is an

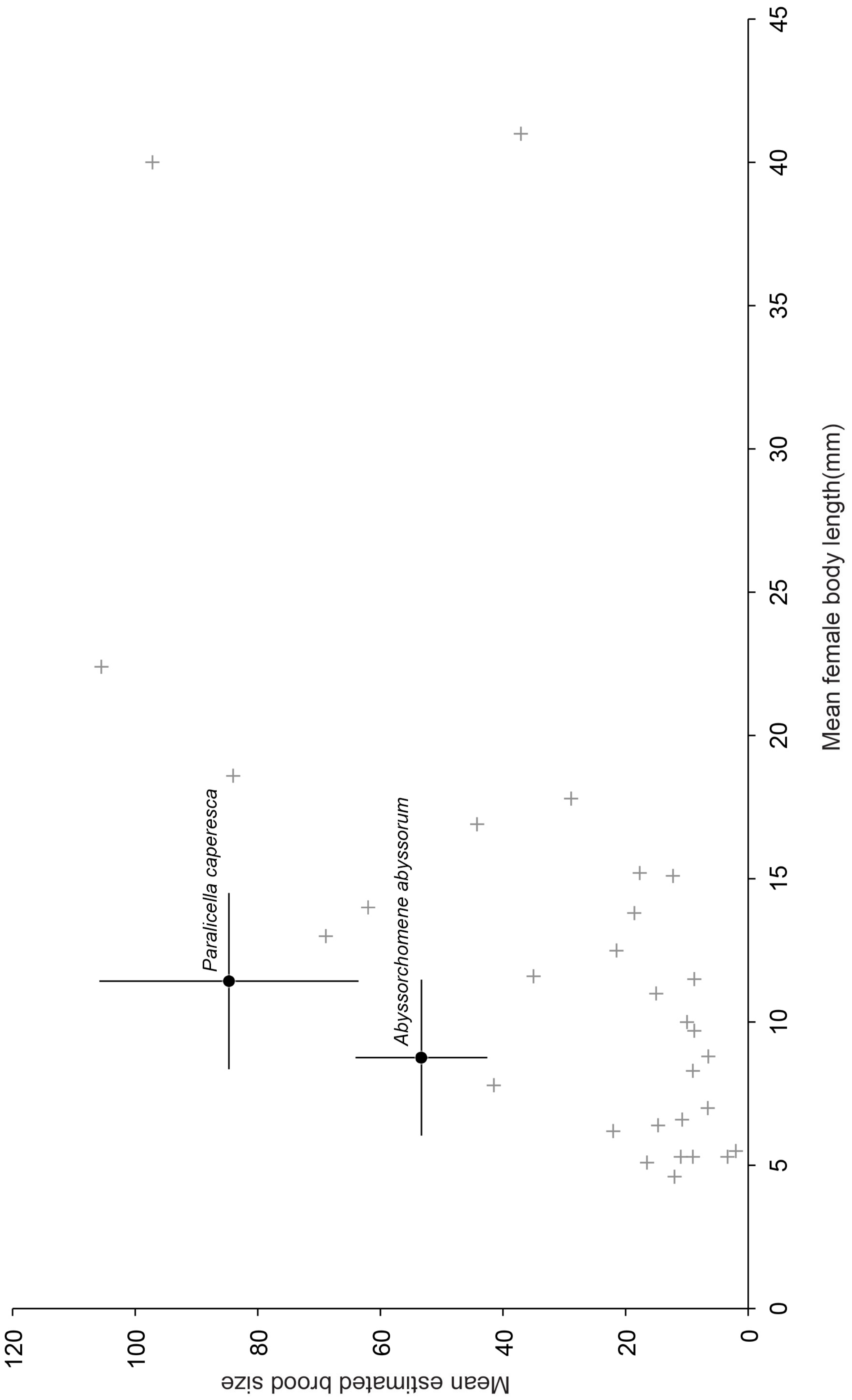


FIGURE 3.21: Estimated brood size as a function of mean female body length from lysianassoid species population studies collected by Sainte-Marie (1991). Data from this study for *Abyssorchomene abyssorum* and *Paralicella caperesca* are shown in black with standard deviations indicated by black bars.

indicator of sexual maturity in female amphipods with setae found in lysianassoids, and some other groups, interlocking to form a brood pouch (Steele, 1991).

Although calculation of the HMFBL ratio (Sainte-Marie, 1991) for *A. abyssorum* proved inconclusive, the finding of mature F5 females suggests that *A. abyssorum* practices iteroparity and is capable of having multiple broods in a lifetime. The variability of oocyte size with body size also adds weight to this theory, with the largest oocytes found in a mid-size female. This hypothesis is further supported by the presence of mid-size, and on two occasions mature, females with empty ovaries, suggesting females return to food-falls following brood-release. An iteroparous lifestyle is advantageous in an unpredictable environment where conditions and food availability are variable. By dividing reproductive investment across multiple broods A. abyssorum increases its chances of reproductive success and reduces the risk of failing to reach sexual maturity, not successfully reproducing, or losing all offspring in a failed brood.

The absence of ovigerous females in any of the samples is expected. With few exceptions (Blankenship et al., 2006; Kaïm-Malka, 2003, 2005), brooding deep-sea scavenging amphipods have not been recorded at food-falls (Ingram & Hessler, 1987; Sainte-Marie, 1991; Thurston et al., 1995). Aggregations of amphipods at food-falls increase the risk of predation by fish (Janßen et al., 2000; Jones et al., 1998; Lampitt et al., 1983), decapods (Jamieson et al., 2009), and other amphipods (Jamieson et al., 2011). Brooding females will also be at greater risk of predation due to reduced mobility when carrying a brood, and more vulnerable as a result of a softened cuticle, as was recorded in an ovigerous individual of *Eurythenes gryllus* by Thurston et al. (1995) and post-release individuals of the same species (Ingram & Hessler, 1987). Many scavenging amphipod species have modified digestive tracts enabling significant food storage (Dahl, 1979) and elastic ventral arthrodial membranes allowing distension and ventral expansion of the pereon to maximise food intake (Shulenberger & Barnard, 1976; Thurston, 1979). While *A. abyssorum* does not exhibit the same degree of pereon extension as highly specialised *Paralicella* spp., the degree of gut distension may be sufficient to impinge on the brood pouch, resulting in partial or total extrusion of the brood.

3.4.1.3 Population characterisation and comparison

Abyssorchomene abyssorum appears to pass through at least two juvenile size-classes (J1, J2), three male (M2 – M4), and five to seven female size-classes (F2 – F8; Table 3.4). Calculated linear growth factors are close to or above 1.26 implying at least a doubling of body volume following the moult process. These factors are comparable to those found for early instars of *E. gryllus* (Ingram & Hessler, 1987; Thurston, 1979), larger than those of *P. caperesca* and *Orchomenella gerulicorbis* (Thurston, 1979, as *Orchomene*) and much higher than the factors derived for *Scopelocheirus hopei* Costa, 1851 (Kaïm-Malka, 2003), and *Tmetonyx similis* Sars, 1891 (Kaïm-Malka, 2005). It is not clear whether these high growth factors are an adaptation to a necrophagous lifestyle or occur for another reason. Amongst females from both northern and southern stations there is a trend for decreasing growth factors with increasing body size, which is probably a reflection on the changing balance between somatic and gametic growth. The relatively low growth factor between stages F2 and F3 may be explained by the problems in resolving normal distributions of earlier size-classes. The group of juveniles that could not be resolved as a normally distributed population (J2) is likely to be composed in part of individuals, mainly from size-class F2 in which sexual characters could not be detected. The earliest stage of oostegite development can be very difficult to identify, particularly in small individuals.

The variability of juvenile abundances, in particular of J1, is responsible for a large amount of amongst sampling area variation. In most instances, juveniles formed a higher proportion of the total population at northern stations than at southern stations. This was particularly apparent at the northeast sampling area in 2007 and 2009. The increased proportions of juveniles remained for successive years and differed substantially from the other sampling areas and years. A high number of juveniles was not recorded in 2010, but the number of males and females was higher than in previous years. This may be due to the sampling method (e.g. weak local currents at this area may permit high numbers of small juveniles to reach the baited trap), however it may also be indicative of a large size-class within the population. *Abyssorchomene abyssorum* may exhibit a seasonal breeding cycle tied to peaks in secondary production in the overlying waters. However, if breeding cycles were tied to peaks in production, numerous juveniles would be recorded at all 4 sampling areas across all years studied, which is not the case.

An alternate hypothesis is that favourable local conditions (e.g. influx of large or abundant food-falls such as whale carcasses) at the NE sampling area result in increased breeding success. The skewing of the population composition toward the juvenile end of the size spectrum, as increased recruitments are not reflected in subsequent size-classes, suggests that either mortality is high at this sampling area or that favourable conditions are temporary and previous generations have not experienced similarly high levels of recruitment. The uncertainty regarding the cause of these juvenile-dominated populations at the NE sampling area in 2007 and 2009 warrants further investigation.

All male size-classes were present at all sampling areas and in all samples, with little variation in relative abundance and consistent size-classes either side of the CGFZ. On the other hand, differences in female size-classes north and south of the CGFZ are particularly interesting. It was not possible to identify separate size-classes through examination of the entire dataset but when samples were separated by position relative to the fracture zone (north, south), distinct normal distributions were apparent. Females north and south of the CGFZ fall into distinct size-classes with different distributional parameters. Female size-classes south of the CGFZ had consistently higher mean body lengths than their counterparts in the north. Differences in the composition of scavenging amphipod assemblages from the northern and southern sampling areas were also recorded at the community level (Horton et al., 2013).

The major environmental differences between sampling areas in the north and south are tied to productivity and correlated POC flux (Abell et al., in press; Niedzielski et al., in press). The northern boundary of the Sub-Polar Front runs along the CGFZ. The position on this front means that surface waters south of the CGFZ are warmer than those north of the fracture zone (Abell et al., in press). Estimates of primary production from satellite measures of chlorophyll confirm that surface productivity also differs either side of the CGFZ (Abell et al., in press), a trend that is mirrored in pelagic assemblages in the underlying waters (Andrew Brierley, University of St Andrews, pers. comm., Jan 11th 2012). The coupling between upper ocean processes and deep-sea benthic communities is a well-established relationship (Billett et al., 2010; Ruhl & Smith, 2004). The existence of this coupling is supported at the MAR by sediment trap data, which shows that the difference in surface productivity is reflected in deep-sea organic carbon input, with the highest levels recorded at southern stations.

Large pelagic megafauna, such as big-game fish and cetaceans, have been tracked following oceanic front systems (Doksæter et al., 2008; Skov et al., 2008; Waring et al., 2008). Therefore, owing to the location of the Sub-Polar Front and differences in surface productivity (Abell et al., in press), sampling areas south of the CGFZ are more likely to experience a higher input of food-falls. When food is not a limiting factor, energy reserves can be built-up more readily and invested into growth and subsequent reproduction. As female resource investment is an important factor in determining reproductive success and offspring survival it is possible that females at the higher-nutrient southern sampling areas are maximising growth during each successive size-class as a result of increased food-availability.

The differences between populations to the north and south of the CGFZ provide an interesting contrast. While increased surface productivity south of the fracture zone appears to be driving an increase in the mean length of each size-class, high numbers of juvenile size-classes at northern sampling areas suggest increased recruitment north of the fracture zone. Within the confines of this study, it is not possible to identify what is causing these very different population structures.

3.4.2 *Paralicella caperesca*

3.4.2.1 Sexual dimorphism

Sexual dimorphism, while still apparent, was less pronounced than in *A. abyssorum.* No mature females, indicated by setose oostegites, were observed in any samples. Thurston (1979) identified two mature females from a sample of 330 individuals taken at 4855 m deep in the northeast Atlantic. A relatively low number of mature females compared to studies on other species. Mature females of this species very rarely attend food-falls. While brooding females of most scavenging amphipod species are rarely seen at food-falls (Ingram & Hessler, 1987; Sainte-Marie, 1991; Thurston et al., 1995), mature females of non-*Paralicella* species are often observed. The absence of mature females suggests that *P. caperesca* is a semelparous organism. This has been previously theorised based on a small dataset of individuals taken from a single trap (Thurston, 1979). Once reproductive maturity is reached females raise a brood and subsequently die once the brood is released. Despite the lack of mature individuals, females were marginally larger in terms of estimated body length. This is in agreement with the synthesis of Sainte-Marie (1991). *Paralicella caperesca* shares many characteristics with lysianassoids. As such, the observed size difference between males and females suggests that *P. caperesca* practices non-mate-guarding pre-copulatory behaviour, as recorded in lysianassoid amphipods (Conlan, 1991).

Males had significantly longer antennae with significantly more articles per mm of antenna length. As previously discussed, it is widely accepted that scavenging amphipods use chemoreception to detect food-falls (Bozzano & Sardà, 2002; Busdosh et al., 1982; Ide et al., 2006; Premke et al., 2003; Thurston, 1979) with the possibility that chemosensing abilities extend to detecting chemical cues given off by conspecifics. The elongate antennae of male *P. caperesca* is believed to enhance tactile detection during mate searching (Steele, 1995) and chemosensing ability (Kauffman, 1994). It is characteristic of an amphipod species in which mating occurs freely in the water column without mate-guarding (Conlan, 1991), further supporting the theory that *P. caperesca* practices mating and brooding behaviour similar to that of other lysianssoid amphipods.

3.4.2.2 Sexual development

Based on the contents of all complete ovaries recovered, the maximum possible brood size of *P. caperesca* ranges from 52 – 150 offspring with a mean estimated brood size of 84. Contrary to the findings of Ingram & Hessler (1987), there is no apparent relationship between oocyte number and body length (Figure 3.16b). Thurston (1979) observed that oocyte number in female *P. caperesca* was "at most weakly related to body length". Total oocyte counts were less variable than those of *A. abyssorum* and substantially higher. Once again using lysianassoid amphipods as a reference point, brood size loosely correlates with female body length but varies widely (Sainte-Marie, 1991). The estimated brood size of *P. caperesca* is substantially larger than that of most lysianassoids of similar size (Figure 3.21). The potential to produce large broods is in keeping with the theory that *P. caperesca* is semelparous, investing substantial resources into one large reproductive output.

The theory that *P. caperesca* is semelparous is further supported by the fact that no empty ovaries were identified in any females examined. A semelparous lifestyle has been identified as a successful reproductive strategy in environments with stable and predictable nutrient input (Fritz et al., 1982, and references therein). If, as theorised, a semelparous strategy is practiced by *P. caperesca* this may go some way to explaining the dominance and apparent success of the *Paralicella* genus in submarine canyons (Duffy et al., 2012), where nutrient input is elevated and relatively consistent (De Leo et al., 2010; Gage & Tyler, 1991; Jannasch & Taylor, 1984; Soliman & Rowe, 2008; Van Oevelen et al., 2011; Vetter, 1995).

Four oostegite size classes were identified across 7 oostegite-bearing female size-classes of *P. caperesca.* The frequency of the most developed oostegite stages (OS3, OS4) increased with increasing size-class number. No oostegites were setose regardless of oostegite stage and size-class. This lack of setose oostegites indicates that no female *P. caperesca* were sexually mature suggesting that mature females, and by extension brooding females, do not attend food falls.

The lack of mature and oviparous females leaves an important gap in our understanding of this species. Unfortunately due to the risks of predation (Jamieson et al., 2009, 2011; Janßen et al., 2000; Jones et al., 1998; Lampitt et al., 1983) and the apparent semelparous lifestyle of *P. caperesca* it is unlikely that either of these size-classes will ever be caught using baited traps. Brooding females are particularly unlikely to attend a food fall owing to their increased vulnerability to predation. This is the result of a softened cuticle while brooding (Ingram & Hessler, 1987; Thurston et al., 1995) and modified digestive tract to maximise food intake (Shulenberger & Barnard, 1976; Thurston, 1979) and facilitate food storage (Dahl, 1979), which inhibits the brood-carrying ability of the female.

3.4.2.3 Population characterisation and comparison

Paralicella caperesca has 4 juvenile (J1 – J4) and 5 male (M3 – M8) bait-attending size-classes. There are at least 7 female size-classes (F3 – F10; Table 3.8), with the notable absence of sexually mature females. Linear growth factors were calculated in the range of 1.10 – 1.84. The growth factors determined here for *P. caperesca* are comparable to those previously documented for this species (Thurston, 1979). These factors are lower than those of *A. abyssorum* (Duffy et al., 2013) and early instars of *E. gryllus* (Ingram & Hessler, 1987; Thurston, 1979). They are similar to those reported for *Orchomenella gerulicorbis* (Thurston, 1979, as *Orchomene*), and higher than documented growth factors for *Scopelocheirus hopei* (Kaïm-Malka, 2003), and *Tmetonyx similis* (Kaïm-Malka, 2005).

There are marked differences in the population composition between the canyon samples and the non-canyon samples. The estimated mean total body length for each size-class was consistently higher for canyon size-classes than it was for their counterparts from the non-canyon environments. A number of environmental factors differentiating between these two sampling areas may be responsible for these differences. Canyon environments are inherently shallower than non-canyon environments, and as such the waters within them are marginally warmer. While the non-canyon group included one shallower site (3852‘ m) not from the abyssal plain (D092/9756/008) this sample group was nevertheless skewed toward deeper sampling. Growth experiments examining the effect of temperature on amphipod growth rates have shown a size increase at warmer temperatures (Highsmith & Coyle, 1991; Maranhao & Marques, 2003; Panov & McQueen, 1998; Pöckl, 1992; Sutcliffe et al., 1981). However, the temperature difference between sample sites in canyons and abyssal plains is small compared to the temperature ranges used for laboratory experiments, making this hypothesis unlikely.

Another possible, yet unlikely, hypothesis is that canyons and non-canyon environments house separate subspecies of *P. caperesca.* It is proposed that the species *Eurythenes gryllus* is in fact a species complex composed of similar species or subspecies separated by depth (Havermans et al., 2012). Such speciation remains only a remote possibility for *P. caperesca* as individuals showed no visible species-level morphological variability. *Paralicella caperesca* has been identified throughout the North Atlantic (Duffy et al., 2012; Thurston, 1990) with no reported variance from standard morphotypes. Molecular analysis will be necessary to completely rule-out this hypothesis but it remains unlikely based on current knowledge.

Supported by the differences seen between populations of *Abyssorchomene abyssorum* in areas of different surface productivity, it appears that the most probable reason for larger total body length in canyon size-classes is a result of the increased nutrient input to canyon environments. While the availability of large food-falls to deep canyon sites is yet unknown, increased nutrient availability and heightened secondary production have been frequently documented (De Leo et al., 2010; Gage & Tyler, 1991; Jannasch & Taylor, 1984; Soliman & Rowe, 2008; Van Oevelen et al., 2011; Vetter, 1995). The high abundances of scavenging amphipods found in submarine canyons (Duffy et al., 2012) lends further support to the theory that nutrient availability in an environment has significant effects on scavenging amphipods at both the community and population levels.

While canyon populations had larger total body length for the same size-class than non-canyon populations, non-canyon populations possessed much greater numbers of the largest size-classes (F6 – F10, M6 – M8). These size-classes were represented by few individuals in canyon populations and in come cases absent altogether. Sexual characteristics could often be identified in small individuals from canyon samples but not in similar sized individuals from non-canyon environments. The size distribution of these small individuals overlapped with the most-developed juvenile size-classes (J3, J4). Expression of sexual characteristics in smaller individuals from canyon samples suggests that some factor is causing earlier reproductive development in canyon populations compared to non-canyon populations.

As with size differences between canyon and non-canyon size-class parameters there are a number of possible explanations for this. Temperature variations have been previously attributed to similar trends in other amphipod species (Highsmith & Coyle, 1991; Sheader, 1983) but, as previously discussed, water in the sampled canyons was only marginally warmer than the non-canyon sites. Differences in nutrient availability are the most likely reason. The link between nutrient availability and sexual development in this species has been previously suggested by Thurston (1979). With an abundant food supply, individuals in canyons are able to apply resources to both growth and reproductive output allowing the onset of earlier reproductive development (Sutcliffe et al., 1981). Earlier maturation and oostegite development with nutrient rich conditions has been previously reported in the scavenging amphipod *Tmetonyx similis* (Kaïm-Malka, 2004). This developmental plasticity in response to food supply has also been observed in the estuarine Gammarid amphipod *Gammarus duebeni* (Sheader, 1983) and the vent-dwelling *Bouvierella curtirama* (Sheader et al., 2004). In the food-limited abyssal plains resources are more constrained and therefore input into reproductive development is delayed until further growth has been achieved.

Without mature females is is not possible to ascertain if earlier reproductive development also results in earlier sexual maturity. The evidence to suggest that this is the case is particularly strong if *P. caperesca* is semelparous. Working under the hypothesis of semelparity, evidence suggests that individuals in canyons reach sexual maturity at smaller sizes than their counterparts in non-canyon environments. Following maturity and reproduction individuals die and are therefore no longer found in baited traps, explaining the lack of the largest size-classes in canyon samples. Members of canyon populations will have matured, reproduced, and died before growing to this size.

3.4.3 Species comparison

There is strong evidence that *Abyssorchomene abyssorum* and *Paralicella caperesca* practice contrasting reproductive strategies. These differing strategies have allowed these two species to become highly successful and highy abundant within their respective study environments (Duffy et al., 2012; Horton et al., 2013). At the MAR *A. abyssorum* dominates at all four sampling areas around the CGFZ. While under the nutrient rich conditions provided by the secondary production hotspots of submarine canyons *P. caperesca* is the dominant scavenging amphipod.

Abyssorchomene abyssorum demonstrates the characteristics of an iteroparous organism capable of producing multiple broods. Mature female *A. abyssorum* were found in great abundance and with varying degrees of oostegite and oocyte development. Empty, 'baggy' ovaries were observed in a number of females suggesting these individuals were attending the bait following reproduction. Potential brood size was comparable to other species believed to be iteroparous (Sainte-Marie, 1991). An iteroparous lifestyle has often been identified as a benefit to organisms living under patchy unpredictable nutrient conditions (Fritz et al., 1982, and references therein), such as those expected at the MAR sites. By avoiding the investment of resources into a single reproductive event at the end of life, A. abyssorum reduces the risk of no reproductive output at all resulting from death before reproduction, failed mating, or total brood mortality caused by unfavourable conditions. The ability to opportunistically reproduce when conditions are favourable is of obvious benefit when food supply cannot be guaranteed or predicted.

Paralicella caperesca has the characteristics of a semelparous organism capable of one reproductive event before death. No mature females were found in this study and were found in very low numbers in baited trap deployments reported by Thurston (1979). Oocyte size showed a strong positive correlation with estimated body length with eggs maturing with increasing body length. No evidence of empty ovaries was seen in any female examined. Potential brood size for this species was particularly large owing to the numerous oocytes and three-tiered arrangement of oocytes in the ovary (Figure 3.15). Early sexual development, most probably due to increased nutrient availability, and underrepresentation of the largest size-classes (F7 – F10, M6 – M8) in samples from submarine canyons further supports semelparity. This 'one shot' approach to reproduction is often associated with success in high nutrient environments with continuous predictable food supply. The increased sediment input and associated heightened food availability in submarine canyons (De Leo et al., 2010; Gage & Tyler, 1991; Jannasch & Taylor, 1984; Soliman & Rowe, 2008; Van Oevelen et al., 2011; Vetter, 1995) reduces the risk of a failed brood resulting from unfavourable trophic conditions. This makes investing heavily into one large reproductive event at the end of life a viable strategy.

Although the samples used for each species in this study were taken at different depths, *A. abyssorum* and *P. caperesca* have overlapping distributions (Horton et al., 2013; Thurston, 1990). Hydrostatic pressure and water temperature have often been identified as important factors controlling scavenging amphipod distributions and therefore community composition of baited trap samples (Thurston, 1990; Thurston et al., 2002). Trophic conditions have previously been suggested as affecting scavenging amphipod community composition (Horton et al., 2013; Premke et al., 2006) and our improved understanding of the contrasting life-histories of scavenging amphipod species supports this. Where nutrient availability is high, species like *P. caperesca*, capable of earlier maturation and a large reproductive output, dominate communities (Duffy et al., 2012). While under less predictable and more patchy conditions a shorter-term reproductive strategy with more, smaller reproductive events, such as that practiced by *A. abyssorum*, proves most successful resulting in community dominance (Horton et al., 2013).

3.5 Conclusions

This study has provided an important contribution to our understanding of the population ecology of two common deep-sea scavenging amphipods. Unfortunately, complete life-history data on deep-sea scavenging amphipods are lacking and further research is necessary in order to better understand the contribution of these ubiquitous animals to the deep-sea ecosystem. The lack of brooding females in baited traps is a clear shortcoming in population studies of this group, but is a problem that is difficult to resolve owing to their altered foraging strategy, or lack thereof. In order to better understand the ecology and importance of deep-sea necrophages more regular sampling of deep-sea scavenger populations (as in Arndt & Beuchel, 2006; Nygård et al., 2009; Sheader, 1983) is required, with a particular focus on common species such as *Abyssorchomene abyssorum* and *Paralicella caperesca*. As hypothesised, populations of both target species differed from one another between study areas. Canyon populations of *Paralicella caperesca* exhibited larger body size for each identified size-class than non-canyon populations. Populations of *Abyssorchomene abyssorum* south of the Charlie Gibbs Fracture Zone had larger body sizes for each identified size-class than their counterparts north of the fracture. There is strong evidence to suggest that these population-level differences are tied to nutrient availability.

Chapter 4

Synthesis of deep-sea scavenging amphipod studies in the North Atlantic

4.1 Introduction

The last published review of scavenging amphipod distributions in the North Atlantic was by Thurston (1990) over 20 years ago. Since the publication of this review many new studies of these ecologically important organisms have been made (e.g. Christiansen, 1996; De Broyer et al., 2004; Duffy et al., 2012; Horton et al., 2013; Jones et al., 1998; Kemp et al., 2006; Premke et al., 2006), but these data have yet to be combined as a synthesis. Developments in multivariate statistics over the last two decades (Clarke, 1993) provide us with the means to use the vast amount of data available on scavenging amphipod assemblages of the North Atlantic in order to further understand the distributions of these organisms and the environmental factors controlling them.

Broad-scale distributions of deep-sea species are largely understudied and poorly understood. Barriers to dispersal of deep-sea organisms are difficult to identify (Lessios et al., 2001) although distribution boundaries often follow topographic divides (Vinogradova, 1959). A synthesis of 1 031 deep-sea species from a range of taxa (Cirripedia, Cnidaria and Ctenophora (as Coelenterata), Decapoda, Echinodermata, Isopoda, Porifera, Pycnogonida (as Pantopoda), and Siboglinidae (as Pogonophora)) identified that only 4%

of examined species were found in the Atlantic, Pacific, and Indian Oceans with 84% of species confined to one ocean (Vinogradova, 1959). Genera and families were widely distributed across all three oceans. Species with large depth distributions generally have wide geographic ranges (Vinogradova, 1959; Young et al., 1997) and deep-sea species often have larger geographic ranges than their shallow-water counterparts (Collins et al., 2001; Koslow, 1993; Young et al., 1997). In contrast to dispersal patterns of shallow species, deep-sea species with large eggs have broader geographic ranges than those with small eggs (Collins et al., 2001; Young et al., 1997). Dispersal potential of deep-sea species is still poorly understood and requires a great deal of further research.

There is strong circumstantial evidence for wide distribution of deep-sea scavenging amphipod species across a range of ocean basins and varying environmental conditions (Barnard & Karaman, 1991; Thurston, 1990). This is in spite of the brooding behaviour practiced by peracarids. Many deep-sea organisms believed to have wide geographic distributions have dispersive eggs or a planktonic larval stage as part of their development (Vinogradova, 1959; Young et al., 1997), which may explain their wide distributions. However, this is not the case for scavenging amphipods. Previous studies have shown that gene-flow between basins occurs but that it is severely restricted amongst varying depths, potentially leading to population isolation and even speciation (France, 1994; Havermans et al., 2012; Thurston et al., 2002). The North Atlantic deep sea has been sampled using baited traps for many years, as such, the Discovery Collections (National Oceanography Centre, Southampton, UK) house a large and comprehensive collection of deep-sea scavenging amphipod samples. Thanks to the efforts of M. H. Thurston and T. Horton (National Oceanography Centre, Southampton, UK) the identification of species in these samples are made with confidence and consistency allowing for analysis of this dataset to compare amongst assemblages throughout the North Atlantic and an assessment of the environmental factors affecting and limiting distribution. Using these data it is possible to produce habitat suitability maps for a number of common amphipod species distributed in the North Atlantic.

To produce habitat suitability maps for any organism it is necessary to identify its environmental tolerances and the parameters of its ecological niche. The Ecological Niche Factor Analysis (ENFA; Hirzel et al., 2002) has been used to assess distributions of animals in both terrestrial (e.g. Basille et al., 2008; Dettki et al., 2003; Gallego et al., 2004; Hirzel et al., 2004; Pettorelli et al., 2009; Reutter et al., 2003; Triolo et al., 2011;

Zaniewski et al., 2002) and marine (e.g. Galparsoro et al., 2009; Valle et al., 2011) settings. This analysis works by comparing the observed distribution of a species within ecogeographical space (cells with species present) to the total available ecogeographic space (all cells within study area). From this it is possible to calculate marginality; the difference between the ecogeographic means of inhabited cells and total available ecogeographic space, and specialisation; the difference between variability of inhabited cells and total available ecogeographic space (Hirzel et al., 2002).

The ENFA is particularly well suited for use when presence-only data is available (Hirzel et al., 2002). The lack of true absence data is a common problem with ecological datasets (Hirzel et al., 2002; Soberón & Peterson, 2005) and while for some analyses one must assume absence this is best avoided where alternative tests or models are available. Utilising an ENFA it is possible to identify which factors are closely linked to whether or not an organism inhabits available space and characterise the habitat that an organism prefers (Basille et al., 2008). Using the results of these analysis with ecogeographical variable maps containing environmental data for a study area it is possible to produce a habitat suitability map assigning a suitability value to each cell of of the study area indicative of the species potential distribution.

Using this synthesis it is possible to test the hypotheses that scavenging amphipod communities vary amongst depth zones but remain relatively constant in their composition across abyssal basins in the North Atlantic. It is also possible to test if taxa identified as cosmopolitan are truly capable inhabiting the range of niches necessary for ocean-wide deep-sea distributions.

4.2 Materials and Methods

Distribution data for deep-sea scavenging amphipod species were collated from a range of sources with samples sorted to a varying degree of resolution. Published records of baited-trap deployments in the North Atlantic (Figure 4.1; Appendix B; Christiansen, 1996; Duffy et al., 2012; Horton et al., 2013; Jones et al., 1998; Kemp et al., 2006; Lampitt et al., 1983; Premke et al., 2006; Thurston, 1979, 1990) were combined with unpublished data from the Discovery Collections made available by M. H. Thurston (National Oceanography Centre, Southampton, UK). All samples were collected using

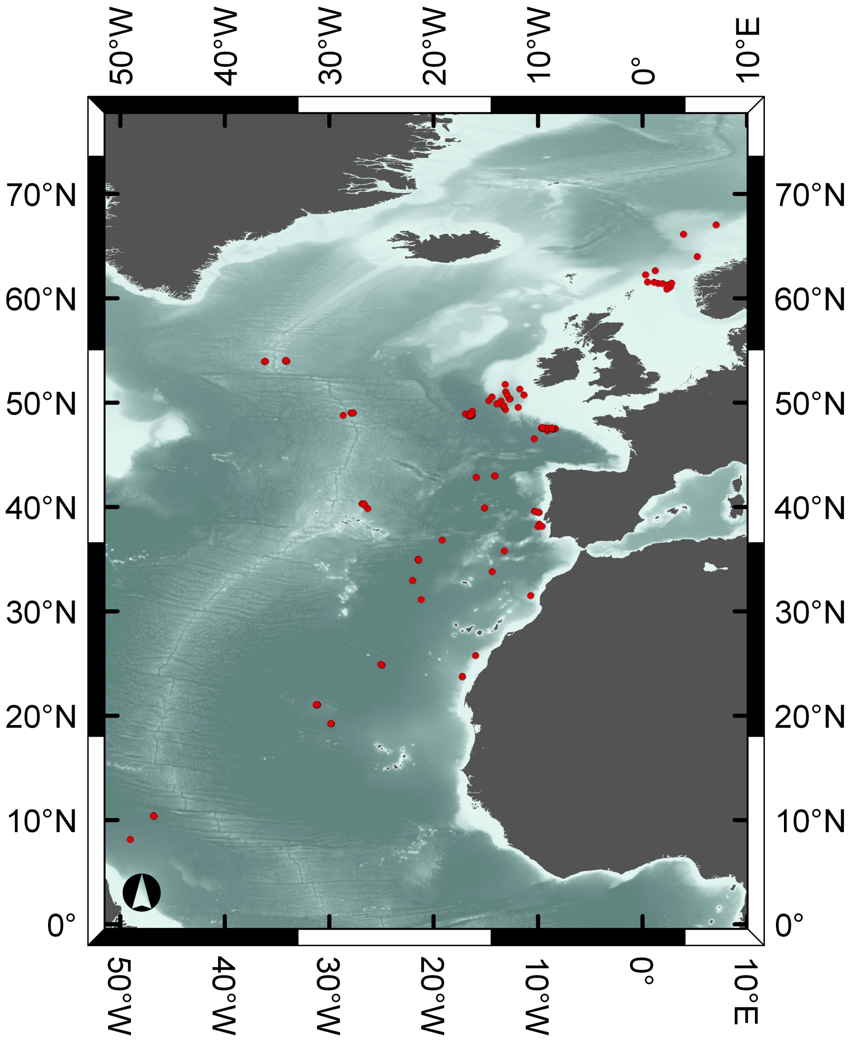


FIGURE 4.1: Map indicating the locations of all samples used in synthesis of scavenging amphipod studies in the North Atlantic.

baited traps deployed on or within close proximity to the seabed. Samples were grouped by sampling area (e.g. Porcupine Abyssal Plain, Madeira Abyssal Plain, Porcupine Seabight) and depth zone (abyssal, > 4000 m; bathyal, 1000 m – 4000 m; dysphotic, 200 m – 1000 m deep). Due to variation in trap design, sampling season, and sampling year, relative abundance data could not be confidently used for comparative analysis. Data were checked to ensure agreement between species classification and transformed to presence/absence for subsequent analyses.

Environmental data were retrieved from published databases. Global temperature (Locarnini et al., 2010), salinity (Antonov et al., 2010), and dissolved oxygen (Garcia et al., 2010) data were retrieved from the 2009 World Ocean Atlas (WOA09; NOAA, USA).

Data were plotted in ArcMap, part of the ArcGIS software suite (Environmental Systems Research Institute, Redlands, CA, USA). Raster layers were created from point data for each cell (1° by 1°) and a mosaic raster was created for each variable using the deepest available data-layer for each cell (Figure 4.2).

Net primary productivity data were retrieved from Oregon State University's Ocean Productivity database. These data were calculated using the Vertically Generalized Production Model (Behrenfeld & Falkowski, 1997) and surface chlorophyll concentrations, sea surface temperature data, and cloud-corrected incident daily photosynthetically active radiation collected using the Moderate Resolution Imaging Spectroradiometer satellite (MODIS; NASA, USA). Monthly productivity data for a 10-year period (2002 – 2012) were added to ArcMap, a decadal mean was calculated, and a mosaic raster created. This raster was down-sampled to match the resolution of the other environmental variable layers (1° by 1°; Figure 4.3a).

4.2.1 Comparison of scavenging amphipod assemblages of the North Atlantic

Environmental variables (bottom temperature, salinity, dissolved oxygen, primary productivity) were exported for each sampling point using the Spatial Analyst toolset in ArcMap. Accurate depth and location data were available for all samples and were used in conjunction with extrapolated data for analyses. All environmental data were normalised to account for different units used for each variable.

Multivariate data analyses were performed in PRIMER 6 statistical software (Clarke & Gorley, 2006). Similarity matrices were created based on Bray-Curtis similarity (Bray & Curtis, 1957) for community composition data and Euclidean distances for environmental data. Multi-Dimension Scaling (MDS) plots were created to visualise sample similarity. An ANOSIM test (Clarke, 1993) was used to compare community composition amongst sampling areas nested within depth zone. Cluster analysis was performed to highlight the grouping of samples and a SIMPER analysis (Clarke, 1993) was used to identify which species were contributing most to community composition differences between depth zones.

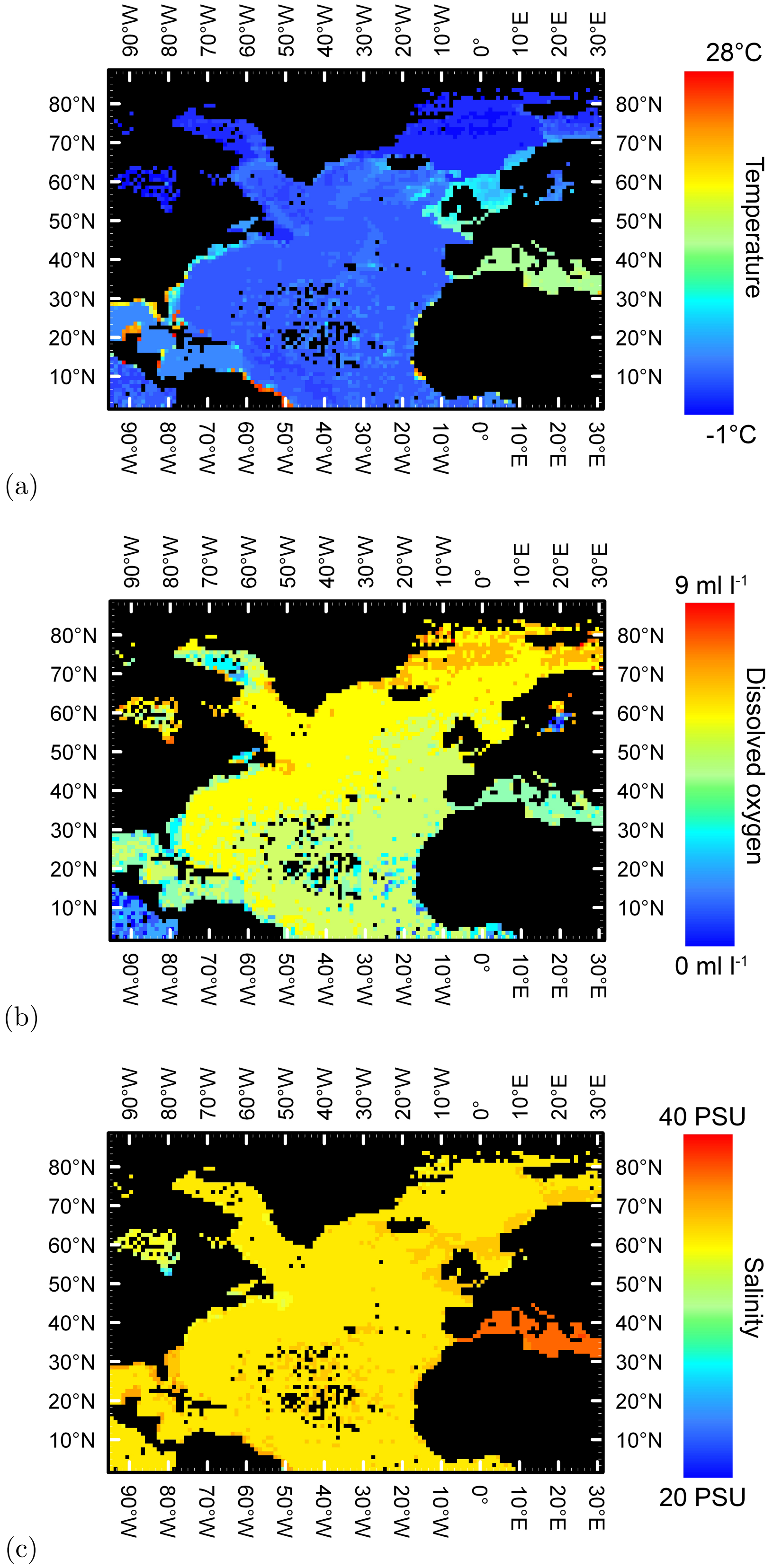


FIGURE 4.2: Ecogeographical variable maps for temperature (4.2a; Locarnini et al., 2010), dissolved oxygen (4.2b; Garcia et al., 2010), and salinity (4.2c; Antonov et al., 2010). Data retrieved from the 2009 World Ocean Atlas (NOAA, USA).

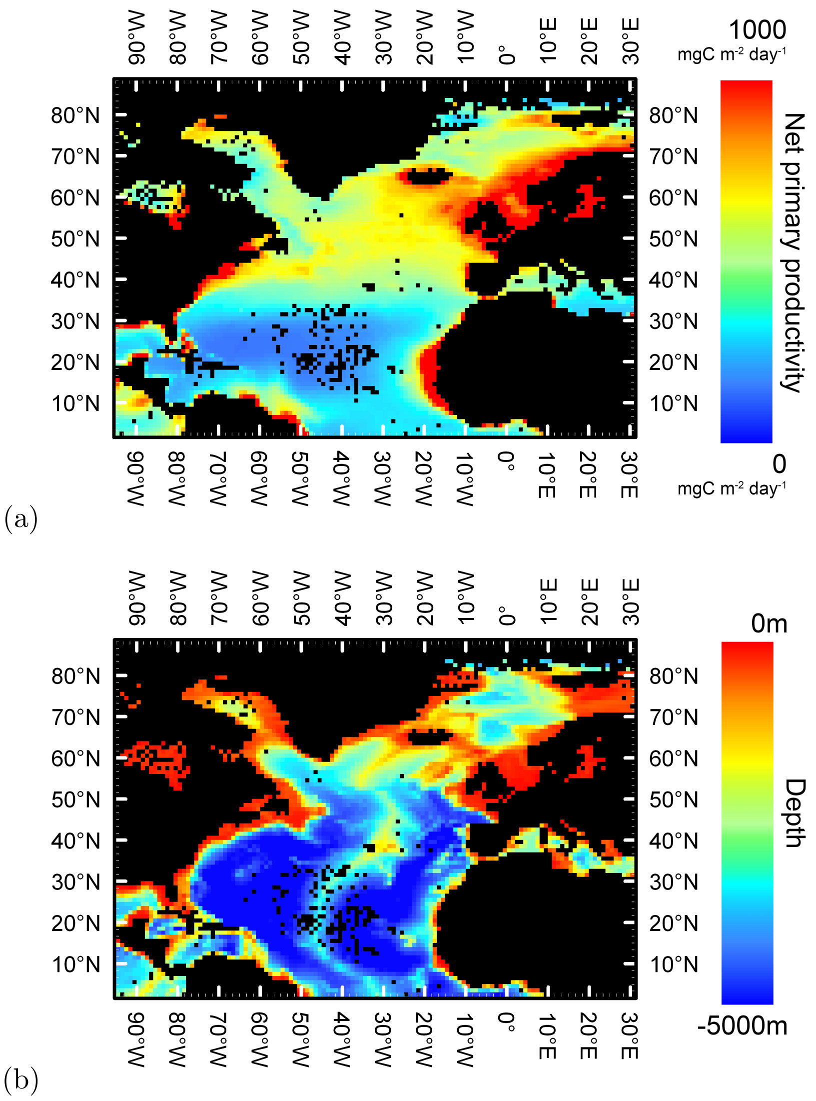


FIGURE 4.3: Maps showing all ecogeographical variables used for analyses.

A second nested ANOSIM, using identical factors, was performed on environmental data to determine if the differences seen in community composition were reflected in environmental variables. SIMPER analysis was used to identify which environmental variables contributed most to variability amongst groups. In order to identify which environmental variables correlated best with variations in community composition a BEST analysis (Clarke, 1993) was performed using both sets of data.

4.2.2 Modelling distributions of common scavenging amphipod species

Raster layers for environmental variables (bottom temperature, salinity, dissolved oxygen, and primary productivity) and a GEBCO (http://www.gebco.net) depth grid were clipped to the extent of the North Atlantic. The depth grid was down-sampled to match the resolution of the environmental variable layers (1° by 1°; Figure 4.3b). All layers were Box-Cox transformed (Box & Cox, 1964) and converted into ASCII grid format for analysis in R statistical software (R Development Core Team, 2012). Using the 'adehabitat' package (Calenge, 2006) an Ecological Niche Factor Analysis (ENFA; Basille et al., 2008; Hirzel et al., 2002) was performed using the ASCII environmental variable layers as ecogeographical variables and presence data for each of the target taxa (*Abyssorchomene* spp., *Paralicella* spp., *Tmetonyx* spp., and *Eurythenes gryllus*). Presence data for *Abyssorchomene* spp., *Paralicella* spp., and *Tmetonyx* spp. were often only available to genus level. Therefore analysis at genus level was considered the most favourable approach when examining dietributions of these three taxa.

A Monte Carlo test was used on each ENFA output to confirm significance of the marginality and specialisation compared to that of random distribution. Using the ENFA output, coupled with environmental variable layers, a habitat suitability map was produced for each taxa. This map indicated the suitability of each cell for the species examined based on the combined environmental variables. From these maps it was possible to infer species distributions.

4.3 Results

A total of 74 species, from 23 described genera, were identified from all data sources (Appendix B). In addition, two undescribed genera were also identified. Not all species have been formerly described and the classification of many taxa requires major revision. Twenty-five species were found at dysphotic depths, 68 at bathyal depths, and 22 at abyssal depths. Four species (*Abyssorchome abyssorum*, *Eurythenes gryllus*, *Hirondellea trioculata* Chevreux, 1889, and *Orchomene* sp. 2) were found inhabiting dysphotic, bathyal, and abyssal depths. Twenty-one species inhabit both the dysphotic and bathyal regions. Eighteen species were found at bathyal and abyssal depths.

4.3.1 Comparison of scavenging amphipod assemblages of the North Atlantic

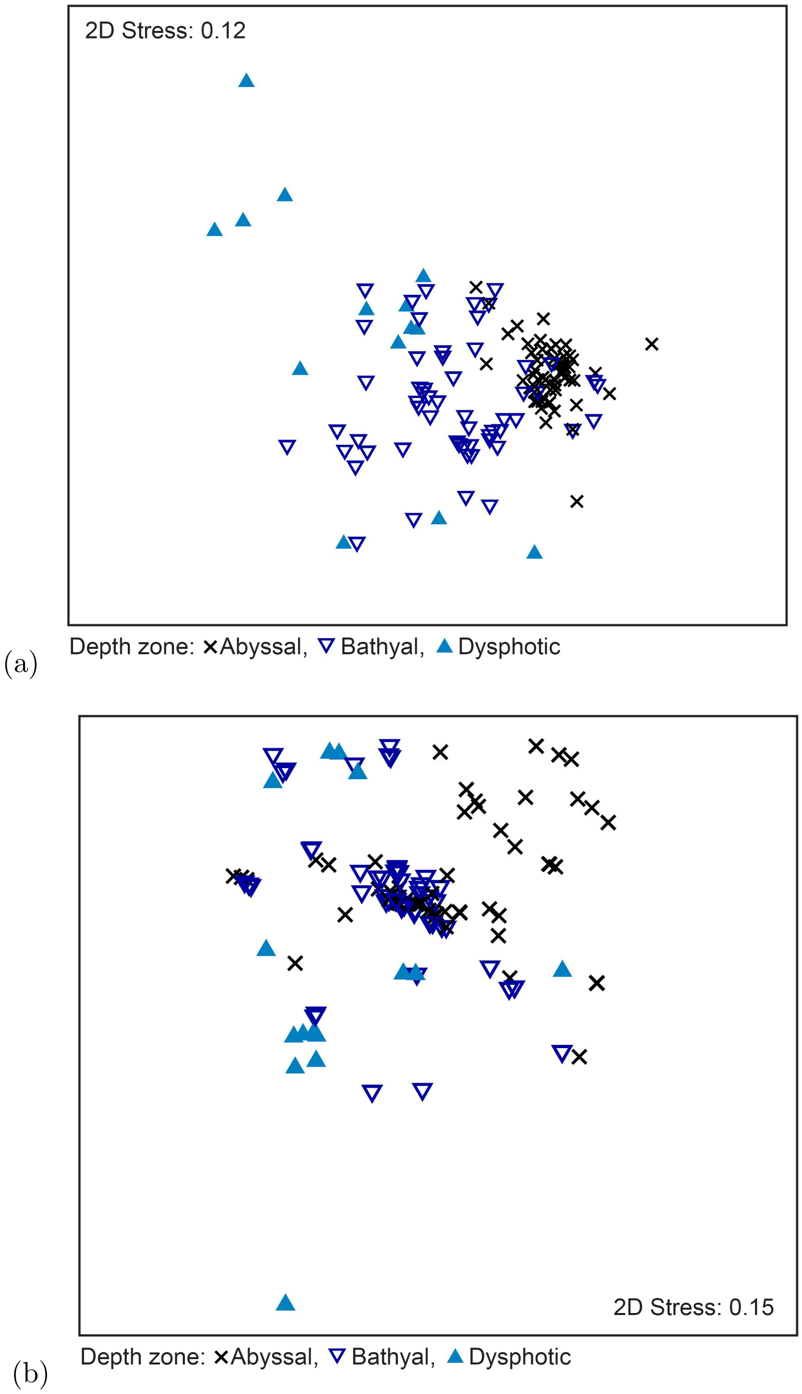
MDS plots identified clear groupings of samples based on depth zone and sampling area (Figures 4.4a; 4.5a). Similar groupings were seen with environmental data (Figures 4.4b; 4.5b). The ANOSIM test confirmed significant differences in community composition in samples from differing depth zones (ANOSIM: $R = 0.334$, $p = 0.001$) with pairwise analysis showing significant difference between all three depth zones (ANOSIM: abyssal/-bathyal, $R = 0.382$, $p = 0.002$; abyssal/dysphotic, $R = 0.800$, $p = 0.002$, bathyal/dysphotic, $R = 0.336$, $p = 0.0013$). The nested analysis comparing areas within each depth zone showed significant difference in community composition amongst areas (ANOSIM: $R = 0.548$, $p = 0.001$). Cluster analysis corroborated the grouping of samples based on depth zone and sampling area.

ANOSIM analysis of environmental data showed significant differences amongst depth zones (ANOSIM: $R = 0.548$, $p = 0.001$) and sampling areas nested within depth zone (ANOSIM: $R = 0.239$, $p = 0.007$). Simper analysis identified temperature as the main contributor to depth zone dissimilarity (35.42 %). Over half (53.77 %) of depth zone dissimilarity was explained by the cumulative contributions of temperature and dissolved oxygen.

Bottom temperature was identified as the single environmental variable with the closest correlation to differences in community composition (BEST: correlation = 0.329). The correlation with bottom temperature combined with primary productivity and temperature combined with dissolved oxygen were comparable to the correlation with temperature alone (BEST: 0.322, 0.320 respectively).

4.3.2 Modelling distributions of target scavenging amphipod species

ENFA models were successfully run on all target taxa allowing for habitat suitability maps to be produced. The distribution of *Eurythenes gryllus* was significantly different from random (Monte Carlo randomisation test: $p = 0.001$) and primarily correlated to depth, as indicated by the arrow length for this variable on the ENFA biplot (Figure 4.6a). Salinity and primary production were the next greatest contributing factors. The directions of each arrow for these environmental factors indicate that *E. gryllus*



(a)

(b)

FIGURE 4.4: MDS plots showing similarity amongst scavenging amphipod samples from the NE Atlantic. Samples labelled by depth zone. 4.4(a) Bray-Curtis similarity of sites based on community composition. 4.4(b) Euclidean distance of sites based on environmental variables.

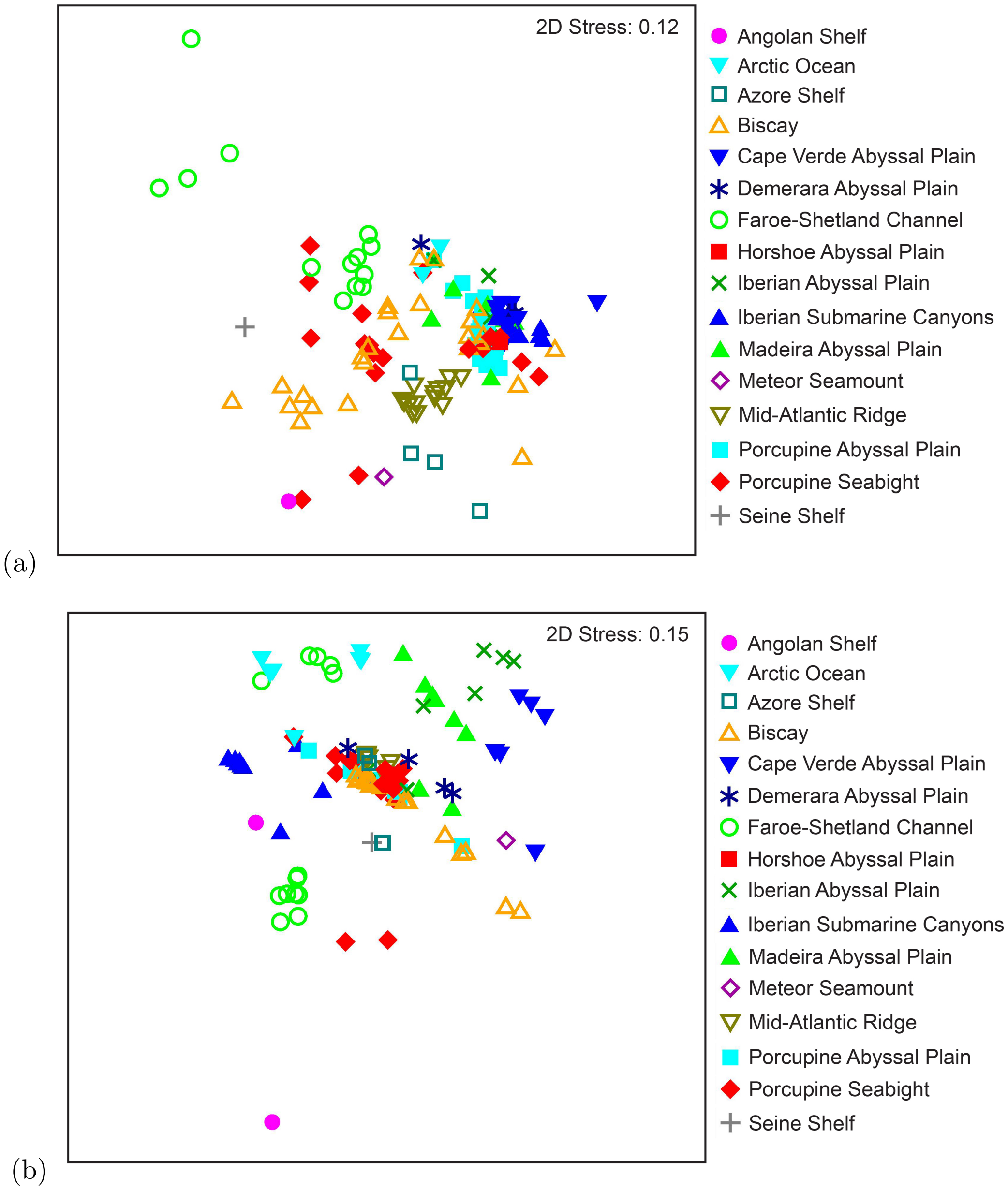


FIGURE 4.5: MDS plots showing similarity amongst scavenging amphipod samples from the NE Atlantic. Samples labelled by sampling area. 4.5(a) Bray-Curtis similarity of sites based on community composition. 4.5(b) Euclidean distance of sites based on environmental variables.

shows preference toward deep habitats with relatively low salinity and high primary productivity in overlying surface waters. The habitat suitability map (Figure 4.6b) indicates highly suitable habitat for this species across the majority of the deep sea of the North Atlantic, with the notable exception of the Mediterranean Sea.

Paralicella spp. distribution was also significantly different from random (MC: $p = 0.001$) and primarily linked to depth (Figure 4.7a) with salinity and temperature the second and third closest correlated variables. Primary productivity had the lowest impact of the five variables. The biplot plotted from the ENFA results suggests *Paralicella* spp. prefer deep, cold habitats with relatively low salinity. The habitat suitability map (Figure 4.7b) indicates suitable conditions for *Paralicella* spp. across almost all deep-sea areas of the North Atlantic with high suitability across all abyssal plains. Once again the Mediterranean Sea is the exception with low suitability despite deep water.

Abyssorchomene spp. distribution was significantly different from random (MC: $p = 0.001$). The biplot produced from the ENFA performed for *Abyssorchomene* spp. (Figure 4.8a) closely resembles that of *E. gryllus* (Figure 4.6a). As such, the habitat suitability map for *Abyssorchomene* spp. (Figure 4.8a) is very similar to that of *E. gryllus.* In descending order, salinity, primary production, and depth were identified as the main contributing factors to *Abyssorchomene* spp. distribution.

In contrast to the three previous target taxa, *Tmetonyx* spp. appears to show a preference for shallower deep-sea habitats (Figure 4.9a). Distribution of this species was significantly different from random (MC: $p = 0.008$). Depth is the dominant factor with primary productivity, dissolved oxygen, and salinity contributing in roughly equal measure. The habitat suitability map for this genus (Figure 4.9b) once again shows the Mediterranean Sea to have low suitability. The most suitable habitats are confined to continental slopes and the Mid-Atlantic Ridge with abyssal plains shown as poorly suited habitats.

Eurythenes gryllus

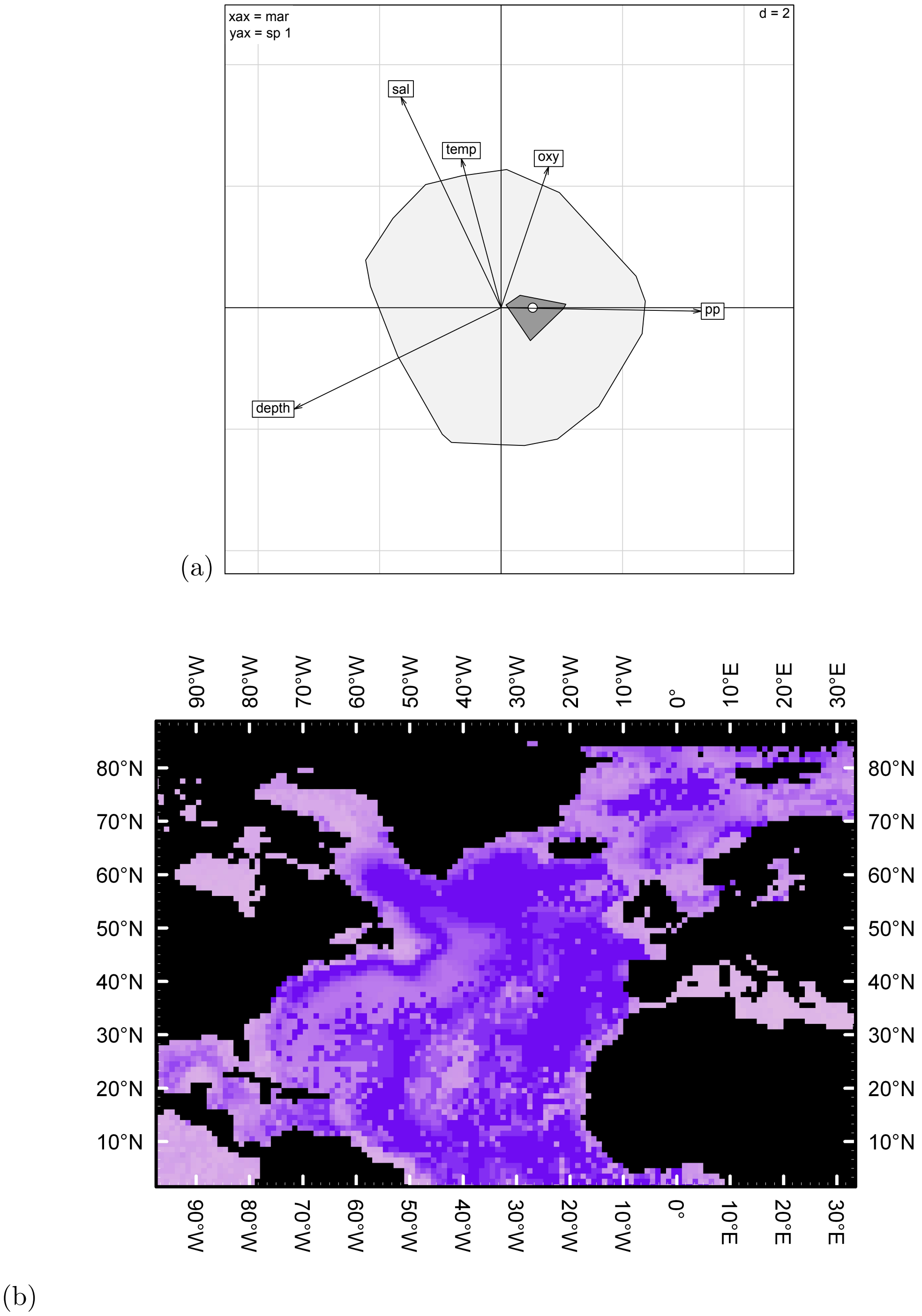
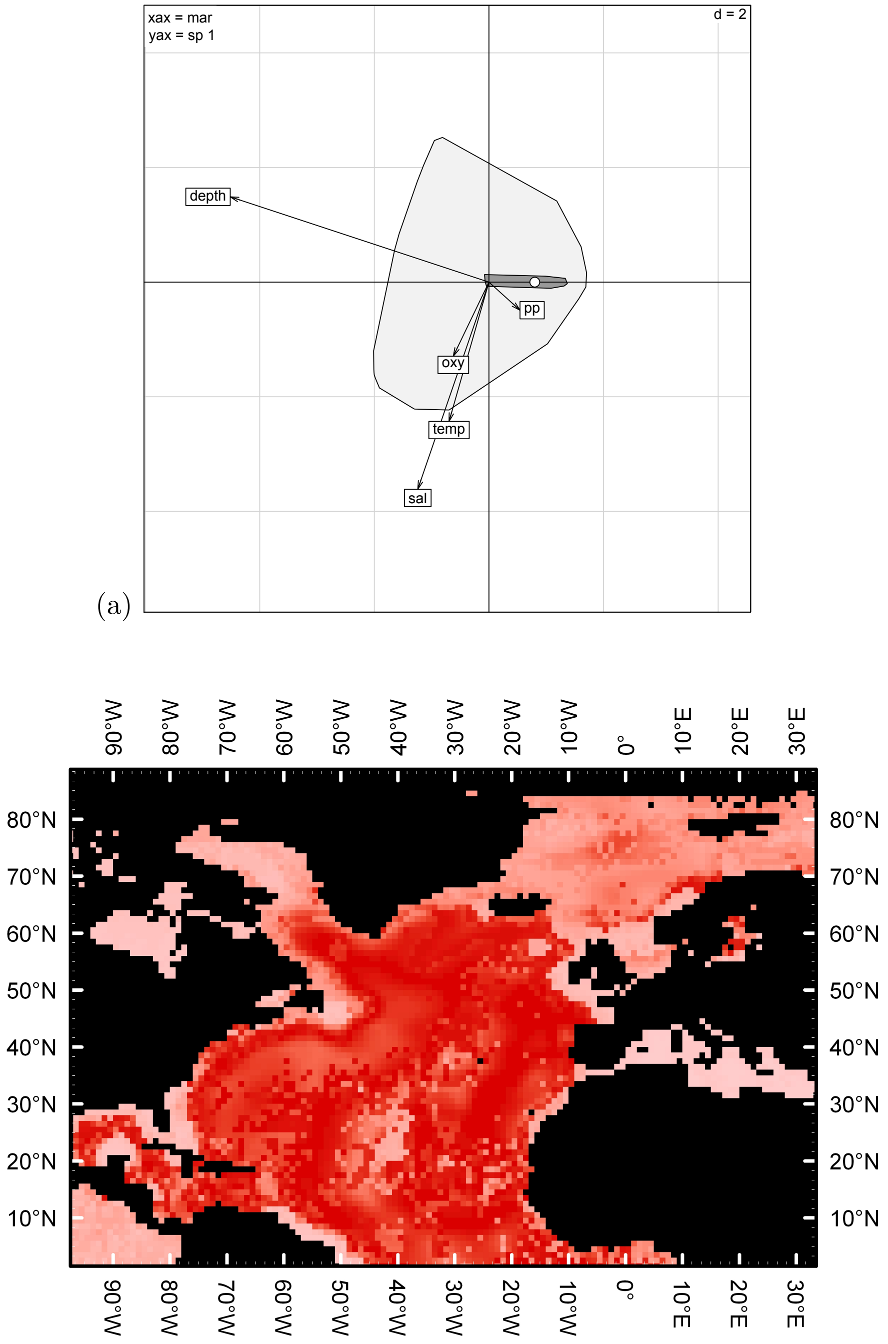


Figure 4.6: Graphical output of Ecological Niche Factor Analysis for the scavenging amphipod *Eurythenes gryllus* in the North Atlantic. 4.6(a) Biplot of the ENFA on *E. gryllus* (x-axis = marginality, y-axis = primary specialisation) with white dot representing centroid of used habitat, light grey area representing projection of available habitats, and dark grey area representing used habitats. Arrows represent projection of environmental variables ('depth' = water depth, 'oxy' = dissolved oxygen, 'pp' = primary production, 'sal' = salinity, 'temp' = bottom water temperature). 4.6(b) Habitat suitability map calculated based on ENFA results for *E. gryllus* with dark areas indicating high habitat suitability and light areas representing low habitat suitability based on an arbitrary scale.

***Paralicella* spp.**



(a)

(b)

FIGURE 4.7: Graphical output of Ecological Niche Factor Analysis for the scavenging amphipod genus *Paralicella* in the North Atlantic. 4.7(a) Biplot of the ENFA on *Paralicella* spp. (x-axis = marginality, y-axis = primary specialisation) with white dot representing centroid of used habitat, light grey area representing projection of available habitats, and dark grey area representing used habitats. Arrows represent projection of environmental variables ('depth' = water depth, 'oxy' = dissolved oxygen, 'pp' = primary production, 'sal' = salinity, 'temp' = bottom water temperature). 4.7(b) Habitat suitability map calculated based on ENFA results for *Paralicella* spp. with dark areas indicating high habitat suitability and light areas representing low habitat suitability based on an arbitrary scale.

***Abyssorchomene* spp.**

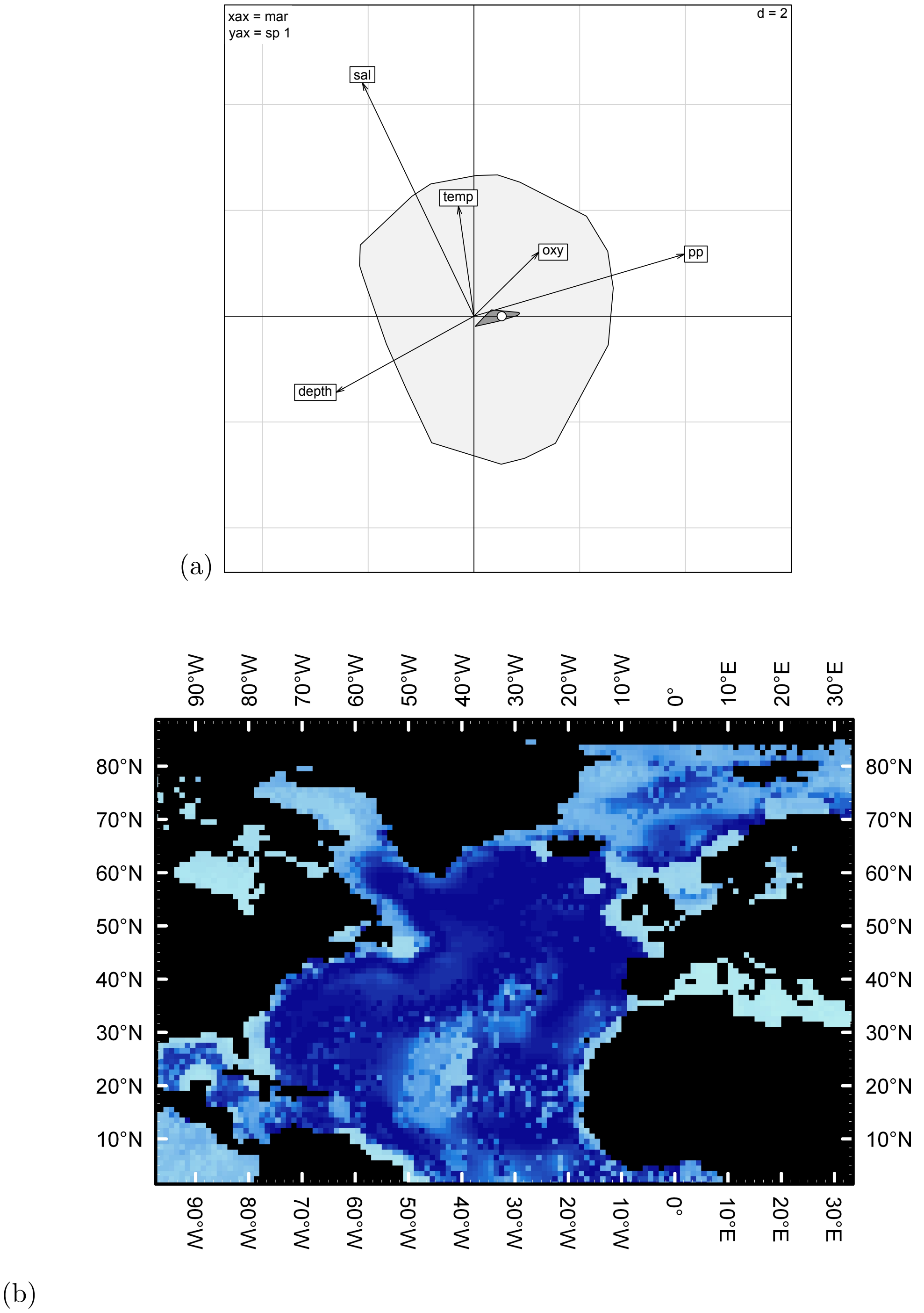


FIGURE 4.8: Graphical output of Ecological Niche Factor Analysis for the scavenging amphipod genus *Abyssorchomene* in the North Atlantic. 4.8(a) Biplot of the ENFA on *Abyssorchomene* spp. (x-axis = marginality, y-axis = primary specialisation) with white dot representing centroid of used habitat, light grey area representing projection of available habitats, and dark grey area representing used habitats. Arrows represent projection of environmental variables ('depth' = water depth, 'oxy' = dissolved oxygen, 'pp' = primary production, 'sal' = salinity, 'temp' = bottom water temperature). 4.8(b) Habitat suitability map calculated based on ENFA results for *Abyssorchomene* spp. with dark areas indicating high habitat suitability and light areas representing low habitat suitability based on an arbitrary scale.

***Tmetonyx* spp.**

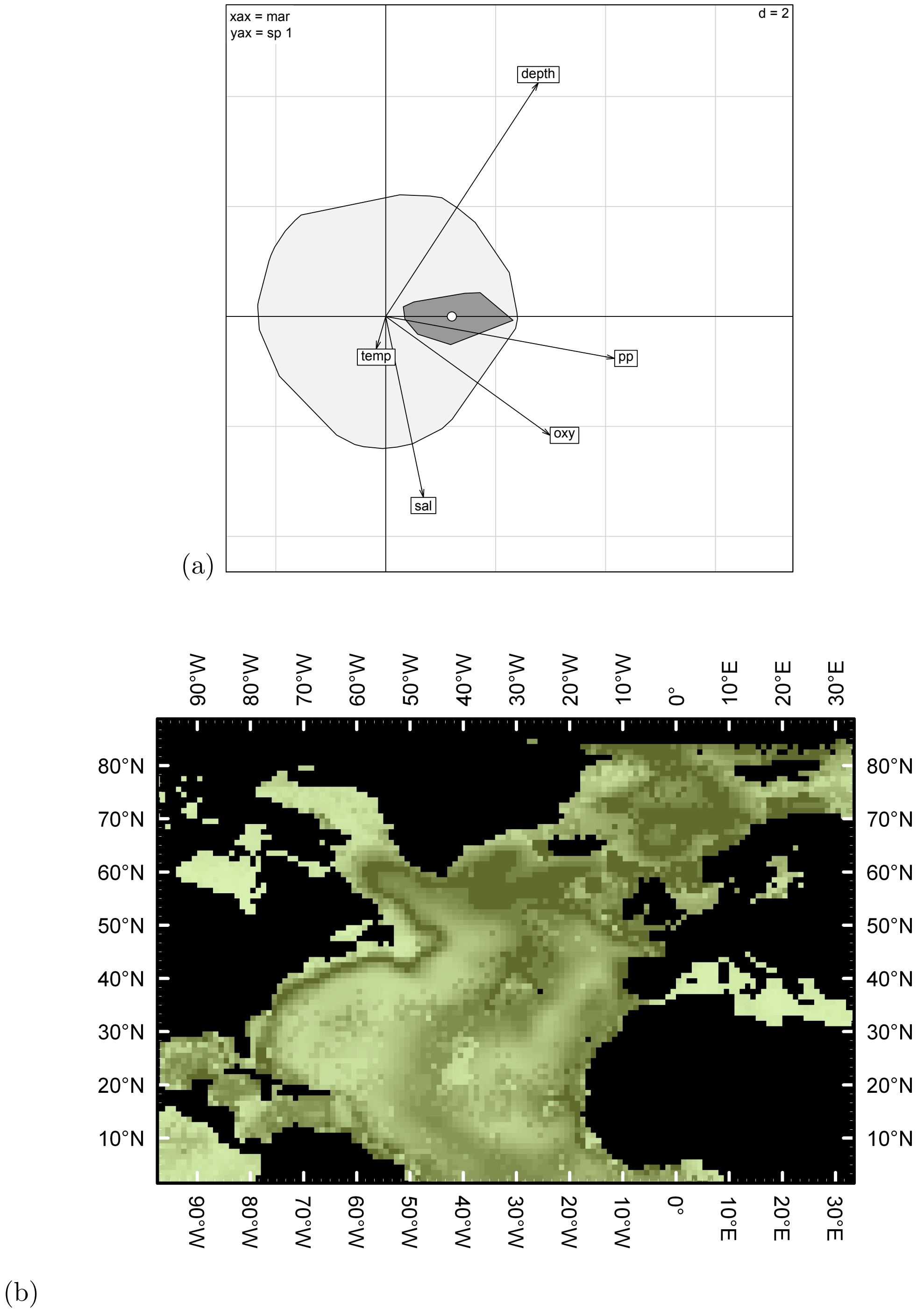


FIGURE 4.9: Graphical output of Ecological Niche Factor Analysis for the scavenging amphipod genus *Tmetonyx* in the North Atlantic. 4.9(a) Biplot of the ENFA on *Tmetonyx* spp. (x-axis = marginality, y-axis = primary specialisation) with white dot representing centroid of used habitat, light grey area representing projection of available habitats, and dark grey area representing used habitats. Arrows represent projection of environmental variables ('depth' = water depth, 'oxy' = dissolved oxygen, 'pp' = primary production, 'sal' = salinity, 'temp' = bottom water temperature). 4.9(b) Habitat suitability map calculated based on ENFA results for *Tmetonyx* spp. with dark areas indicating high habitat suitability and light areas representing low habitat suitability based on an arbitrary scale.

4.4 Discussion

Differences in community composition amongst all three depth zones are as expected. Community change with depth has been recorded on numerous occasions (Carney, 2005; Howell et al., 2002; Rex et al., 1999; Tietjen, 1971) and as such significant community differences amongst these three discrete depth zones are not surprising. The abyssal, bathyal, and dysphotic zones each experience significantly different environmental variables and provide different habitats suitable for different species. Temperature variation was identified as the main factor contributing to environmental differences and combined with dissolved oxygen accounted for over half of dissimilarity amongst abyssal, bathyal, and dysphotic sites.

Within depth zones the significant differences in community composition between sampling areas is not expected and in contrast to past studies on scavenging amphipod communities in the North Atlantic (Thurston, 1990). The most common deep-sea scavenging amphipod species are identified as having cosmopolitan distributions and ENFA analysis indicates tolerance of a range of environmental conditions. As such, these are expected to be found throughout the study region. The finding of significant differences in community composition amongst abyssal sites indicates that, while a select few species may have truly cosmopolitan distributions, on the whole community composition does vary due to distribution limitations of other less ubiquitous taxa. A comparable trend has been identified with deep-sea fish species with dominant species widespread and less dominant species more constrained (Koslow, 1993). Differences in community composition are supported by similar significant differences in environmental conditions amongst sites from different sampling areas.

4.4.1 Factors affecting community composition

Water temperature was identified as the environmental variable with greatest influence on community composition variability. The interaction of temperature with primary production and dissolved oxygen was also similarly correlated to changes in scavenging amphipod community composition. The physiological limits of deep-sea scavenging amphipods are largely untested but past ecological studies (e.g. Duffy et al., 2012; Horton et al., 2013; Jamieson et al., 2011; Thurston, 1990) and the limited experimental studies (Brown & Thatje, 2011) on this group can provide valuable insight into the environmental preference of these organisms. Although most scavenging amphipod species examined in this study are believed to be exclusive to the deep sea, *E. gryllus* has been found at shallower than expected depths at the poles (Ainley et al., 1986; Thurston et al., 2002). This suggests that scavenging amphipod distributions are not restricted by hydrostatic pressure alone. A similar trend has been identified in physiological studies of deep-sea scavenging amphipods (Brown & Thatje, 2011) with temperature and hydrostatic pressure exerting a combined influence on respiration and survival rates. Deep-sea scavenging amphipod species have also been recovered alive using insulated containers (Yayanos, 1978) and in areas with colder surface waters (Brown & Thatje, 2011; De Broyer et al., 2004; Premke, 2003; Premke et al., 2003). This further supports the hypothesis that temperature rather than hydrostatic pressure plays the most important role in controlling amphipod distributions.

At abyssal depths water temperature is generally stable and varies very little between abyssal plains of the North Atlantic (Gage & Tyler, 1991). However, the analyses presented here show significant community and environmental differences amongst abyssal sampling areas. Therefore while temperature appears to control vertical distribution of scavenging amphipod species and is behind community composition changes with depth, other factors, either environmental, historical, or biological, are affecting differences amongst assemblages from sampling areas within the abyssal depth zone.

The notable exception to the homogeneity of temperature at abyssal depths is the Mediterranean Sea which is considerably warmer at a bottom temperature of 13°C (Gage & Tyler, 1991). This temperature difference, along with the correlated salinity and oxygen differences, results in the abyssal Mediterranean Sea providing a very different habitat than that of other abyssal regions of the North Atlantic. This habitat differentiation is reflected in the habitat maps produced for all target taxa where the Mediterranean Sea is consistently identified as poorly suited to the requirements of these organisms. Some amphipod species have been identified in both the Mediterranean Sea and in the North Atlantic (e.g. *Scopelocheirus hopei* Costa, 1851, Kaïm-Malka, 2003; *Tmetonyx similis* Sars, 1891, Kaïm-Malka, 2004), however these species may represent a species complex and require taxonomic revision (pers. comm., T. Horton, National Oceanography Centre, UK). Most abyssal scavenging species found in the North Atlantic have not been observed in the Mediterranean (Jones et al., 2003). Scavenging activity in general in the Mediterranean Sea is substantially lower than that of the rest of the North Atlantic (Dumser & Türkay, 2008; Jones et al., 2003).

4.4.2 Distribution of scavenging amphipods in the North Atlantic

With the exception of *Tmetonyx* spp., the taxa examined in detail have potentially ocean-wide distributions in the deep North Atlantic. Habitat suitability maps indicate highly suitable environmental conditions in deep-sea basins ocean-wide for *Paralicella* spp., *Abyssorchomene* spp., and *Eurythenes gryllus*. It is important to note that high suitability of an area does not necessarily insinuate the presence of the tested taxa. Species distributions, while dependent on favourable environmental conditions, are also controlled by dispersal ability and historical factors. Accounting for these factors is not possible within the confines of this study using the ENFA model (Basille et al., 2008; Hirzel et al., 2002), therefore any inferences on faunal distributions must be made with caution.

The main barriers to species dispersal in the deep sea are thought to be topographic divides (Vinogradova, 1959). Within the deep North Atlantic the main topographical barrier to dispersal of deep-sea organisms is the Mid-Atlantic Ridge. Other, less pronounced, topographic divides between abyssal plains do not appear to act as barriers to dispersal of amphipods (Thurston, 1990), cephalopods (Collins et al., 2001), echinoderms (Young et al., 1997), or fishes (Koslow, 1993). The Mid-Atlantic Ridge does not act as a physical barrier to scavenging amphipods, with no significant difference in community composition either side of the ridge (Horton et al., 2013). Abyssal species of deep-sea fish, another motile taxa, have also been found to have distributions spanning the entire width of the North Atlantic, uninhibited by the MAR (Koslow, 1993). The MAR also does not appear to act as a distribution barrier to bathyal species of polychaete (Shields & Blanco-Perez, 2013).

Deep-sea fish species inhabiting shallower continental slope areas do not have the same wide geographic distributions recorded for their abyssal counterparts (Koslow, 1993). Different species of deep-sea fish are found on the continental slopes either side of the Atlantic Ocean. Deeper dwelling species of echinoderms also have wider geographic ranges than their shallower counterparts (Young et al., 1997). This provides interesting insight into the potential distribution of *Tmetonyx* spp., which is found on deep-shelf and continental slopes. Slope environments either side of the Atlantic and the Mid-Atlantic Ridge were identified as highly suitable environments for this genus. Based on evidence from fish distributions (Koslow, 1993) it is likely that species of *Tmetonyx* will differ on opposing continental slopes with a clear east-west divide. This theory is supported by the finding of large numbers of two previously undescribed species of *Tmetonyx* at the Mid-Atlantic Ridge (Horton et al., 2013), strong evidence that, while this genus may have a cosmopolitan distribution in the North Atlantic, individual species are restricted in their distribution. Unfortunately data on *Tmetonyx* spp. on the West Atlantic slope are not available to determine if species level differences exist between the East and West Atlantic. The genus *Tmetonyx* is also in need of major taxonomic revision, further confounding such analyses.

Ideally, analyses of distribution of deep-sea scavenging amphipods would be performed at a species level for all taxa. As some samples have only been sorted to genus level this is not possible without excluding a large number of data points. Even if all samples were sorted to species level absolute certainty of identification could not be guaranteed. Phylogenetic studies have identified a species complex in *Eurythenes gryllus* (Havermans et al., 2012) and it is likely that such complexes exist for other species considered to be cosmopolitan. Thus far genetic variance appears to be greatest amongst individuals from different depths with horizontal gene flow less restricted (France, 1994).

When examining the factors controlling the habitat suitability of individual taxa, temperature rarely plays a contributing role. Depth is consistently identified as the controlling factor for all target taxa used for the ENFA. While not a true environmental variable depth is representative of and often closely correlated with hydrostatic pressure, temperature, salinity, and dissolved oxygen. As such, it is difficult to determine which of these contributing variables is limiting the distribution of each species. Depth is best viewed as the combined synergistic effect of these variables. All modelled taxa except *Tmetonyx* spp. showed high affiliation with deep water.

Tmetonyx spp. showed greatest affinity to mid-depth water with productive overlying surface waters. The habitat suitability map for this genus reflects the tendency toward such conditions with areas of high suitability focussed on the continental slopes and Mid-Atlantic Ridge. Members of this genus are often found in baited traps deployed on continental slopes and large numbers of a potentially new species of this genus were found on the Mid-Atlantic Ridges as part of the ECOMAR project (Horton et al., 2013). Evidence supports the low suitability of abyssal depths, *Tmetonyx* spp. have never been identified in samples taken from abyssal plains in the North Atlantic (Thurston, 1990).

Primary productivity was identified as an important environmental variable in determining habitat suitability of *E. gryllus*, *Abyssorchomene* spp., and *Tmetonyx* spp. as indicated by the biplots and habitat suitability maps for these taxa. Communities at bathyal depths have recently been shown to differ based on variation in surface productivity (Horton et al., 2013), with *E. gryllus* being notably more abundant in productive areas (Premke et al., 2006). While this has not been directly tested with abyssal scavenging amphipod communities, the findings presented here suggest a similar influence of productivity on abyssal species distributions and hence community composition. *Eurythenes gryllus*, *Abyssorchomene* spp., and *Tmetonyx* spp. all show strong affiliation to areas with high surface primary productivity. Areas with productive surface waters are expected to support greater numbers of large fishes and cetaceans, increasing the number of subsequent food falls.

Paralicella spp. habitat suitability shows a much weaker correlation to primary productivity than other target taxa. While still having an affinity for more productive areas the biplot for this genus indicates this affinity is weak. The ability of *Paralicella* spp. to grossly distend and expand its pereon in order to maximise food intake (Shulenberger & Barnard, 1976; Thurston, 1979) sets this genus apart from *E. gryllus*, *Abyssorchomene* spp., and *Tmetonyx* spp. that still possess modified digestive tracts (Dahl, 1979) but cannot distend their pereon to such an extent. While abyssal plains under less productive surface waters are less likely to experience frequent food falls, the ability of *Paralicella* spp. to distend its pereon and assimilate very large quantities of food may allow it to capitalise on any food parcels that reach abyssal depths. This may may make *Paralicella* spp. better able to tolerate lower nutrient environments.

The apparent semelparous lifestyle of *Paralicella* spp. (Chapter 3) also sets *Paralicella* spp. apart from *E. gryllus* and *Abyssorchomene* spp., which are believed to be iteroparous (Chapter 3; Duffy et al., 2013; Thurston, 1979). This longer term reproductive strategy may prove beneficial in areas with constant but relatively poor nutrient input. Members of this genus are believed to follow different growth patterns under different trophic conditions with evidence that sexual maturation in scavenging amphipods may also be tied to nutrient availability (Chapter 3; Sutcliffe et al., 1981). Maturing over a longer period of time, working toward one large reproductive event while capitalising on available food falls, would allow persistence and survival under conditions that may inhibit the success of other species of scavenging amphipod.

4.4.3 Limitations of this synthesis

Despite the apparent tolerance low productivity areas exhibited by *Paralicella* spp. it is also a very successful genus in the nutrient rich environments provided by submarine canyons (Chapter 2; Chapter 3; Duffy et al., 2012). This highlights one of the problems of the ENFA and the dependence on presence-only data rather than abundance or community composition data. Presence is not necessarily an indicator of success of a species in the sampled environment. Suitability could be better estimated if reliable quantitative data were available for all samples. This would allow for more confidence in determining not only what niches of the available environment the target organisms can inhabit but how successful they are, allowing for marginal habitats to be identified as such. Due to variability in data sources, different trap configuration, local conditions, and our reliance on remote sampling it is not possible to confidently use the abundance data where it is available.

The coarse resolution used for environmental data may also confound the ENFA. There are a number of topographic features of the deep sea measuring smaller than the cell size used in this study (1° by 1°) and therefore small-scale habitats and the environmental variability they provide are not accounted for. Higher resolution environmental data are not available for the entire study are of the North Atlantic and the remote sensed data from the World Ocean Atlas (Antonov et al., 2010; Garcia et al., 2010; Locarnini et al., 2010) was the highest resolution available. While primary productivity and depth data were available at higher resolutions these were down-sampled as all ecogeographical variable maps had to be of the same extent and resolution for the ENFA model to be run.

Net primary productivity of surface waters does not necessarily correlate directly with food fall availability at abyssal depths. While productivity of overlying waters is closely linked to food input into the deep sea (Drazen et al., 2012; Ruhl & Smith, 2004), the link is unlikely to be a direct one because of the influence of ocean circulation and currents.

There have been a number of proposed models to estimate POC flux to the sea floor (Berelson, 2001; Johnson et al., 2007; Lutz et al., 2002; Pace et al., 1987) however large food falls will not necessarily follow the same patterns as smaller organic carbon packages. They are expected to experience faster sinking rates and be less influenced by small-scale currents (Smith, 1985). The outputs from these models also represent a combination of environmental factors which would have added further difficulty in identifying the primary environmental factors affecting distributions.

4.5 Conclusions

This study has made use of the large dataset available from baited trap deployments in the North Atlantic. Use of multivariate statistics has identified depth, temperature, and primary production as factors affecting horizontal and vertical distributions of deep-sea scavenging amphipods. The hypothesis that communities changed with depth appears to be correct but amongst abyssal basins there also appears to be variability. This is in contrast to the originally proposed hypothesis. The Environmental Niche Factor Analysis identified the main factors affecting taxon-level distributions. Habitat suitability maps show that some scavenging amphipod taxa have the potential to exhibit ocean-wide distributions. *Paralicella* spp. has a particularly broad tolerance of environmental conditions and most of the deep North Atlantic has been identified as a suitable habitat for this genus. While this synthesis of the available data has provided new insight into the factors influencing distribution our understanding could be greatly aided via experimental testing of the physiological limits of these organisms.

Chapter 5

Megafaunal ecology of the submarine canyons of Southern California

5.1 Introduction

Forming deep incisions into the continental shelf, submarine canyons are large topographic features with unique hydrographical, sedimentary, and geochemical characteristics (Shepard & Dill, 1966). It is estimated that 1 824 large submarine canyons incise continental shelves around the world, with a further 4 025 canyons confined to the continental slope (Harris & Whiteway, 2011). These canyons exhibit a high degree of biological variability on both the intra-canyon and inter-canyon level (Gage & Tyler, 1991; Tyler et al., 2009). This heterogeneity is the result of a number of biotic and abiotic factors including shelf morphology, proximity to river systems, bottom topography, substrate lithology oceanographic conditions, sediment transport events, sedimentation rates, nutrient input, and depth. The cross-section of many submarine canyons has been described as being V-shaped (Shepard & Dill, 1966) as they contain a narrow axial channel which is flanked on both sides by steep walls composed of rocky outcrops. Examples of these include the Nazaré Canyon, off the coast of Portugal, and the Monterey Canyon off the Central California coast (e.g. Arzola et al., 2008; Greene et al., 2002; Tyler et al., 2009). While these larger canyons represent the submarine canyon archetype, many smaller canyons, sometimes referred to as submarine valleys, are also found on continental margins throughout the globe (De Leo et al., 2010; Shepard & Dill, 1966). Small submarine canyons demonstrate the same spatial and temporal heterogeneity seen in larger submarine canyons, albeit across a much smaller spatial scale.

Sediment interception results in many canyons experiencing high levels of organic matter input, although this varies based on surface productivity and proximity to estuarine input (Vetter & Dayton, 1998). By channelling sediment and expediting its movement from the continental shelf to the associated basin, canyons provide an important means to supply organic carbon to the deep sea. The difficulty of studying fauna in such complex environments means that only a limited number of studies have examined the effect of activity on community composition (Okey, 1997, 2003), and these have examined patches of low and high activity within an individual submarine canyon rather than between canyon systems.

Submarine canyons have been classified using various criteria. While attempts at quantitative classification have occurred (e.g. Goff, 2001), most classification is qualitative. One classification system of particular interest to both biologists and geologists is that of canyon activity, where canyons are categorised based upon their rate of sediment throughput. All submarine canyons intercept sediment that is being laterally transported along the continental shelf (Cúrdia et al., 2004). Large, active canyons, such as Nazaré, which penetrates almost the entire width of the continental shelf, intercept a greater amount of sediment than those with reduced shelf penetration (Covault et al., 2007; Van Weering et al., 2002). Active submarine canyons channel this down from the continental shelf to the abyssal plain, while inactive canyons have less of a role in sediment transport and are more likely to have sediment accumulating within the canyon over time.

While active canyons can be distinguished from inactive canyons by the position of the canyon head with respect to the shoreline, the impact of the canyon activity on the fauna that colonizes the canyons flanks is unclear. The processes that move sediment within these canyons are primarily focused within the axial channel of these canyons during energetic episodic sediment transport events (Paull et al., 2010). Megafaunal communities that are exposed to these events will be physically destroyed. Thus, slow growing megafaunal communities will not exist where the sediment transport/disturbance events occur at a frequency which is less than the lifetime of the organisms (Paull et al., 2009). However, energetic sediment transport events may only impact the axial channel floor and an area immediately adjacent to the axial channel (Paull et al., 2013, 2011, 2010). Thus, the extent to which fauna living on the canyon walls above the axial are impacted by the episodic passage of sediment through the canyon floor is unclear. Moreover, while it is lethal for the organisms in the axial channel that are exposed to the full force of these events, organisms that are on the canyon walls and survive the events may benefit from their proximity to event as fresh nutrient rich sediments are exposed or the availability of carrion is increased.

In spite of their importance as hotspots of secondary production and role in connecting the continental shelf to the deep sea (Vetter & Dayton, 1998), our understanding of submarine canyons, their formation, processes, and ecosystems, is relatively limited (Ramirez-Llodra et al., 2010). In recent years there have been a number of programmes targeting European (e.g. EUROSTRATFORM; HERMES; HERMIONE; Tyler et al., 2009), Californian (e.g. Goffredi et al., 2004; Lundsten et al., 2010a; McClain & Barry, 2010; Paull et al., 2011, 2005, 2010; Robison et al., 2010), Hawaiian (e.g. De Leo et al., 2012; Vetter et al., 2010) and New Zealand (e.g. De Leo et al., 2010; Lewis & Barnes, 1999) submarine canyons. However, numerous submarine canyon systems remain unstudied and therefore our understanding of these complex systems is limited.

This study makes use of an extensive video dataset collected using remotely operated vehicles (ROVs) in an effort to understand the ecology of nearby canyons, with particular emphasis on the role of canyon activity in controlling community structure that exists on the canyon flanks. The hypothesis to be tested is that megafauna communities in active submarine canyons differ significantly to communities in inactive canyons. The effect of depth on community composition and species richness will also be examined within the targeted submarine canyon systems.

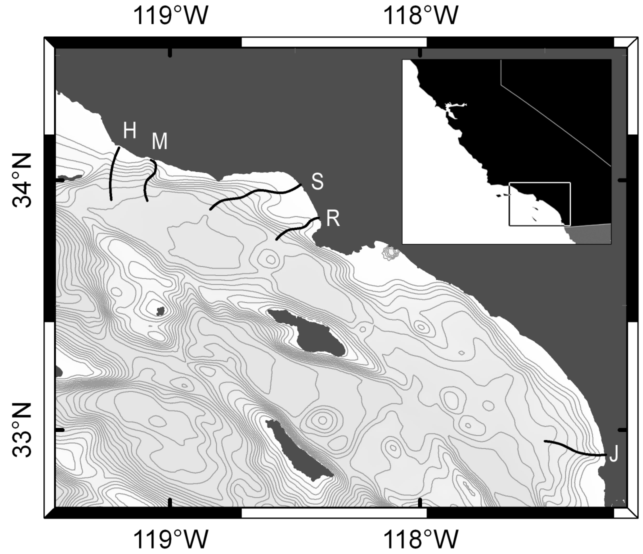


Figure 5.1: Map of study area off the Southern California, USA, coastline with main canyon axes indicated. H; Hueneme Canyon (Axis length 28 km), M; Mugu (16 km), S; Santa Monica (22 km), R: Redondo (18 km), J; La Jolla (27 km). 100 m contours shown. Inset map shows location of main map with respect to California.

5.2 Materials and Methods

5.2.1 Study sites

Video surveys were conducted within five Southern California submarine canyons by Monterey Bay Aquarium Research Institute (MBARI) ROVs (Paull et al., 2008; in prep.) in an effort to better understand the geological processes occurring within them (Figure 5.1). A total of 25 ROV dives were made with the majority of dives starting on the axial channel floor and climbing up the canyon wall, perpendicular to the main axis.

Hueneme, Redondo, and Santa Monica Submarine Canyons were surveyed during an expedition in 2005 using MBARIs ROV *Tiburon*, equipped with a standard definition (SD) video camera. In 2010, Mugu and La Jolla Submarine Canyons were surveyed using MBARIs ROV *Doc Ricketts*. ROV *Doc Ricketts* was equipped with a high definition (HD) video camera. Both ROVs were deployed from the RV *Western Flyer*. While these surveys were conducted primarily with a geological focus, video data were collected such that analysis of megafauna communities was possible.

Based upon geological sampling and detailed bathymetric data analysis these canyons have been characterised as being active or inactive. Hueneme, Mugu, Redondo, and La Jolla Canyons are identified as active submarine canyons because their axial channels are characterised by recurring crescent shaped bedforms and are underlain with coarse-grained sediments (Beer & Gorsline, 1971; Normark et al., 2009; Paull et al., 2013, 2008, 2010). In contrast, Santa Monica Canyon is characterised as being inactive (Paull et al., 2008; in prep), as its axial channel lacks crescent shaped bedforms and contains hemipelagic sediment fill.

5.2.2 Analysis of video footage

Over the course of the surveys, 81.5 hours of ROV dive footage was recorded. Duration and distance travelled during each ROV dive varied greatly and was dictated by the geological sampling requirements and operational considerations. For this reason each dive was subsequently divided into a number of randomly selected 50 m long transects, calculated from ROV navigation data (Table 5.1). All video footage was annotated in detail using the Video Annotation and Reference System (VARS, http://www.mbari.org/vars; Schlining & Stout, 2006), a software database system designed for input and retrieval of video observation data. Trained video laboratory staff performed initial outline annotations then all footage was reviewed in greater detail by the author to identify any potential sources of error and to ensure consistency across all dives.

Due to the nature of this study no voucher specimens were collected during dives and ROV altitude, and consequently the height of the camera above the seabed, also varied substantially. Therefore while a limited number of organisms were viewed close-up, many were observed at some distance and were difficult to identify to lower taxonomic levels. This, coupled with the use of standard definition video during the 2005 dives and HD video during the 2010 dives, resulted in variation in the level of confidence in the identification of organisms. MBARI video lab staff have observed much of the fauna found during previous surveys in Southern California and along the west coast of the United States during its 25 years of conducting deep-sea research (Lundsten et al., 2009a,b, 2010a,b), therefore some organisms could be consistently and confidently identified to species level (e.g *Strongylocentrotus fragilis* Jackson, 1912) or grouped as a morphologically-recognisable species (e.g. Asteroid sp. 1). Other organisms were grouped to family level to ensure consistency between footage of varying quality. For this reason analysis was performed using benthic megafauna classified as operational taxonomic units (OTUs), with organisms identified to the taxonomic level that provided the most confidence of consistent identification across all dives. These data were subsequently converted into a presence/absence matrix.

Using video observations, high-resolution multi-beam bathymetry, and knowledge obtained during the primary geological survey, habitat was classified based on parameters including slope steepness, Bathymetric Position Index (BPI; calculated using the Benthic Terrain Modeler ArcGIS plugin, http://www.csc.noaa.gov/digitalcoast/tools/btm), and substratum. Using these data three discrete slope zones ($< 45°$ slope; $> 45°$ slope; vertical wall), and four substrata types (sandy substratum; soft, sedimented substratum; sedimented areas with exposed rock making a rocky substratum; hard substratum composed exclusively of exposed rock) were characterised (Table 5.1).

5.2.3 Statistical analysis

Using PRIMER (Plymouth Routines In Multivariate Ecological Research; Clarke & Gorley, 2006), a resemblance matrix of presence/absence data was created using Bray-Curtis similarity. Study areas were compared on the basis of megahabitat (canyon) and macrohabitat (slope zone, depth zone, substrata) to facilitate a comparative analysis between locales (Greene et al., 1999).

Data were analysed using the PERMANOVA+ (Anderson, 2001; McArdle & Anderson, 2001) add-on for PRIMER. The PERMANOVA test is a permutation based test, analogous to a MANOVA. It is capable to comparing community composition of sampling areas grouped by a number of factors forming a more complex test design than is possible using an ANOSIM. Macrohabitats were nested within megahabitat. The environmental factors hydrostatic pressure, temperature, oxygen concentration, and salinity were all closely correlated to depth; as such only depth was used as a representative factor. In order to assess the effect of canyon activity, a contrast was built into this design grouping active canyons (Hueneme, Mugu, Redondo and La Jolla) against the inactive canyon (Santa Monica). The PERMANOVA test produced the test statistic ‘pseudoF’ where a large value is indicative of significant differences in community composition amongst sampling groups. The significance level of the test is calculated by comparing observed community composition to randomly assigned communities produces through random permutation (Anderson, 2001).

TABLE 5.1: List of dives made in Southern Californian canyons, number of 50 m transects in each dive, and zones represented by each transect. Organised by canyon and dive number.

Canyon	**Dive #**	**Date**	**Transects**	**Slope**			**Substrata**				**Depth**				
		yyyy-mm-dd	50m each	Flat	Slope	Wall	Sand	Soft	Rocky	Hard	300-400	400-500	500-600	600-700	700-800
Hueneme	T783	2005-02-10	3	2	–	1	1	1	–	1	–	–	3	–	–
	T784	2005-02-10	3	–	–	3	–	–	–	3	–	1	2	–	–
	T805	2005-02-18	4	4	–	–	2	2	–	–	2	2	–	–	–
	T806	2005-02-18	6	3	3	–	3	3	–	–	–	–	6	–	–
	T807	2008-02-18	4	1	–	3	–	1	–	3	–	4	–	–	–
	T808	2005-02-18	5	5	–	–	3	1	–	–	2	3	–	–	–
La Jolla	DR127	2010-03-24	7	2	2	3	1	3	–	3	–	–	–	7	–
	DR128	2010-03-24	4	3	–	1	–	3	–	1	–	–	4	–	–
	DR130	2010-03-25	7	3	1	3	3	–	1	3	–	–	1	6	–
	DR131	2010-03-26	5	–	5	–	–	4	1	–	–	–	–	1	4
	DR132	2010-03-26	4	–	–	4	–	–	–	4	–	–	–	3	1
	DR133	2010-03-26	5	1	4	–	–	–	5	–	–	–	3	2	–
Mugu	DR120	2010-03-20	5	5	–	–	–	5	–	–	–	–	–	–	5
	DR121	2010-03-21	5	1	3	1	1	4	–	–	–	–	1	4	–
	DR122	2010-03-22	5	5	–	–	5	–	–	–	–	–	–	5	–
Redondo	T786	2005-02-12	7	–	7	–	–	7	–	–	–	–	7	–	–
	T787	2005-02-12	6	1	3	2	1	3	–	3	–	2	4	–	–
	T788	2005-02-23	5	3	2	–	–	5	–	–	–	–	4	1	–
	T800	2005-02-17	5	1	1	3	1	1	–	3	–	3	2	–	–
	T801	2005-02-17	4	–	2	2	–	2	–	2	–	4	–	–	–
S. Monica	T789	2005-02-13	5	2	3	–	–	5	–	–	–	1	4	–	–
	T790	2005-02-13	4	–	4	–	–	4	–	–	–	1	3	–	–
	T791	2005-02-13	5	3	2	–	–	5	–	–	1	4	–	–	–
	T794	2005-02-14	4	1	1	2	–	2	–	2	–	–	1	3	–
	T795	2005-02-15	5	2	3	–	4	–	1	–	2	3	–	–	–

Local effects of canyon activity were tested for using a nested ANOSIM on data from all canyons. Nested within depth, community composition for transects within the central 50 m section of the main canyon axis were compared against transects that were more than 100 m from the main canyon axis. Species richness (S) was calculated for each 50 m transect and compared between each 100 m depth zone using a Kruskal-Wallis test.

5.3 Results

In total, 127 transects of 50 m in length were used for analysis, covering a combined linear distance of 6.35 km across a range of slopes, substrata, and depth zones (Figure 5.2). Over 11 000 biological observations were classified into 35 OTUs (Table 5.2). Across all depths and canyons rockfishes of the family Scorpaenidae were the most commonly observed organisms. The echinoderms *Asteronyx longifissus* Döderlein, 1927, Asteroidea sp. 1, and *Pannychia moseleyi* Théel, 1882 were the most commonly observed invertebrates. Of particular note is the abundance of *Pleuroncodes* Stimpson, 1860, which in spite of being observed almost exclusively during the deepest dives, was the sixth most commonly recorded organism.

Organisms found over most of the surveyed depth range included: a sea star (Asteroidea sp. 1), between 430 m and 716 m; *Dromalia alexandri* Bigelow, 1911, a benthic siphonophore, from 414 m to 719 m; Subsessiliflorae, sea pens in the genus *Funiculina* De Lamarck, 1816 or *Halipteris* Kölliker, 1880 (indistinguishable from each other in video observations), from 430 m to 711 m; the holothurian *Pannychia moseleyi* between 383 m and 720 m depth. Asteroidea sp. 1 was frequently observed in high numbers during shallow transects and was numerically dominant in a number of transects below 500 m. Transects below 725 m deep were dominated by the squat lobster *Pleuroncodes* sp., which was found at high densities in the deeper dives at the mouths of the canyons.

There was no significant difference amongst canyons (PERMANOVA; *d.f.* = 4, pseudoF = 1.2689, P(Perm) = 0.2353) or between active and inactive canyons (*d.f.* = 1, pseudoF = 0.81419, P(Perm) = 0.6716). The effect of slope zone was not significant (*d.f.* = 9, pseudoF = 1.9404, P(Perm) = 0.0523) but a relatively high pseudoF value, coupled with the near-significant P(Perm) value, suggests that the slope of the seafloor influences community composition. Substratum was found to have no significant effect upon

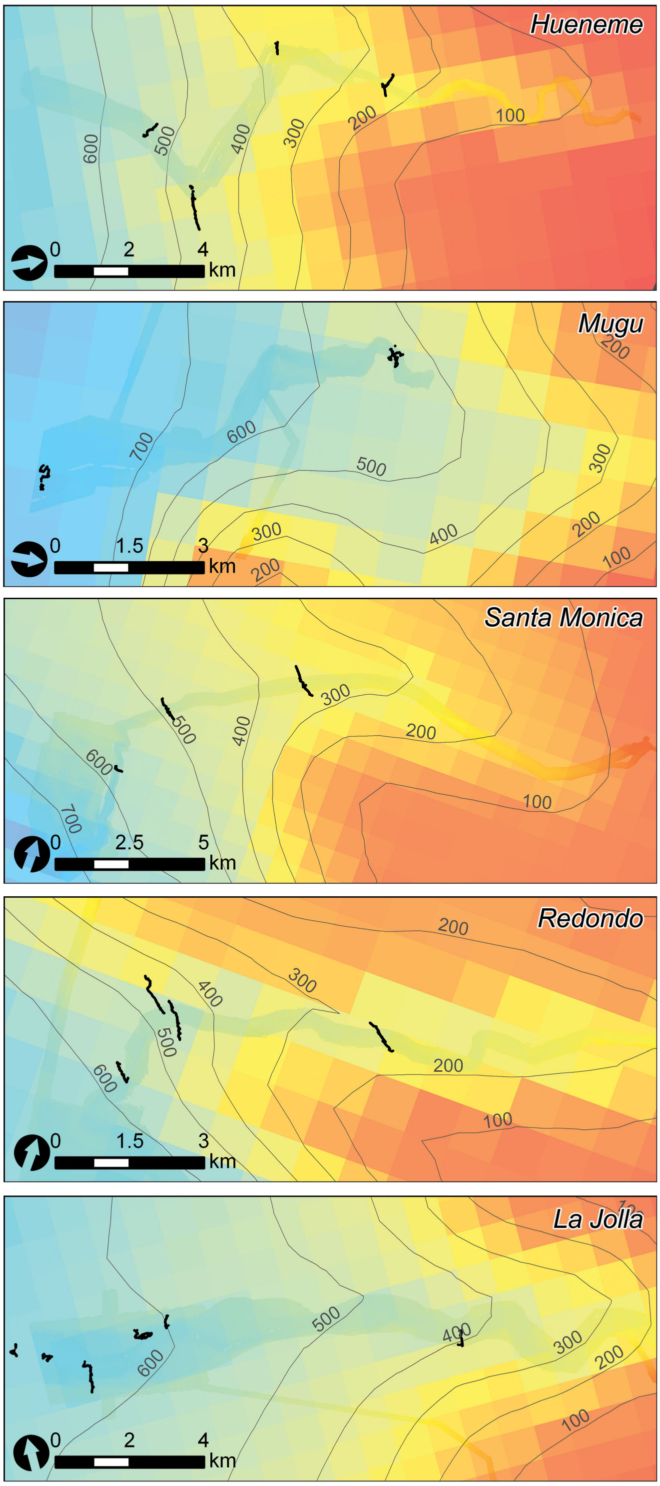


FIGURE 5.2: Location of ROV dive transects (black lines) with respect to the bathymetry of Hueneme, Redondo, Santa Monica, Mugu, and La Jolla submarine canyons. Areas of detailed mapping surveys (Paull et al., 2008), will be published elsewhere.

Table 5.2: Taxa grouped into operational taxonomic units (OTU) used in this study. Ordered alphabetically by taxa.

Phylum	**OTU**	**Common Name**	**Level**	**Exclusions**
Arthropoda	Lithodidae	king crabs	Family	–
	Majidae	spider crabs	Family	–
	Pleuroncodes sp.	squat lobster	Genus	–
Chordata	Pleuronectiformes	flatfish	Order	–
	Liparidae	snail fish	Family	–
	Macrouridae	grenadiers	Family	–
	Scyliorhinidae	catsharks	Family	–
	Scorpaenidae	rockfish	Family	–
	Zoarcidae	eelpouts	Family	*L. diapterus*
	Eptatretus sp.	hagfish	Genus	–
	Lycodes diapterus	black eelpout	Species	–
	Raja rhina	longnose skate	Species	–
Cnidaria	Anthozoa	soft corals	Class	Actiniaria Pennatulacea
	Actiniaria	anenomes	Order	*L. brevicornis*
	Pennatulacea	sea pens	Order	Subsessiliflorae *U. lindahli*
	Subsessiliflorae	sea pens	Suborder	–
	Dromalia alexandri	benthic siphonophore	Species	–
	Liponema brevicornis	pom pom anenome	Species	–
	Umbellula lindahli	sea pen	Species	–
Echinordermata	Brisingida	sea stars	Order	–
	Pterasteridae	sea stars	Family	–
	Brisaster spp.	heart urchin	Genus	–
	Florometra sp.	crinoid	Genus	–
	Solaster sp.	sea star	Genus	–
	Asteroidea sp. 1	sea star	Species	–
	Asteronyx longifissus	basket star	Species	–
	Pannychia moseleyi	sea cucumber	Species	–
	Psolus squamatus	sea cucumber	Species	-
	Rathbunaster californicus	sea star	Species	–
	Strongylocentrotus fragilis	urchin	Species	–
Mollusca	Gastropoda	gastropods	Class	Octopoda Pleurobranchomorpha
	Octopoda	octopuses	Order	–
	Pleurobranchomorpha	pleurobranchs	Order	–
Porifera	Porifera	sponges	Phylum	–

community structure (*d.f.* = 8, pseudoF = 0.51386, P(Perm) = 0.8123). Depth was found to have a significant effect upon the community composition (*d.f.* = 9, pseudoF = 2.9992, P(Perm) = 0.002).

Nested within depth, community composition did not vary between inside and outside the central canyon axis (ANOSIM, R = -0.179, p = 0.8040). Species richness (based on OTUs) varied significantly based on depth zone (Figure 5.3; Kruskal-Wallis test, n = 122, *d.f.* = 4, χ^2 = 24.415, p < 0.001). Richness initially increased steadily with depth but then declined at deeper depths nearing the basin.

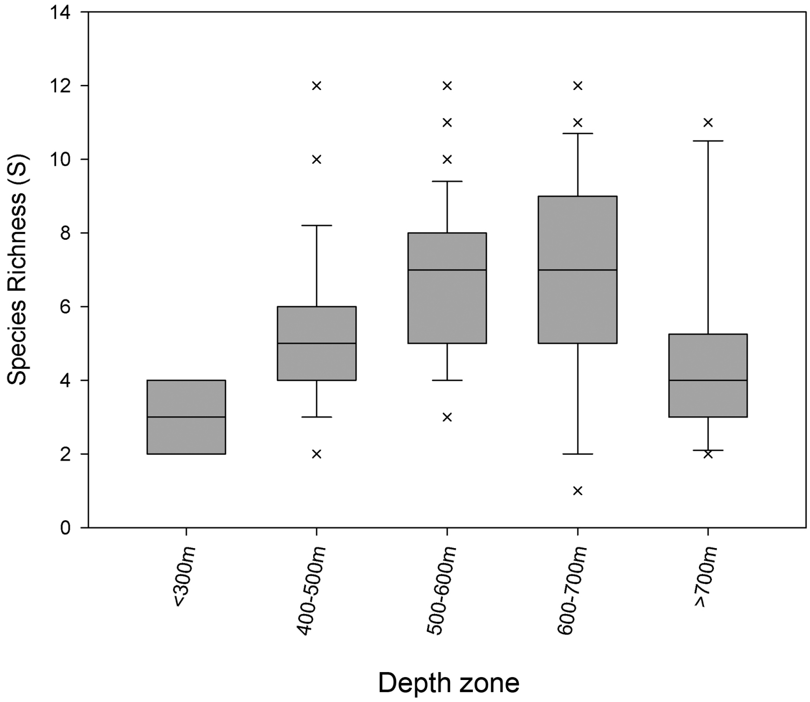


FIGURE 5.3: Stem and leaf plot of species richness, based on OTUs, for combined 50 m transects from all canyons grouped by depth zone. Median and interquartile ranges shown, outliers indicated by crosses. Species richness varied significantly between depth zones (Kruskal-Wallis test, $n = 122$, $d.f. = 4$, $\chi^2 = 24.415$, p = textless 0.001).

5.4 Discussion

5.4.1 Canyon activity

No significant differences in megafaunal community composition were observed between active and inactive canyons. Based upon current knowledge on the effects of reduced canyon activity upon the morphology of submarine canyons (e.g. reduction of main channel width and size, fewer steep slopes, build-up of soft muddy sediments), one would expect to see megafaunal community differences at the between-canyon level as fewer small macrohabitats (e.g. sandy flats) would occur in the less active, more homogenous canyons. Local variability in community composition was observed, particularly in the axis of the main channel where teleost fish dominated communities and less motile fauna were rarely seen. Statistical analysis did not, however, indicate a significant difference in community composition based on distance away from the canyon axis.

The lack of detectable community differences based on the interpreted activity of the canyons (Paull et al., 2008) may be a consequence of the ROV survey locations. As the depths and slopes surveyed and analysed were not consistent between canyons direct comparisons with sufficient replicate transects proved difficult. The necessity to standardise to presence/absence also substantially reduced the ability to identify community change with no discernment between changes in relative abundance of various taxa. Equal and representative surveying of all canyons will be necessary to identify with certainty the presence or absence of megafauna driven by differing levels of canyon activity. Sampling of infaunal organisms in these canyons may also elucidate further community variation patterns.

5.4.2 Factors affecting community composition

Although not significant, there is a trend for the effect of slopes on community composition. Fauna commonly found on gentle slopes and flats may lack the ability to remain affixed to steeper slopes greater than 45° and that of near-vertical walls. Other fauna such as sponges require the harder substratum commonly found forming walls in order to anchor securely (Gage & Tyler, 1991). Indeed, Porifera and Subsessiliflorae, another taxon requiring hard substratum for attachment, were most commonly observed on the steepest slopes and walls. The lack of statistical significance in these data may be an artefact of the data analysis approach as local changes in slope occur within individual transects which were adequately captured within the 50 m transect lengths (e.g. small sections of flat terrace within areas characterised as being steep, or short intervals of steep slope within areas characterised as having more gentle average slopes). The difficulty of assessing substrate types from video may also have confounded our results. It may not have been possible to recognise and classify hard substrate covered in a veneer of sediment accurately. Biological community structure was expected to vary based on substratum type as demonstrated in previous studies (Hecker, 1990; Lessard-Pilon et al., 2010).

There was a significant change in community composition as one traverses depth zones. The effect of water depth upon community composition has been observed on numerous occasions in a wide variety of habitats over a range of fauna (e.g. Cartes & Sarda, 1993; Haedrich et al., 1980; Lundsten et al., 2009a,b, 2010a; Williams et al., 2011; Yeh & Drazen, 2009; Zintzen et al., 2011). Observations of the most abundant taxa plotted by depth (Figure 5.4), shows that the depth range of a number of the organisms, such

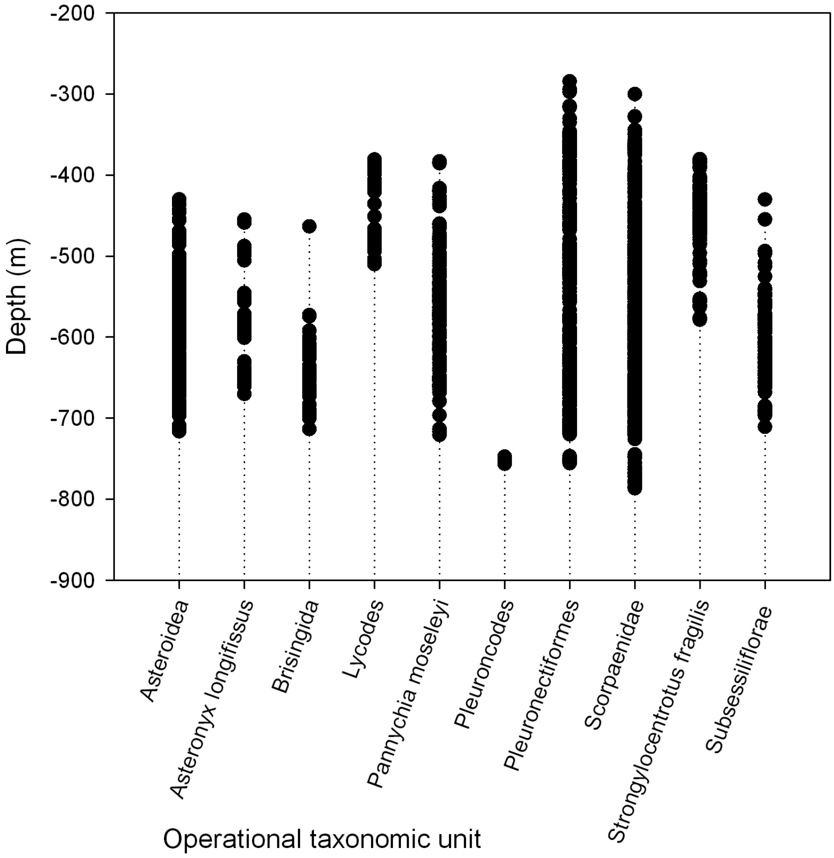


FIGURE 5.4: Occurrences of the 10 most frequently observed OTUs in the submarine canyons of Southern California plotted against depth observed.

as *Strongylocentrotus fragilis* and *Lycodes* spp., is restricted, while other taxa span the entire range observed. Overall, assemblages of detritivorous fauna appear to form a continuum across a wide depth-range within the canyons.

Dromalia alexandri, a benthic siphonophore which anchors itself to the seafloor (Pugh, 1983), was not found on transects which were focused on the main canyon channel. While the strength of the tentacles used by this siphonophore to tether itself to the seafloor has not been tested, the currents in the canyon axis may be too strong for this organism to settle and remain tethered (pers. comm., P. R. Pugh, National Oceanography Centre, UK). At sites deeper than 500 m, abundances of sea pens from the sub-order Subsessiliflorae were especially high on both gentle and steep slopes. On almost all occasions, the basket star *Asteronyx longifissus*, an organism that was rarely seen on the benthos, was observed attached to these animals. This behaviour has been observed in ophiuroids, which use sea pens as an attachment location in high current environments when other hard substrata are unavailable (Hochberg, 1998).

Sessile organisms, which were found in low numbers in the main channel, are unlikely to survive the fast water and sediment flow of an active canyon. In contrast, the shallowest transects in main canyon channel (approximately 375 m to 500 m deep) were dominated by *Lycodes diapterus* Gilbert, 1892, a teleost fish which is comparatively motile and can easily recolonise after an energetic event.

Detritivorous heart urchins, *Brisaster* Gray, 1855 spp., were frequently observed on gentle slopes at shallow depths; their occurrence was sporadic below 500 m, with none below 600 m. Heart urchins readily burrow, so their numbers are underestimated in video observations. The urchin *Strongylocentrotus fragilis*, another detritivore, was found in very high numbers on slopes and flats with soft muddy sediment shallower than 600 m, an observation also made to the north in Carmel Canyon (Harrold et al., 1998). Below this depth it was rarely observed.

When the occurrence of one detritivore began to decline, the niche was filled by other taxa practicing similar foraging behaviour. The action of *S. fragilis* and *Brisaster spp.* in the shallower zones is succeeded by an increased abundance of Asteroidea sp. 1 at deeper sites. The continuous representation of abundant detritivores within submarine canyons is not surprising given their associated high sediment and inorganic carbon input and identification as hotspots of secondary production (De Leo et al., 2010; Gage & Tyler, 1991; Jannasch & Taylor, 1984; Soliman & Rowe, 2008; Van Oevelen et al., 2011; Vetter, 1995).

The restrictions in depth distributions of the majority of the taxa may be an indication of their physiological tolerance limits with regard to depth-related environmental variables. Zonation of megafaunal communities with depth has been described on numerous occasions (Bett, 2001; Carney, 2005; Grassle et al., 1975; Haedrich et al., 1975, 1980; Hecker, 1990, 1994; Howell et al., 2002; Rex et al., 1999; Rowe & Menzies, 1969). Variation in ranges of each species results in continuous community change along depth gradients (Rowe & Menzies, 1969) with steeper slopes increasing this rate of change (Hecker, 1990). While direct displacement of species does not appear to occur (Rowe & Menzies, 1969) trophic feeding strategy shifts have been observed (Howell et al., 2002).

Community changes along depth gradients can be altered or disrupted by variability in water masses and is related to other environmental conditions including substrata, temperature, and productivity variation (Bett, 2001; Hecker, 1990, 1994; Howell et al., 2002; Levin et al., 2000; Rex, 1981). The effect of oxygen minimum zones on disrupting standard community depth trends are particularly striking (Levin & Gage, 1998; Levin et al., 2000) with only a few highly specialised organisms able to inhabit these low oxygen environments. It is difficult to discern between the specific effects of hydrostatic pressure and other depth-correlated variables, such as temperature, oxygen concentration, and salinity, due to the close correlation between these environmental variables (Lundsten et al., 2010a). Information regarding the nutrient availability within the studied canyons is not currently available. In the food-limited deep sea, there may also interspecific competition dictating which species are found within each depth band.

5.4.3 Species richness

The observed increase in species richness with depth between 200 m and 700 m follows previously reported trends of megafaunal diversity. On open continental slopes diversity has been reported to increase from the shallows down the slope before plateauing and declining at abyssal depths (Haedrich et al., 1975, 1980; Howell et al., 2002; Rex & Etter, 2010; Vinogradova, 1962). The diversity trend reported here shows a sharp decline in species richness at depths $>$ 700 m, in contrast to previously reported depth-diversity trends.

The Santa Monica Basin, into which the sampled canyons filter, has been previously identified as a low oxygen environment (Eldridge & Jackson, 1993; Hagadorn et al., 1995) and all transects below 700 m recorded relatively low oxygen levels (<0.23 ml l^{-1}). The deepest dives in Mugu submarine canyon were characterised by an abundance of *Pleuroncodes* sp. coupled with particularly low oxygen levels (~ 0.1 ml l^{-1}). With the exception of *Pleuroncodes* sp., organisms were observed in very low abundances during the deep transects in Mugu. While *Pleuroncodes* sp. is adapted to live in low oxygen conditions (Quetin & Childress, 1976), many other organisms are unable to maintain a population in these low oxygen environments. The La Jolla submarine canyon empties into the San Diego trough rather than the Santa Monica Basin, as such, the deepest transects in La Jolla submarine canyon, while at a comparable depth to those in Mugu, experienced marginally higher oxygen levels ($0.20 - 0.23$ ml l^{-1}). These transects showed more variation in megafauna than in Mugu, albeit in much lower abundances and less diverse than seen during shallower dives.

Low oxygen environments have been found to depress diversity and interrupt the standard depth-diversity trend (Levin & Gage, 1998; Levin et al., 2000). This provides a potential explanation for the sharp decline in diversity at these depths. Oxygen concentrations of less than 0.20 ml l^{-1} have been shown to depress diversity in deep-sea environments (Levin & Gage, 1998; Levin et al., 2000). The great abundance of *Pleuroncodes* sp. reflects the specialisation of this species to low oxygen environments and lack of competition from other organisms that are unable to tolerate the low oxygen concentration. This trend of high organism density but depressed diversity has been previously observed in oxygen minimum zones (Gooday et al., 2000). The standard depth-diversity trend is expected to continue below the oxygen minimum zone once oxygen concentrations rise (Levin et al., 2000), however topography levelled out at the mouths of each canyon upon meeting the Santa Monica Basin so deeper surveys were not possible.

5.5 Conclusions

While it has not been possible to determine the effect of canyon activity upon the communities found within them, this study has nevertheless shown an interesting result with regards to the role that depth-related factors play in controlling community composition and species distributions in these submarine canyons. In order to confidently determine if canyon activity affects community composition it is necessary for a more rigorous and uniform survey to be carried out in order to encompass a more even spread of transects in a range of depth-bands and slope-zones within all canyons. This study has, however, highlighted the value to biologists in reviewing and analysing video footage collected during ROV dives intended for primary studies in other scientific fields.

Chapter 6

Conclusions

Both scavenging amphipods and submarine canyons play important roles in the deep-sea ecosystem. Through the studies presented here it has been possible achieve the aims of this project, furthering our understanding of submarine canyon ecology, scavenging amphipod ecology at the community and population level, and the interaction of these two ecological aspects with each other. The objectives outlined at the outset of this thesis have been completed as summarised below

Submarine canyons of the Iberian Peninsula were found to house large assemblages of scavenging amphipods that were of low evenness, a consequence of the dominance of the genus *Paralicella* and the species *Paralicella caperesca* in particular. There is strong evidence that *Paralicella caperesca* is a semelparous organism capable of producing one large brood toward the end of its lifespan. Analyses comparing canyon populations to those from abyssal plains demonstrate that *P. caperesca* canyon cohorts have larger mean body lengths than their counterparts from the abyssal plain with strong evidence to suggest they also reach sexual maturity and reproduce at an earlier stage of their life cycle. The theory that observed differences between canyon and plain populations of *P. caperesca* is due to the increased food availability in submarine canyons rather than depth or temperature was supported by population analysis of *Abyssorchomene abyssorum* populations under differing trophic conditions at the Mid-Atlantic Ridge. Populations of female *A. abyssorum* from north of the Charlie-Gibbs Fracture were composed of cohorts with consistently smaller average body lengths than those from the more-productive south. *Abyssorchomene abyssorum* showed many characteristics of an iteroparous organism, and was classified as such.

The synthesis of studies of scavenging amphipod communities of the North Atlantic revealed the wide environmental tolerance of many scavenging amphipod species with habitat suitability maps suggesting the most common species have the potential to inhabit the majority of the deep-sea habitat. Nevertheless significant differences in community composition were seen between abyssal plains and between depth zones. The effects of depth on community composition were also observed in megafauna of the Southern Californian submarine canyon systems. Remotely operated vehicle surveys provided a unique opportunity to study these complex systems at a higher resolution than is possible using traps or trawls and to further study the environmental factors driving community changes in canyons and the wider deep-sea ecosystem.

6.1 Limitations and future direction

While providing vital new information on scavenging amphipod life histories, distributions, and ecological limits there remain many unknowns with regards to this important group of deep-sea organisms. The same can also be said of our knowledge of canyon ecosystems whose complexity and heterogeneity warrants a great deal of future research. Many gaps in our knowledge are the result of the limitations of our current sampling techniques and the difficulties associated with remote sampling. However with well-planned, targeted sampling it may be possible to fill some of these gaps in the future.

6.1.1 Experimental studies

The physiological limitations of deep-sea scavenging amphipods remain largely untested. Few laboratory studies have been carried on these organisms with Brown & Thatje, 2011 being a notable exception. In order to carry out controlled tests of the physiological limits of various scavenging amphipod species it is first necessary to collect live specimens. Specimens are sometimes alive on recovery of baited traps, particularly in polar regions, and live recovery rates can be increased using insulated traps (Yayanos, 1978), which limit fatality from increasing water temperatures.

While recovery of deep-sea organisms is possible without using pressure-sealed vessels (Brown & Thatje, 2011; Yayanos, 1978), laboratory experiments ideally need to be carried out at environmental pressures. This is due to the effect of hydrostatic pressure on amphipod physiology and the potential for synergistic effects with the environmental variables being tested (Brown & Thatje, 2011). The facilities necessary to maintain and perform experiments on organisms at pressure are often costly and are not always widely available. Pressure vessels also carry the problem of confining the test organism to a relatively small space which may influence behaviour and produce unrepresentative physiological responses.

Controlled experiments on the physiological constraints of deep-sea scavenging amphipod species are necessary to further our understanding of the variables controlling scavenging amphipod distributions. Such experimentation would complement existing ecological studies. The collection of live specimens may also provide the opportunity to closely study the life cycles of deep-sea species. While it has been possible to infer some aspects of life histories from ecological studies, keeping deep-sea scavenging amphipods under controlled conditions and tracking their growth would prove undoubtedly beneficial.

6.1.2 Limitations of using baited landers

In spite of all of the benefits of sampling scavenging fauna using baited landers, there are some disadvantages inherently associated with this method meaning that this and similar methods can only be considered as semi-qualitative samples (De Broyer et al., 2004). If, as expected, scavenging amphipods use chemical cues to locate bait, then the sample area is constricted by local conditions and currents affecting the dispersal of the bait's odour plume. In turn, the velocity and direction of currents can affect the numbers of individuals attending food-falls (Lampitt et al., 1983; Wilson & Smith, 1984). This means traps deployed at different sites will have varying catchment areas, making direct comparisons between samples complicated with a number of assumptions necessary (Bailey et al., 2007). As such, the estimation of background populations of the scavenging organisms based on catches from traps must be approached cautiously and in the case of scavenging amphipods may not be possible at all with our current understanding and techniques.

A number of models have been proposed to estimate bait-plume dispersal and trap catchment area (Farnsworth et al., 2007; Heagney et al., 2007; Sainte-Marie & Hargrave, 1987), and furthermore to estimate background population size of scavengers (Priede & Merrett, 1998). These models have been successfully applied in studies examining scavenging fish species in relatively homogenous deep-sea environments with consistent current regimes but it is difficult, if not impossible, to apply these models within highly heterogenous environments or to scavenging amphipod populations.

The accurate measurement of current flow and diffusion rates required for bait-plume estimations are rarely available for heterogenous deep-sea environments such as submarine canyons (Bailey et al., 2007). Even where data is available from these environments local currents are found to vary so much in space and time that modelling bait-plume dynamics and estimating the subsequent area of attraction would require a model of incredible complexity. Even the most simple area of attraction models also require accurate swim speeds for the target organisms. Swim speeds have been measured for a handful of deep-sea scavenging amphipod species including two species frequently caught at abyssal plain and submarine canyon sites in the North Atlantic (Duffy et al., 2012; Thurston, 1990; *Paralicella caperesca*, 2.46 cm s^{-1}; *Eurythenes gryllus* 8.05 cm s^{-1}; Smith & Baldwin, 1982). It is, however, improbable that these measured speeds are true representations of maximum swim speeds. Data from one of the few current meters deployed near an amphipod trap site indicate that current speeds in canyons are frequently too fast for any *P. caperesca* to swim against (King et al., 2008). Large numbers of this species in baited traps suggest that this species is fully capable of reaching a food fall in a submarine canyon (Duffy et al., 2012). It is possible that *P. caperesca* uses an alternative means of locomotion, such as crawling, to circumvent swimming into strong currents. Crawling along the seabed has been noted where locomotion of amphipods was observed (Conlan, 1991; De Robertis et al., 2001; Sainte-Marie, 1986b; Vetter & Smith, 2005) but it is believed that deep-sea scavenging amphipods swim, rather than crawl, to food falls (Hessler et al., 1978; Thurston, 1979).

The methods used in determining swim speeds are the most likely source of error when measuring these speeds in deep-sea scavenging amphipods. In the case of *P. caperesca*, Smith & Baldwin (1982) used towed bait and a video camera to measure swimming speed. While this remains the *de facto* way to measure swim speeds of these organisms, their swim speed in close proximity to a food-fall is unlikely to be the same speed at which they swim when further from bait. A slower searching speed is expected on approaching a food source in order to pinpoint the food fall location. Behaviour near food falls has also been observed to alter based on the activity of conspecifics in the area (Ingram & Hessler, 1983).

It may be possible to accurately measure long-distance swim speeds for large amphipod species using scanning sonar (Premke et al., 2003), but owing to the small size of other scavenging species they are most probably undetectable using this method. The use of multiple cameras positioned at various points along a bait plume may provide more accurate measures of long-distance swim speeds but again the small size of many scavenging amphipod species makes video survey a difficult technique to apply.

It is almost impossible to identify scavenging amphipod taxa from photographs or video footage. This not only makes measuring swim speeds for specific species difficult to determine but also confounds population estimation once bait plume and catchment area have been estimated. Past population estimation methods applied to larger scavengers rely on video or photographs to pinpoint the time of first arrival for each species (Priede & Merrett, 1998). The inability to identify all but the largest amphipods from these data means that these methods cannot be used to estimate amphipod populations with current technology. Time of first arrival from small scavenging amphipod species could theoretically be determined using time-delay traps, which seal off after a given period of deployment. However, past deployments of complex time-release landers has not proven to be particularly successful (Blanco et al., 2013; Priede, 2010) and the sampling methods require further development before they can be realistically applied in real-world situations.

One proposed resolution to estimating population size was using the mark and recapture method (Smith & Present, 1983). A mark and recapture technique for use on scavenging amphipods was developed utilising the submersible *Cyana* (IFREMER, France; Gaunt, 1986; Thurston, 1985 but technical difficulties marred early deployments of this trap. Attempts to use this method to estimate scavenging amphipod populations have largely been abandoned.

Another potential problem in estimating population size using baited traps is that samples from these traps may not be a true representation of scavenging amphipod community composition. The deployment duration of a trap coupled with local current speed may directly affect the abundance and community composition of amphipods able to enter the trap (Lampitt et al., 1983; Thurston et al., 1995). Short deployment times and fast currents may exclude less motile species, with more motile scavengers dominating the sample due to their superior swimming ability, while extended deployments may result in catches with artificially high numbers of less motile species. Unpublished data suggests that catches from deployments with very long durations ($>$ 100 hours) differ from those of more standard duration ($\sim$ 24 hours; pers. comm., T. Horton & M. H. Thurston, National Oceanography Centre, UK). This difference is negligible but for consistency amphipod trap deployments are targeted to last approximately 24 hours and the comparison against extremely long deployments is avoided whenever possible.

Other potential sources of error that may affect the overall composition of trap catches include the threat of predation at a specific deployment site (Zamzow et al., 2010), the natural availability of food-falls in the sample area (Janßen et al., 2000), the size (Sainte-Marie, 1986a), amount (Bailey et al., 2007), type, and preparation method of bait (Lampitt et al., 1983), the varying life cycles of target species (Kaïm-Malka, 2003, 2005), the configuration of the trap (Bailey et al., 2007), and the rarity of brooding females at food falls (Ingram & Hessler, 1987; Sainte-Marie, 1991; Thurston et al., 1995). All of these factors should ideally be accounted for if at all possible, however this is not always feasible owing to the inherent difficulties of deep-sea sampling.

6.2 Study of submarine canyons

Submarine canyons are difficult to study with trawls, a technique often applied to studying other deep-sea habitats (Priede & Merrett, 1998). This is a result of their rugged topography and associated fast currents. Baited traps and cameras can only provide a snapshot of submarine canyon ecosystems, specifically targeting scavenging organisms. Although scavenging fauna are an important component of deep-sea ecosystems, better understanding of non-scavenging fauna in canyon ecosystems is required to move toward complete understanding of these complex environments. Remotely operated vehicles (ROVs) have proven to be an incredibly useful sampling tool for sampling rugged terrain. In recent years ROV surveying and sampling has provided new insight into submarine canyon ecosystems (Goffredi et al., 2004; Lundsten et al., 2010a; McClain & Barry, 2010; Paull et al., 2011, 2005, 2010; Robison et al., 2010; Tyler et al., 2009).

Video survey and sampling using standard ROV toolsets (e.g. suction sampling, push coring) is ideal for studying megafauna and infauna. It is also possible for baited traps to be deployed using ROV technology.

Using ROVs to deploy traps is a rare practice as freefall landers are often available and require less direct input for deployment and recovery. This is an unfortunate result of the relative ease of use and low cost of use of freefall landers compared to using an ROV for trap deployment. The cost of running ROVs means that dive time is often in great demand. Using an ROV for trap deployment in submarine canyons, with recovery via ROV or ballast with acoustic release, would allow targeted deployment of the traps and ensure accurate environmental data can be recorded for a specific macrohabitat within these complex and heterogenous environments.

6.3 Concluding remarks

The studies presented here provide novel insight into the ecology of submarine canyons and of scavenging amphipods. The complexity and heterogeneity of submarine canyon environments was demonstrated through the study of benthic megafauna communities. For the first time, canyon effects have been identified for scavenging amphipods at the community and population level. Important life-history characteristics have been inferred for two species of deep-sea scavenging amphipod. This was made possible by via the most comprehensive population studies yet reported for any deep-sea amphipod species. The application of multivariate analyses and niche suitability modelling provided new understanding of the environmental factors affecting scavenging amphipod distribution. While there is still a great deal unknown, the work presented here has contributed to the field of deep-sea ecology and paved the way for numerous future research projects to address the as yet unanswered questions.

Appendix A

Supporting publications

Duffy, G. A., Lundsten, L., Kuhnz, L. A., & Paull, C. K. (in press). Megafaunal community structure in the submarine canyons of Southern California. Deep-Sea Research II.

Duffy, G. A., Horton, T., Sheader, M., & Thurston, M. H. (2013). Population structure of *Abyssorchomene abyssorum* (Stebbing, 1888) (Amphipoda: Lysianassoidea), a scavenging amphipod from the Mid-Atlantic Ridge in the vicinity of the Charlie-Gibbs Fracture Zone. Deep-Sea Research II.

Horton, T., Thurston, M. H., & Duffy, G. A. (2013). Community composition of scavenging amphipods at bathyal depths on the Mid-Atlantic Ridge. Deep-Sea Research II.

Duffy, G. A., Horton, T., & Billett, D. S. M. (2012). Deep-sea scavenging amphipod assemblages from the submarine canyons of the Western Iberian Peninsula. Biogeosciences, 9, 48614869.

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Population structure of *Abyssorchomene abyssorum* (Stebbing, 1888) (Amphipoda: Lysianassoidea), a scavenging amphipod from the Mid-Atlantic Ridge in the vicinity of the Charlie-Gibbs Fracture Zone

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ABSTRACT

This study focussed on the common and ubiquitous scavenging amphipod *Abyssorchomene abyssorum* collected from a section of the Mid-Atlantic Ridge with one pair of sampling areas at 49°N and the other at 54°N, north and south of the Charlie Gibbs Fracture Zone (CGFZ) and east and west of the ridge, at a water depth of 2500 m. Baited-trap samples of necrophagous amphipods were collected during three research expeditions on the RRS *James Cook* in 2007, 2009, and 2010, allowing for direct comparisons to be made amongst populations of *A. abyssorum* at the four sample areas. Random subsamples of 200 individuals from nine trap samples were sexed, dissected, and measured.

Males, females, and juveniles were found in all samples but no ovigerous females were identified. The finding of sexually mature mid-sized females, variability of oocyte size with body size, and presence of mature females with 'empty' ovaries, suggest that *A. abyssorum* is capable of having multiple broods in a lifetime. This reproductive strategy is beneficial to a scavenging organism living under a variable and unpredictable nutrient regime, allowing for a rapid reproductive response to advantageous conditions. Females north and south of the CGFZ fall into distinct cohorts with different distributional parameters. The total body lengths of female cohorts south of the CGFZ were consistently larger than those in the north. This is likely due to increased nutrient availability at the southern sampling areas.

Males were significantly smaller than females and possessed longer, more articulate antennae. Longer antennae are thought to facilitate mate-searching by males. Estimates of the maximum brood size ranged from 36–78 offspring with actual brood size expected to be at the lower end of this scale. This places the estimated brood size of *A. abyssorum* in a similar range to that of other scavenging amphipods of comparable size. The juvenile:non-juvenile ratio differed north and south of the CGFZ with significantly more juveniles in the north. Possible reasons for this difference are discussed.

1. Introduction

Through their role in recycling organic carbon from large food-falls, scavenging organisms, and in particular scavenging amphipods, are a vital component of secondary production cycles that support numerous deep-sea ecosystems (Stockton and DeLaca, 1982; Christiansen and Diel-Christiansen, 1993; Britton and Morton, 1994; Payne and Moore, 2006). In spite of this, our understanding of the ecology of these organisms remains poor. A concerted effort in the field has furthered our understanding of deep-sea scavenging amphipods and their distribution at the community level (e.g. Thurston, 1990; Jamieson et al., 2011; Duffy et al., 2012; Horton et al., this issue), but few studies have examined the factors affecting population structure and distribution of deep-sea scavenging amphipods.

Numerous population studies have been carried out on shallow water amphipods (see Sainte-Marie, 1991, for a comprehensive review of pre-1990 literature; Arndt and Beuchel, 2006; Nygård et al., 2009). The study of deep-sea populations is, however, largely limited to the giant amphipods *Eurythenes gryllus* Lichtenstein 1822 (Ingram and Hessler, 1987; Premke et al., 2006) and *Alicella gigantea* Chevreux, 1899 (Barnard and Ingram, 1986), and species inhabiting hydrothermal vent (Sheader et al., 2000, 2004; Sheader and Van Dover, 2007), submarine canyon (Kaïm-Malka, 2003, 2004, 2005), and trench environments (Thurston et al., 2002; Blankenship et al., 2006). Without detracting from the importance of these studies, *E. gryllus* is rarely the most abundant species in deep-sea scavenging communities, and vent, canyon, and trench environments account for a very small part of the deep-sea by area.

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Mid-ocean ridges, on the other hand, represent a large area of the deep-sea benthic habitat, yet they have been poorly studied beyond their hydrothermal vent systems.

The Mid-Atlantic Ridge (MAR) bisects the Atlantic Ocean and accounts for 45.7% (3 704 404 km^2) of seabed in lower bathyal (800–3500 m) depths in the North Atlantic (Priede et al., this issue). Prior to the commencement of the MARECO and ECOMAR projects very little was known of the ecosystems of this environment. Following 19 research expeditions, involving partners from 17 countries, our understanding has progressed substantially.

The ECOMAR project provided a unique opportunity to study deep-sea scavenging amphipod communities at a single depth (~2500 m) across four geographically separated sampling areas at the MAR over a four-year period. Distinct scavenging amphipod assemblages were found at each sampling area with significant differences north and south of the Charlie-Gibbs Fracture Zone (CGFZ; Horton et al., this issue). All samples were dominated by the lysianassoid amphipod *Abyssorchomene abyssorum* Stebbing, 1888. The presence of this species in high abundances at all sampling areas provided the opportunity to study these organisms at the population level.

Abyssorchomene abyssorum, like all other scavenging amphipods, has a limited dispersive ability, obligate brooding, and direct development; yet evidence suggests it has a wide-ranging, cosmopolitan distribution (Barnard and Karaman, 1991; Thurston 1990). An in-depth analysis of the populations of *A. abyssorum* inhabiting the MAR, including observations of sexual characteristics, will provide vital information concerning the life history of this species and will help us to understand its success in the deep sea. Sampling across four distinct areas at a constant depth allows for direct comparisons to be made amongst these populations. Analysing how populations vary between sampling areas may facilitate the identification of the environmental factors responsible for population-level variation amongst sampling areas.

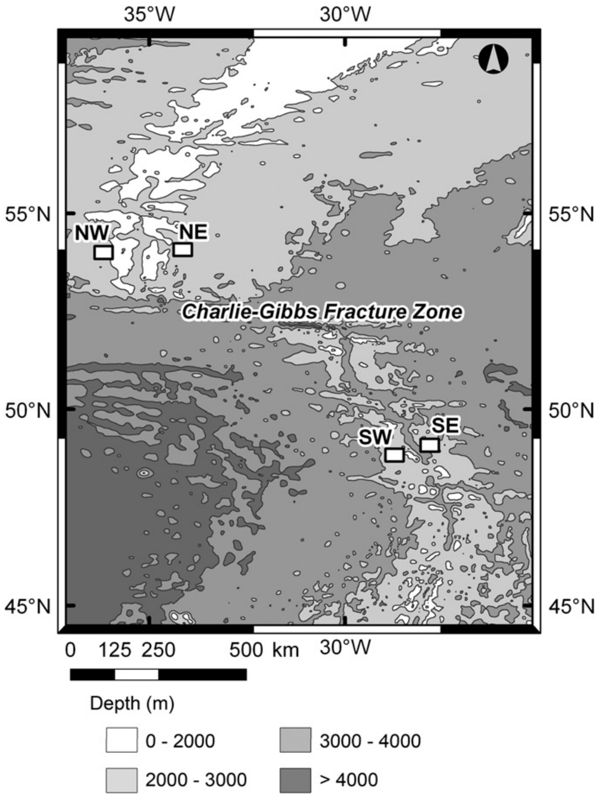

Fig. 1. Bathymetric map of study area coloured by water depth. Sampling areas highlighted by white boxes.

2. Materials and methods

2.1. Sample collection

Four ECOMAR sampling areas were studied (Fig. 1) during research expeditions in the boreal summers of 2007, 2009, and 2010 (RRS *James Cook* expeditions JC011, JC037, and JC048 respectively). Amphipods were collected using baited traps attached to free-fall landers. The lander design and trap arrangement varied across years (see Horton et al., this issue, for further discussion) however the basic trap design was consistent. A funnelled entrance led to the bait of a whole mackerel (*Scomber scombrus*), either in a meshed off section of the trap or wrapped in muslin cloth. Soak time varied (from 13–101 h) as a result of weather conditions and operational constraints. For this reason samples were selected such that the effects of variable soak time were minimised with particularly long deployments excluded in favour of shorter deployments at the same sampling area where possible (Table 1).

Due to operational constraints the southwest sampling area was only sampled in 2010 and the southeast area was sampled during two years (2009, 2010). Both northern areas were sampled successfully on all three expeditions. The contents of the traps were fixed in either 100% ethanol or 4% buffered formaldehyde–saline solution. Formalin-fixed material was subsequently transferred to 80% industrial methylated spirit. Samples were sorted to species level (Horton et al., this issue) with the *A. abyssorum* component of selected samples used for population analysis in this study.

2.2. Data collection

Every individual was assigned a unique identification number and 200 individuals were randomly selected from each sample using a random number generator. Selected individuals were dissected and measured under a stereo-dissecting microscope. Specimens were preserved in a variety of postures and many were damaged, making it difficult or impossible to accurately measure total body length for all individuals. Previous studies have resolved this problem by measuring an individual body-part as a proxy for total body length. A range of proxies have been used previously, including coxal plate 4 diagonal length (Chapelle, 1995; Blankenship et al., 2006), pereonite 1 dorsal length, (Thurston et al., 2002; Nygård et al. 2009), the length of the dorsal margin of pleonite 1 (Sheader et al., 2004; Sheader and Van Dover, 2007), dorsal margin length of pleonite 3 (Sheader et al., 2000). In this study coxal plate 4 was used as a proxy for total body length.

The total body length (distance along the dorsal margin between the anterior margin of the head and the tip of the telson) of all intact individuals from sample JC048/032 was measured. This was performed using a digital graphics tablet and HTML-assisted Measuring System (HaMS) calibrated using a stage graticule of known length. Use of HaMS permitted accurate measurement of a curved line. These data were subsequently correlated to the diagonal linear measure of coxal plate 4 (as in Chapelle, 1995), which were made using a stage graticule. Estimation of total body length for all remaining specimens was possible using the coxal plate 4 measurement as a proxy.

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Table 1
Baited trap deployments whose *Abyssorchomene abyssorum* component was used for this study.

Station	Area	Location Latitude	Longitude	Depth (m)	Date deployed (dd/mm/yyyy)	Bottom time (hh:mm)
JC011/098	**NE**	54°04.08′N	34°09.43′W	2500	09/07/2007	46:58
JC037/083	**NE**	54°02.31′N	34°09.54′W	2452	02/09/2009	32:21
JC048/020	**NE**	54°03.95′N	34°09.12′W	2505	08/06/2010	24:09
JC011/079	**NW**	53°56.44′N	36°11.56′W	2564	05/05/2007	42:09
JC037/052	**NW**	53°59.32′N	36°08.12′W	2570	25/07/2009	35:13
JC048/008	**NW**	53°59.32′N	36°08.07′W	2628	02/06/2010	101:20
JC037/013	**SE**	49°02.00′N	27°43.44′W	2501	08/07/2009	41:45
JC048/046	**SE**	49°02.01′N	27°43.44′W	2507	23/06/2010	70:45
JC048/032	**SW**	48°47.34′N	28°38.45′W	2448	16/06/2010	75:28

Identification of primary and secondary sexual characteristics allowed for accurate sexing of all but the smallest individuals, which were classified as unsexed juveniles. Along with coxal plate 4, antenna 1 (length, number of articles, accessory flagellum length), antenna 2 (length, number of articles), and secondary sexual characteristics (oostegite length and presence of oostegite setae in females, presence of genital papillae in males) were also measured. Oocytes of females at varying stages of sexual maturity were measured and counted. The half-range of mature female body length (HMFBL) ratio for *A. abyssorum* was calculated from the maximum and mean female body length (Sainte-Marie, 1991).

2.3. *Population characterisation*

Identification of cohorts of amphipods is possible using measurements of total body length or a correlated proxy (Sheader et al., 2000, 2004; Thurston et al., 2002; Kaïm-Malka, 2003, 2004, 2005; Blankenship et al., 2006; Premke et al., 2006; Sheader and Van Dover, 2007). Oostegite measurements for females and coxal plate 4 measurements for each sex, including a separate histogram for unsexed juveniles, were plotted as probability density histograms. Identification of normal distributions, each representing an oostegite stage or cohort, was initially performed by eye. The presence and parameters of each of these distributions were confirmed using the probability paper method (Harding, 1949; Cassie, 1954) and the 'mixdist' package (Macdonald and Pitcher, 1979; Macdonald and Du, 2011) in R statistical software (R Development Core Team, 2012). The accuracy of each of the modelled distributions was confirmed using the ANOVA function included in the 'mixdist' package.

2.4. *Comparison of populations*

Nonparametric statistical tests were used to compare male:female, mature:immature female, and juvenile:non-juvenile ratios amongst sampling areas (Kruskal–Wallis test) and either side of the MAR and CGFZ (Mann–Whitney U test). Once parameters for cohorts were accurately determined, all 200 individuals from each sample were assigned to the appropriate cohort based on 95% confidence limits (2 standard deviations from the mean). Where overlap of these limits occurred individuals were assigned to cohorts based on the relative proportions of each cohort. Once classified, data were analysed using PRIMER 6 statistical software (Clarke and Gorley, 2006). Each cohort was treated as a 'species' in each sample in order to perform multivariate analyses to compare the cohort composition of populations at each sampling area.

Data were root transformed to minimise the skewing effect of highly dominant cohorts. A similarity matrix was created based on Bray–Curtis similarities (Bray and Curtis, 1957) and a multidimensional scaling (MDS) plot was created to visualise population similarity. Cluster analysis was used to group stations based on similarity. Populations were compared using ANOSIM tests with sampling area (NE, NW, SE, SW) and sampling year as factors. Stations north and south of the CGFZ and east and west of the MAR were grouped and compared using ANOSIM tests (N/S; E/W). A SIMPER analysis was used to identify which components of the population were contributing most to the variability seen (Clarke, 1993).

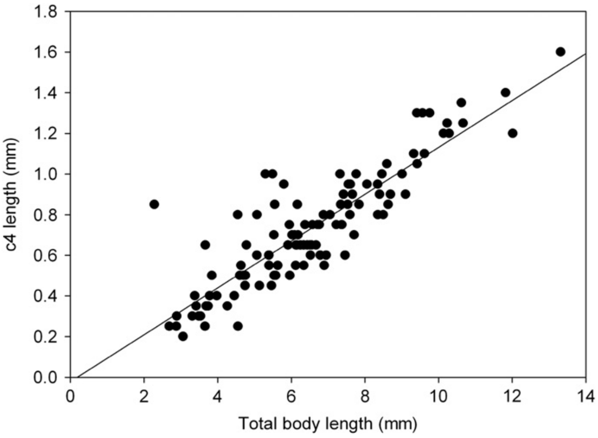

Fig. 2. Linear correlation between total body length and coxal plate 4 (c4) length. $n=110$, $y=0.1153x-0.0215$, $R^2=0.7700$. Measurements of all intact individuals from sample JC048/032.

3. Results

In total, 1800 amphipods were dissected and measured from the collected samples. Males, females, and juveniles were identified in all samples, but no ovigerous females were identified. There was a strong positive correlation between total body length and coxal plate 4 length (Fig. 2; $n=110$, $R^2=0.7700$). This relationship permitted the use of coxal plate 4 measurements as a proxy for total body length using the equation

$$L=\frac{C+0.0215}{0.1153}$$

where L is the estimated total body length and C is the linear measure of coxal plate 4. Estimated total body length ranged from 1.92 mm to 16.67 mm. No individuals smaller than 4.09 mm showed primary or secondary sexual characteristics and were identified as juveniles. With few exceptions individuals larger

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Table 2
Mean body size for all cohorts identified. Linear growth factor between successive cohorts in parentheses.

	Male		North females	South females
Cohort	Body length (mm)	Cohort	Body length (mm)	Body length (mm)
J1	2.61	J1	2.61	2.61
	(1.51)		(1.51)	(1.51)
J2	3.89	J2	3.89	3.89
	(1.42)		(1.38)	(1.50)
M1	5.45	F1	5.30	5.74
	(1.37)		(1.19)	(1.19)
M2	7.40	F2	6.26	6.78
	(1.44)		(1.26)	(1.24)
M3	10.60	F3	7.82	8.43
			(1.35)	(1.33)
		F4	10.51	11.20
			(1.20)	(1.22)
		F5	12.59	13.72
			(1.11)	
		F6	13.98	-
			(1.18)	
		F7	16.41	-

than this exhibited both primary and secondary sexual characteristics.

3.1. *Sexual dimorphism*

The total body lengths of males were significantly smaller than those of females (Table 2: Fig. 3a; Mann–Whitney U: $n=997$, $U=72\ 416$, $p<0.001$). Males ranged in total body length from 4.09 mm to 11.90 mm (Median=7.12 mm, IQ range=5.82 mm to 7.99 mm). Females ranged in body size from 5.39 mm to 16.67 mm (Median=8.43, IQ range=6.69 mm to 11.03 mm). The largest individuals (>12 mm total body length) were exclusively female. Males possessed significantly longer antenna 1 and antenna 2, relative to total body length, than those of the females (Fig. 3b; MWU: $n=990$, $U=231\ 997$, $p<0.001$; $n=980$, $U=222\ 405$, $p<0.001$ respectively) with differences becoming more pronounced with increasing body size. As a function of antenna length (articles mm^{-1}), males possessed significantly more articles on antenna 1 and antenna 2 than females (MWU: $n=990$, $U=176\ 935$, $p<0.001$; $n=979$, $U=133{,}049$, $p=0.001$ respectively).

3.2. *Sexual development*

Two ovaries, lying dorso-laterally either side of the gut, could be identified between pereonites 3 and 7 in some females as small as 5.39 mm. Complete ovaries were recoverable from only 40 individuals due to the poor condition of specimens. Both ovaries contained equal numbers of ellipsoid oocytes of approximately equal size in a linear arrangement. Ooctye size, calculated as the area of an ellipse ($\pi r_1 r_2$), generally increased with body size but was not closely correlated (Fig. 4a). Some large females had relatively small oocytes and some small females possessed large oocytes. The total number of oocytes within each ovary ranged from 18 to 39 and had a weak, inverse correlation to oocyte size. There was no apparent relationship between oocyte number and total body length (Fig. 4b).

Oostegite buds were visible on females as small as 5.82 mm in length but the majority (94.5%) of females of this size lacked any trace of oostegites. Larger females possessed oostegites of varying size. A probability density histogram of oostegite length as a ratio of gill length (Fig. 5) identified three distinct oostegite stages (OS1–OS3; Table 3) with limited overlap. The presence and parameters of these stages were confirmed using the probability paper method.

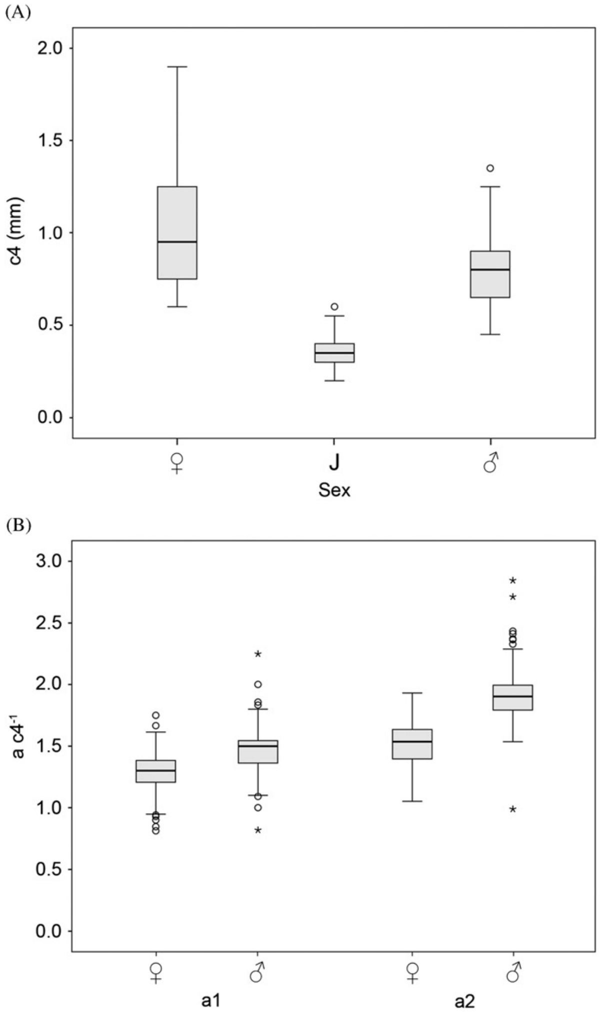

Fig. 3. Comparison between sexes from all stations at all sampling areas. (A) Length of coxal plate 4 (c4), a proxy for total body length, for males, juveniles, and females. (B) Length of antennae as a function of coxal plate 4 (a c4^{-1}) length for antenna 1 and antenna 2 in male and female *Abyssorchomene abyssorum*. Median and interquartile ranges shown, open circles indicate individuals outside the interquartile range, asterisks indicate statistical outliers.

Setose oostegites, an indicator of female maturity, were observed in individuals from all three stages in differing frequencies. Of 73 individuals of OS3, 61 (83.6%) possessed setose oostegites. Only 2 out of 69 individuals (2.9%) of OS2 and a single specimen of the 141 OS1 individuals (0.7%) bore setae on their oostegites.

Testes were identifiable in the majority of males seen however they did not preserve well and were in generally poor condition making developmental classification impossible. Penile papillae in this species were relatively large, extending to the mid-point of the ventral surface and producing marked downward protrusions that were easily identified on examination of pereonite 7.

3.3. *Population characterisation*

Individuals that could not be sexed were assigned to two juvenile stages (Fig. 6a). The smaller individuals met the conditions

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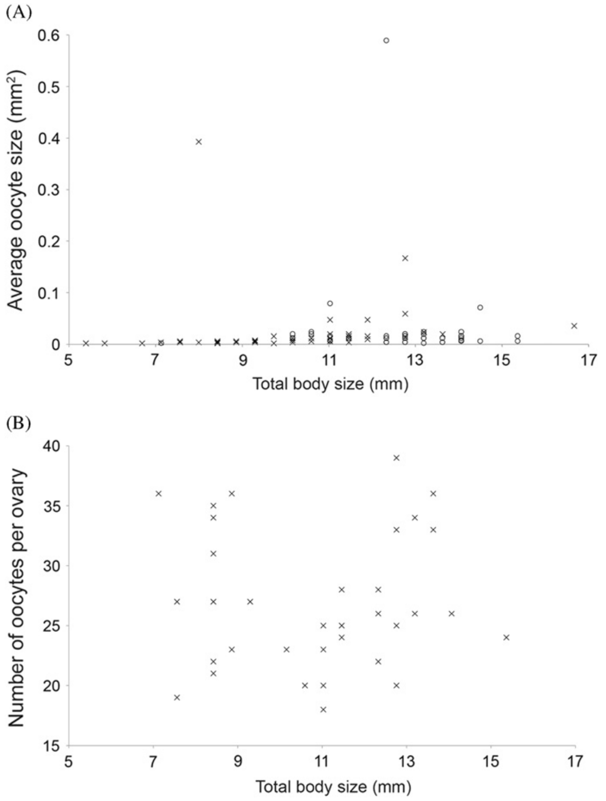

Fig. 4. (A) Average oocyte size relative to body length for all females from all samples where ovaries or partial ovaries could be identified. Immature females represented by '*x*', mature females with setose oostegites represented by open circles. (B) Total oocyte count for all complete ovaries identified compared to total female body length.

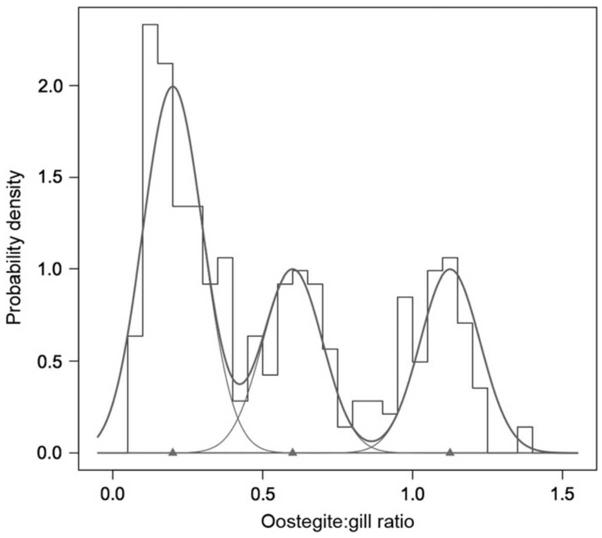

Fig. 5. Probability density histogram for oostegite:gill ratios for all females possessing oostegites from all samples. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Thin lines represent the distribution of each oostegite stage, thick line represents entire population.

Table 3
Counts of oostegite stage, identified based on oostegite:gill ratios, for each female cohort. (Setose oostegite count for OS3).

Oostegite stage	Oostegite: Gill ratio (μ)	F1	F2	F3	F4	F5	F6	F7
OS0	–	69	50	45	3	1	0	0
OS1	0.20	4	16	102	17	1	1	0
OS2	0.60	1	0	2	64	2	0	0
OS3	1.20	0	0	0	29	37	6	1
(setose)					(23)	(33)	(6)	(1)

of a normal distribution and could confidently be grouped as such (J1). Unsexed individuals that could not be sexed but were more than 2σ larger than J1μ were grouped as J2 juveniles. The distribution of J2 overlapped with the smallest sexed individuals (M1, F1; Fig. 6a). Males from all sampling areas were found to fall into three distinct cohorts (M1, M2, and M3; Fig. 6b). The presence and number of these cohorts were confirmed using the probability paper method. The boundaries, mean, standard deviation, and relative proportion of each of these cohorts (Table 2) were further refined using a 'mixdist' model, which satisfactorily fitted the data (ANOVA: d.f.=6, $\chi^2=17.00$, $p=0.2562$).

A total of 7 cohorts were identified for females (F1–F7). The five smallest cohorts (F1–F5) were observed in samples from north and south of the CGFZ but the parameters of these cohorts varied north and south of the CGFZ. Cohorts of females from north of the CGFZ (Fig. 6c) were consistently smaller than those at southern areas (Fig. 6d). The occurrence and parameters of these cohorts were confirmed using the probability paper method and a 'mixdist' model fitted to the data (ANOVA: north, d.f.=9, $\chi^2=8.42$, $p=0.4925$; south, d.f.=12, $\chi^2=12.37$, $p=0.4165$). Cohorts F6 and F7 were represented by a handful of individuals at the northern sampling areas only. Linear growth factors between cohorts J1 and J2, and J2 and F1/M1 were high (Table 2). Increments between cohorts of females from the northern sampling areas fell in the range of 1.11–1.35 and those from the southern sampling areas in the range of 1.19–1.33.

Oostegite stages were distributed across female cohorts. Individuals with no oostegites (OS0) were found in all but the two largest female cohorts (F6, F7). The smallest oostegites (OS1) were found in all cohorts apart from F7, which was represented by one large individual with setose OS3 oostegites. The sole amphipod with OS1 oostegites in the F6 cohort possessed setose oostegites in spite of their small size. Setose OS3 oostegites were found in individuals from cohorts F4–F7. The HMFBL ratio (Sainte-Marie, 1991) was calculated as 0.2297, placing *A. abyssorum* between the expected ratios for iteroparous (>0.3478) and semelparous (<0.1304) species.

3.4. Population comparison

The male:female and mature:immature female ratios did not differ significantly amongst sampling areas (Table 4; Kruskal–Wallis: $n=9$, d.f.=3, $H=3.489$, $p=0.322$; $n=9$, d.f.=3, $H=0.178$, $p=0.981$ respectively). The juvenile:non-juvenile ratio did not differ significantly amongst sampling areas (Table 4; KW: $n=9$, d.f.=3, $H=5.622$, $p=0.132$) but was significantly different north and south of the CGFZ (MWU: $n=9$, $U=17$, $p=0.048$) with significantly more juveniles north of the fracture zone.

Multivariate analysis showed populations varied significantly based on sampling area (ANOSIM: $R=0.379$, $p=0.045$). Differences were not significant when stations were grouped based on their position relative to the MAR and CGFZ (ANOSIM: north/south, $R=0.198$, $p=0.143$; east/west, $R=0.006$, $p=0.373$) rather than by

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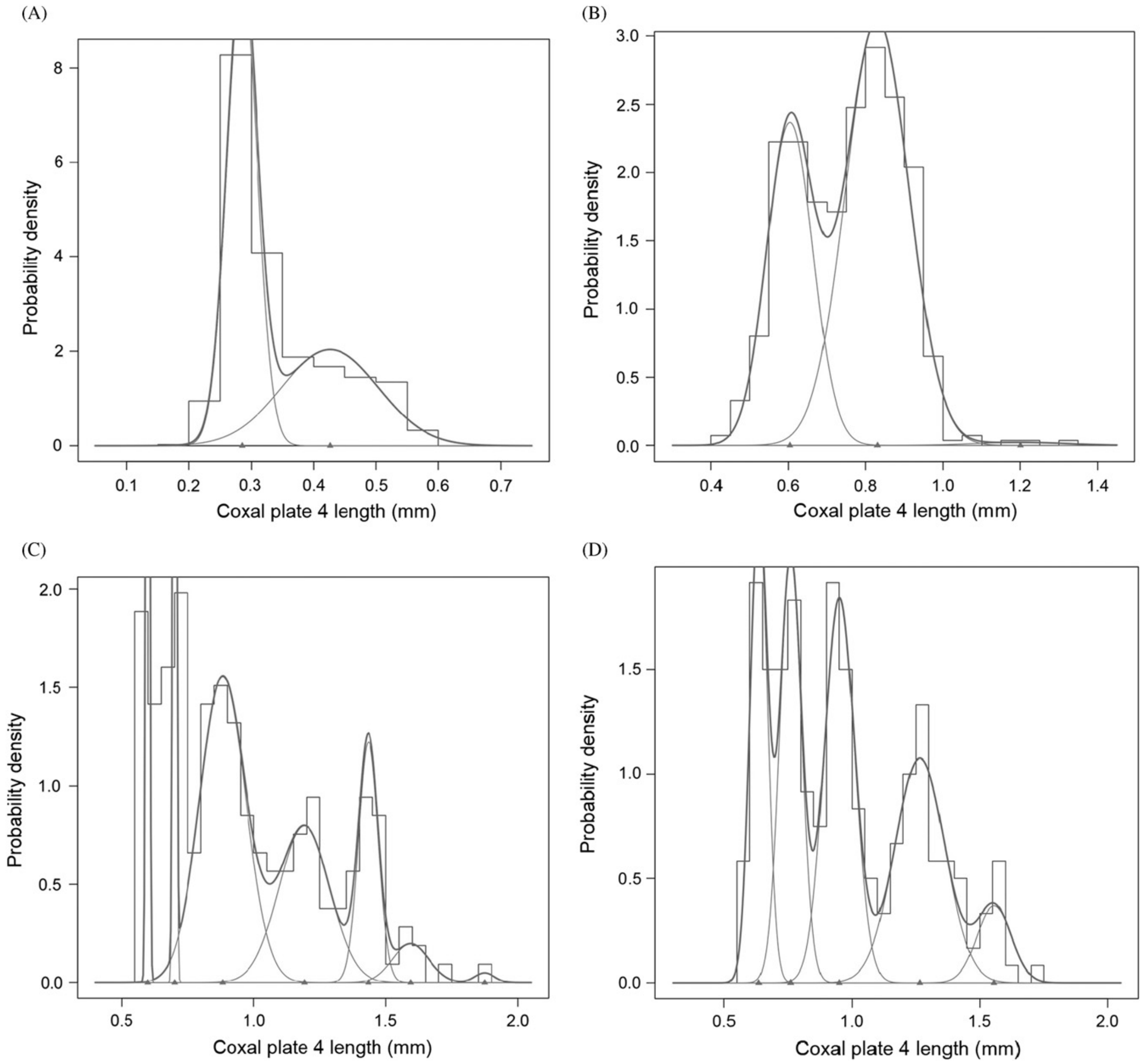

Fig. 6. Probability density histograms of coxal plate 4, a proxy for total body length, measures. (A) Combined data for juveniles from all samples. (B) Combined data for all males. (C) Females from stations north of the CGFZ. (D) Females from stations south of the CGFZ. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Thin lines represent distribution of each cohort, thick line represents entire population.

Table 4
Total counts of males, females, and juveniles for all samples. Population composition ratios used for univariate comparison shown.

Sample	Area	Total males	Total females	Mature females	Total juveniles	**Male: female ratio**	% **Mature females**	**Mature: juvenile Ratio**
JC011/079	NW	53	95	3	102	**0.56**	**0.03**	**1.45**
JC037/052	NW	78	61	16	61	**1.28**	**0.26**	**2.28**
JC048/008	NW	62	43	5	95	**1.44**	**0.12**	**1.11**
JC011/098	NE	15	14	3	171	**1.07**	**0.21**	**0.17**
JC037/083	NE	20	5	0	175	**4.00**	**0.00**	**0.14**
JC048/020	NE	84	44	14	74	**1.91**	**0.32**	**1.73**
JC048/032	SW	28	102	5	70	**0.27**	**0.05**	**1.86**
JC037/013	SE	120	55	14	25	**2.18**	**0.25**	**7.00**
JC048/046	SE	88	83	3	28	**1.06**	**0.04**	**6.11**

sampling area. There was no significant difference amongst stations based on year sampled (ANOSIM: $R=0.100$, $p=0.265$). Cluster analysis showed pre-2010 samples from the NE sampling area (JC011/098 and JC037/083) to be least similar to other samples (Fig. 7). Both of these samples contained large numbers of juvenile cohorts (J1 and J2). SIMPER analysis showed dissimilarity was greatest between NE and SE sampling areas with 24.88% of this dissimilarity attributed to differences in J1 counts. Analysis of grouped stations showed 20.52% of north/south and 18.24% of east/west dissimilarity was also due to J1 count variation.

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4. Discussion

4.1. Sexual dimorphism

Based on total body length estimates using the coxal plate 4 proxy, females, on average, grew larger than males. The largest female measured had a body length greater than 16.5 mm whereas the largest male was less than 13 mm in length. This size disparity is in agreement with the pattern found by Sainte-Marie (1991) of larger females and smaller males amongst lysianassoids, and reflects the non-mate-guarding pre-copulatory behaviour characteristic of the superfamily (Conlan, 1991).

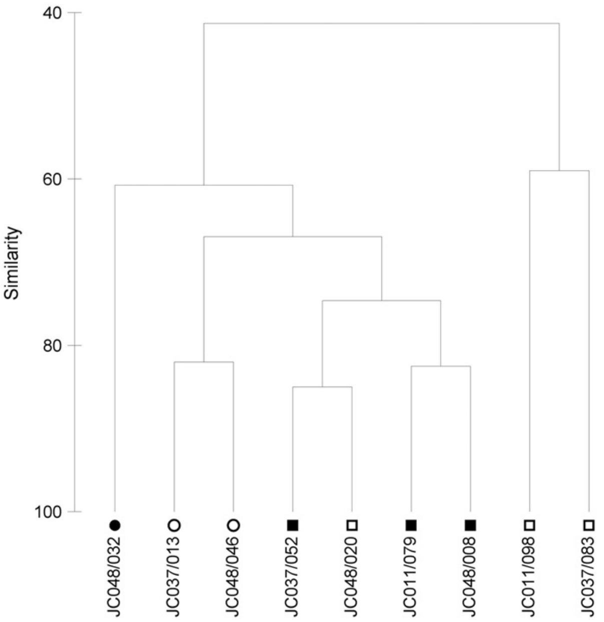

Fig. 7. Dendrogram demonstrating similarity in population composition amongst all stations. Stations south of the CGFZ indicated by circles and northern stations indicated by squares. Filled symbols represent stations west of the MAR and open symbols represent stations east of the MAR.

Relative to body size males had significantly longer antennae with significantly more articles per mm of antenna length. It is widely accepted that scavenging amphipods use chemoreception to detect food falls (Thurston, 1979; Busdosh et al., 1982, Bozzano and Sarda, 2002; Premke et al., 2003; Ide et al., 2006) and it is possible that these chemosensing abilities extend to detecting any chemical cues given off by conspecifics. The elongation of antennae, particularly antenna 2, is characteristic of amphipod species in which mating occurs freely in the water column without any form of amplexus or mate-guarding (Conlan, 1991). The effect of possessing longer antennae on chemosensory ability remains untested but it is hypothesised that longer, more articulate, antennae enhance chemosensing ability due to an increase in chemoreceptor sites (Kaufmann, 1994). Steele (1995) has advanced arguments that elongate antennae and associated organelles may enhance tactile detection of females by searching males prior to mating.

4.2. Sexual development

Each female had two ovaries of approximately equal size and number of oocytes. Based on this symmetry and the contents of complete ovaries recovered, the maximum possible brood size of an individual ranges from 36 to 78 offspring. There is no apparent relationship between oocyte number and body length in *A. abyssorum* (Fig. 4b), as has also been recorded for immature *Paralicella caperesca* Shulenberger and Barnard, 1976 (Thurston, 1979) and *E. gryllus* (Ingram and Hessler, 1987). A reduction in the number of oocytes with ovarian maturation has been recorded for other lysianassoid species including *Hirondellea gigas* Birstein and Vinogradov, 1955 (Hessler et al., 1978), *P. caperesca* (Thurston, 1979), *Pseudorchomene rossi* Walker, 1903 (Stockton, 1982, as *Orchomene*), and *E. gryllus* (Ingram and Hessler, 1987). As such, actual brood size of *A. abyssorum* is most probably toward the lower end of this estimate. Brood size in lysianassoid species correlates with female body length but varies widely (Sainte-Marie, 1991). The estimated brood size of *A. abyssorum* is comparable to that of other lysianassoids of similar size (Fig. 8).

In lysianassoid amphipods oostegites develop over a variable number of instars (Stockton, 1982; Ingram and Hessler, 1987), seven oostegite bearing cohorts have been identified in the case of *A. abyssorum*. Three oostegite size classes are apparent in *A. abyssorum* although the smallest oostegite stage (OS1) may be

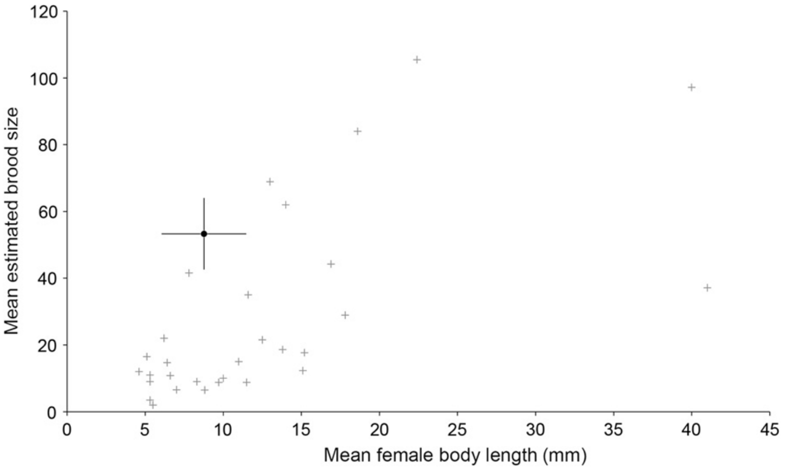

Fig. 8. Estimated brood size as a function of mean female body length from lysianassoid species population studies collected in Sainte-Marie (1991). Data from this study for *Abyssorchomene abyssorum* are shown in black with standard deviations indicated by black bars.

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composed of multiple cohorts as size increases during early oostegite development are often small and potentially confound analyses. The frequency of the most developed oostegite stage (OS3) increased with increasing cohort number. The majority (84%) of oostegites belonging to the most developed stage (OS3) were setose. Setose OS3 oostegites were found in females from F4 onwards. The presence of long apical setae on oostegites is an indicator of sexual maturity in female amphipods with setae found in lysianassoids, and some other groups, interlocking to form a brood pouch (Steele, 1991).

Although calculation of the HMFBL ratio (Sainte-Marie, 1991) for *A. abyssorum* proved inconclusive, the finding of mature F4 females suggests that *A. abyssorum* practices iteroparity and is capable of having multiple broods in a lifetime. The variability of oocyte size with body size also adds weight to this theory, with the largest oocytes found in a mid-size female. This hypothesis is further supported by the presence of mid-size, and on two occasions mature, females with empty ovaries, suggesting females return to food-falls following brood-release. An iteroparous lifestyle is advantageous in an unpredictable environment where conditions and food availability are variable. By dividing reproductive investment across multiple broods *A. abyssorum* increases its chances of reproductive success and reduces the risk of failing to reach sexual maturity, not successfully reproducing, or losing all offspring in a failed brood.

The absence of ovigerous females in any of the samples is expected. With few exceptions (Kaïm-Malka, 2003, 2005; Blankenship et al., 2006), brooding deep-sea scavenging amphipods have not been recorded at food falls (Ingram and Hessler, 1987; Sainte-Marie, 1991; Thurston and Bett, 1995). Aggregations of amphipods at food falls increase the risk of predation by fish (Lampitt et al., 1983; Jones et al., 1998; Janßen et al., 2000), decapods (Jamieson et al., 2009), and other amphipods (Jamieson et al., 2011). Brooding females will also be at greater risk of predation due to reduced mobility when carrying a brood, and more vulnerable as a result of a softened cuticle, as was recorded in an ovigerous individual of *Eurythenes gryllus* by Thurston and Bett (1995) and post-release individuals of the same species (Ingram and Hessler, 1987). Many scavenging amphipod species have modified digestive tracts enabling significant food storage (Dahl, 1979) and elastic ventral arthrodial membranes allowing distension and ventral expansion of the pereon to maximise food intake (Shulenberger and Barnard, 1976; Thurston, 1979). While *A. abyssorum* does not exhibit the same degree of pereon extension as highly specialised *Paralicella* spp., the degree of gut distension may be sufficient to impinge on the brood pouch, resulting in partial or total extrusion of the brood.

4.3. Population characterisation and comparison

Abyssorchomene abyssorum appears to pass through at least two juvenile cohorts (J1, J2), three male (M1–M3) and five to seven female cohorts (F1–F7; Table 2). Calculated linear growth factors are close to or above 1.26 implying at least a doubling of body volume following the moult process. These factors are comparable to those found for early instars of *E. gryllus* (Thurston, 1979; Ingram and Hessler, 1987), larger than those of *P. caperesca* and *Orchomenella gerulicorbis* Barnard and Shulenberger, 1976 (Thurston, 1979, as *Orchomene*) and much higher than the factors derived for *Scopelocheirus hopei* Costa, 1851 (Kaïm-Malka, 2003), and *Tmetonyx similis* Sars, 1891 (KaïmMalka, 2005). It is not clear whether these high growth factors are an adaptation to a necrophagous lifestyle or occur for another reason. Amongst females from both northern and southern stations there is a trend for decreasing growth factors with increasing body size, which is probably a reflection on the changing balance between somatic and gametic growth. The relatively low growth factor between stages F1 and F2 may be explained by the problems in resolving normal distributions of earlier cohorts. The group of juveniles that could not be resolved as a normally distributed population (J2) is likely to be composed in part of individuals, mainly from cohort F1 in which sexual characters could not be detected. The earliest stage of oostegite development can be very difficult to identify, particularly in small individuals.

The variability of juvenile abundances, in particular of J1, is responsible for a large amount of amongst sampling area variation. In most instances, juveniles formed a higher proportion of the total population at northern stations than at southern stations. This was particularly apparent at the northeast sampling area in 2007 and 2009. The increased proportions of juveniles remained for successive years and differed substantially from the other sampling areas and years. A high proportion of juveniles was not recorded in 2010, but the number of males and females was higher than in previous years. This could be indicative of a large cohort within the population. *Abyssorchomene abyssorum* may exhibit a seasonal breeding cycle tied to peaks in secondary production in the overlying waters. However, if breeding cycles were tied to peaks in production, numerous juveniles would be recorded at all 4 sampling areas across all years studied, which is not the case.

An alternate hypothesis is that favourable local conditions (e.g. influx of large or abundant food falls such as whale carcasses) at the NE sampling area result in increased breeding success. The skewing of the population composition toward the juvenile end of the size spectrum, as increased recruitments are not reflected in subsequent cohorts, suggests that either mortality is high at this sampling area or that favourable conditions are temporary and previous generations have not experienced similarly high levels of recruitment. The uncertainty regarding the cause of these juvenile-dominated populations at the NE sampling area in 2007 and 2009 warrant further investigation.

There is a chance that the method used may affect the population structure of the samples collected. While it is known that ovigerous females often avoid baited traps (Ingram and Hessler, 1987; Sainte-Marie, 1991; Thurston and Bett, 1995), it is unclear if any other components of the population (e.g. large males) also avoid baited traps for whatever reason. Although unlikely, it is not possible to know with absolute certainty based on current knowledge. The openings of all traps used were large enough so as not to occlude the entry of any size class of *A. abyssorum*. Local conditions may also have impacted the structure of samples collected (e.g. weak local currents may permit higher than expected numbers of small juveniles to reach the baited traps), however it is not possible to account or correct for this.

All male cohorts were present at all sampling areas and in all samples, with little variation in relative abundance and consistent cohorts either side of the CGFZ. On the other hand, differences in female cohorts north and south of the CGFZ are particularly interesting. It was not possible to identify separate cohorts through examination of the entire dataset but when samples were separated by position relative to the fracture zone (north, south), distinct normal distributions were apparent. Females north and south of the CGFZ fall into distinct cohorts with different distributional parameters. Female cohorts south of the CGFZ had consistently higher mean body lengths than their counterparts in the north. Differences in the composition of scavenging amphipod assemblages from the northern and southern sampling areas were also recorded at the community level (Horton et al., this issue).

The major environmental differences between sampling areas in the north and south are tied to productivity and correlated POC flux (Abell et al., this issue; Niedzielski et al., this issue). The northern boundary of the Sub-Polar Front runs along the CGFZ.

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Due to the position on this front, surface waters south of the CGFZ are warmer than those north of the fracture zone (Abell et al., this issue). Estimates of primary production from satellite measures of chlorophyll confirm that surface productivity also differs either side of the CGFZ (Abell et al., this issue), a trend that is mirrored in pelagic assemblages in the underlying waters (Brierley, 2012). The coupling between upper ocean processes and deep-sea benthic communities is a well-established relationship (Ruhl and Smith, 2004; Billett et al., 2010). The existence of this coupling is supported at the MAR by sediment trap data, which shows that the difference in surface productivity is reflected in deep-sea organic carbon input, with the highest levels recorded at southern stations.

Large pelagic megafauna, such as big-game fish and cetaceans, have been tracked following oceanic front systems (Waring et al., 2008; Doksæter et al., 2008, Skov et al., 2008). Therefore, owing to the location of the Sub-Polar Front and differences in surface productivity (Abel et al., this issue), sampling areas south of the CGFZ are more likely to experience a higher input of food falls. When food is not a limiting factor, energy reserves can be built-up more readily and invested into growth and subsequent reproduction. As female resource investment is an important factor in determining reproductive success and offspring survival it is possible that females at the higher-nutrient southern sampling areas are maximising growth during each successive cohort as a result of increased food-availability.

The differences between populations to the north and south of the CGFZ provide an interesting contrast. While increased surface productivity south of the fracture zone appears to be driving an increase in the size of each cohort, high numbers of juvenile cohorts at northern sampling areas suggest increased recruitment north of the fracture zone. Within the confines of this study, it is not possible to identify what is causing these very different population structures.

This study has provided an important contribution to our understanding of the population ecology of a common deep-sea lysianassoid amphipod. Unfortunately, complete life-history data on deep-sea lysianassoids are still lacking and further research is necessary in order to better understand the contribution of these ubiquitous animals to the deep-sea ecosystem. The lack of brooding females in baited traps is a clear shortcoming in population studies of this group, but is a problem that is difficult to resolve due to their altered foraging strategy, or lack thereof (Sainte-Marie, 1991). In order to better understand the ecology and importance of deep-sea necrophages more regular sampling of deep-sea populations is required, with a particular focus on common species such as *A. abyssorum*.

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Community composition of scavenging amphipods at bathyal depths on the Mid-Atlantic Ridge

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ABSTRACT

This study focussed on a section of the Mid-Atlantic Ridge with one pair of sampling areas at 49°N and the other at 54°N, north and south of the Charlie–Gibbs Fracture Zone and east and west of the ridge, at a water depth of 2500 m. Sixteen baited-trap samples of necrophagous amphipods were collected during three research cruises on the R.R.S. *James Cook* in 2007, 2009 and 2010. Amphipods of the superfamily Lysianassoidea are numerically dominant and taxonomically diverse and form the most important group of necrophages in most deep-sea environments. A total of 39 scavenging species from 253,306 specimens were identified at the four sampling areas over the 4-year study period. Less than half of the entities could be ascribed to known species. More than 25% of the species recorded were found at all of the sampling areas, supporting the view that necrophagous amphipods are widely distributed animals. The number of lysianassoid species (31) was higher than expected when compared with other studies of necrophagous amphipods, particularly as all sampling was done at one depth (2500 m). Deep-sea scavenging amphipods are generally thought to have low diversity and previous studies have supported this view. Sample sizes were large with some traps containing more than 40,000 specimens. The most abundant species, *Abyssorchomene abyssorum*, dominated all trap samples with percentage compositions over 90% at the NE sites in 2009–2010. Univariate and Multivariate analyses indicated a significant difference in community composition and species richness between the northern and southern stations. There are at least 15 new species to be described from these samples, and particular effort is required in the genus *Paracallisoma* and the genus *Tryphosella*.

1. Introduction

Non-vent mid-ocean ridge environments are some of the least studied of the world's ecosystems. Considering the size of these environments and their likely contribution to biodiversity and pelagic and benthic biomass, this lack of study results in a major gap in the understanding of biological ocean structure and processes. The complex topography of ridge environments poses significant problems of access and technological difficulties associated with sampling. The Census of Marine Life program (http://www.coml.org) has aimed to assess the diversity, distribution and abundance of life in all marine environments including those of mid-ocean ridges. Between 2002 and 2010 there have been 19 research expeditions to the Mid-Atlantic Ridge involving 17 countries within two major scientific programmes: MARECO (http://www.mar-eco.no/) and the ECOMAR project (Ecosystems of the Mid-Atlantic Ridge at the Sub-polar Front and Charlie–Gibbs Fracture Zone) (http://www.oceanlab.abdn.ac.uk/ecomar). The ECOMAR project was devised to investigate how physical and biogeochemical factors influence the structure, distribution and diversity of deep-sea communities, focussing on the Mid-Atlantic Ridge.

The Mid-Atlantic Ridge (MAR) extends from the Gakkel/MAR junction (83°N, 07°W) to the Bouvet Triple Junction (55°S, 01°W) and is the largest topographic feature in the Atlantic Ocean. The MAR is dissected by a number of fracture zones between Iceland and the Azores, the largest of which is the Charlie–Gibbs Fracture Zone (CGFZ), a double transform fault system at 52–53°N (Fleming et al., 1970). The North Atlantic Current (NAC) crosses the MAR between 45°N and 53°N (Krauss, 1986) with the northern branch largely constrained by the CGFZ and forming the Sub-Polar Front (Sy, 1988; Sy et al., 1992). Read et al. (2010) have shown that the circulation of the NAC is dominated by long lasting, slow moving mesoscale eddies. Despite high variability, the long-term mean surface current flow is easterly and the velocity is low. North of the CGFZ in the Sub-Polar Gyre the residual current flow is weaker and westerly. The water masses north and south of the Sub-Polar Front lie under contrasting areas of surface primary productivity, with intense, seasonal production to the north, and less intense, more prolonged periods of production, to the south.

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The MAR environment is distinct from continental margin environments at similar depths owing to an absence of terrigenous input of sediments and organic matter. Therefore, while it is likely that the MAR harbours species known from elsewhere, the fauna is expected to have unique characteristics as a result of differences in primary productivity and organic matter flux. Working on the hypothesis that differing regimes of surface productivity would result in differences in benthic species populations and biodiversity, the ECOMAR project focussed on a section of the MAR with sampling sites north and south of the CGFZ, at a water depth of 2500 m. Two pairs of study sites were selected, one pair at 49°N and the other at 54°N. One site in each pair was located to the west of the ridge axis and the other to the east.

The zonation of bottom-living species with depth is a well-known phenomenon (Carney, 2005; Howell et al., 2002; Rex et al., 1999) and is generally thought to be characterized by gradients of adaptation to high hydrostatic pressure, low food supply, low temperature, current regime and substrate characteristics. At the four ECOMAR sites, pressure and substrate type were relatively consistent (all at 2500 m), therefore it was hypothesized that the influence of the MAR and the Sub-Polar Front would affect the food supply, current regime, and possibly bottom temperature of the four stations.

Amphipods of the superfamily Lysianassoidea are numerically dominant and taxonomically diverse, and form one of the most important groups of necrophages in most deep-sea environments (Christiansen, 1996; Hessler et al., 1978; Smith, 1985; Thurston, 1990; Wolff, 1971). Necrophagous amphipods are ubiquitous in the deep-sea and play a key role in the recycling and dispersal of nutrient input in the form of larger packets of carrion (Britton and Morton, 1994; Smith, 1985).

Systematic studies of the deep-sea scavenging fauna of the North Atlantic Ocean by means of baited traps began in 1888 during an expedition of the Prince of Monaco, and between 1892 and 1912, 21 deployments of baited traps deeper than 3000 m were undertaken (Richard, 1934). After these early studies it was not until the advent of more advanced technology that the use of baited cameras (see Bailey et al., 2007, for a review) revealed the existence of an active guild of mobile scavengers comprised largely of crustaceans and fish. A majority of studies of these fauna have focussed on the larger, more readily identified components, namely the larger decapods crustaceans and fish (Jones et al., 1998; Kemp et al., 2006; Thurston et al., 1995). Comprehensive studies of scavenging amphipods other than the conspicuous and well-studied giant amphipod *Eurythenes gryllus* are rare, yet numerically it is the smaller species that make up the vast majority of any such collection (Christiansen, 1996). It is probable that these smaller amphipods have a higher capacity for food conversion and a more important role in dispersal of nutrients, at least in the near field, than the larger *E. gryllus*.

Few studies have fully analysed replicate baited traps for species composition. In the North Atlantic Ocean Thurston (1979) studied material from a single trap-set at 3852 m and Thurston (1990) analysed 44 trap-sets taken on three different abyssal plains and over a wide bathymetric range (3144–5940 m). De Broyer et al. (2004) analysed 31 trap-sets taken over a wide bathymetric range (171–3739 m) in the Southern Ocean. The ECOMAR study is unique in studying the scavenging amphipod faunal composition at a single depth (2500 m) in detail by fully analysing replicate samples taken over a 4-year time period.

2. Materials & methods

2.1. Study region and baited trap operations

Samples were collected during three research cruises on the R.R.S. *James Cook* in 2007, 2009 and 2010. All sampling took place between June and September. Samples were collected at each of the four ECOMAR sampling areas, two to the south of the CGFZ under the influence of the North Atlantic Current (Read et al., 2010) and two to the north in the Sub-Polar Gyre (Fig. 1). One of each pair of sampling areas was located west of the Mid-Atlantic Ridge and one to the east. The sampling areas were chosen to be of comparable depth and seabed topography to allow for deep-ocean moorings, bottom trawling and benthic ROV survey work.

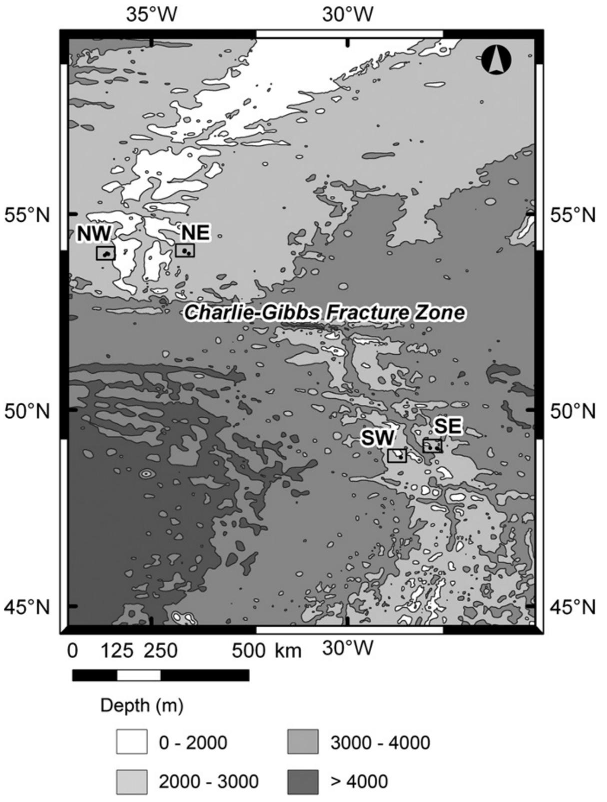

Fig. 1. Mid-Atlantic Ridge bathymetry and location of ECOMAR sampling areas.

Scavenging amphipods were collected by means of baited traps. In total, 15 trap deployments took place over the three cruises, 12 of which were successful and have been used in this study (Table 1). Trap designs changed and soak times were very variable as a result of gear losses, weather conditions and other technical problems at sea (Priede, 2007, 2009; Priede and Bagley, 2010). As a consequence southern sites are represented by only three samples—one from the south-west site (2010), and two from the south-east site.

The trap-rig consisted of a frame, traps, buoyancy, an acoustic release (OCEANO 2500 Universal, IXSEA, France) and a ballast weight located in a recess on the underside of the frame.

For samples collected in 2007, the rig included a benthic and an epibenthic trap. The benthic trap measured 500 mm × 500 mm × 200 mm, had a solid top and bottom, and four walls each with a large rectangular window into which was fitted a 500 μm mesh funnel with a 40 mm square aperture. A cylindrical bait container of 10 mm mesh was located centrally in the trap. Bait consisted of two whole mackerel (*Scomber scombrus*) wrapped in muslin. The epibenthic trap, suspended 1 m above the bottom, consisted of a 725 mm × 300 mm internal diameter tube with a mesh funnel entrance (45 mm aperture) at each end, and was baited with a single muslin wrapped mackerel.

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Table 1
Station data for baited lander deployments.

Site	Station #	Latitude	Longitude	Depth (m)	Deployed	Soak (hh:mm)
NE	JC011/098	54°04.08′N	34°09.43′W	2500	09/VIII/2007	22:58
NE	JC011/114	54°02.31′N	34°09.60′W	2453	12/VIII/2007	22:15
NE	JC037/076	53°58.94′N	34°02.94′W	2552	31/VIII/2009	22:08
NE	JC037/083	54°02.31′N	34°09.54′W	2452	02/IX/2009	32:21
NE	JC048/020	54°03.95′N	34°09.12′W	2505	08/VI/2010	24:09
NW	JC011/079	53°56.44′N	36°11.56′W	2564	05/VIII/2007	42:09
NW	JC037/052	53°59.32′N	36°08.12′W	2570	25/VIII/2009	35:13
NW	JC037/060	53°58.46′N	36°06.12′W	2340	27/VIII/2009	61:32
NW	JC048/008	53°59.32N	36°08.07′W	2628	02/VI/2010	101:20
SE	JC037/013	49°02.00′N	27°43.44′W	2501	08/VIII/2009	41:45
SE	JC048/046	49°02.01′N	27°43.44′W	2507	23/VI/2010	70:45
SW	JC048/032	48°47.34′N	28°38.45′W	2448	16/VI/2010	75:28

In 2009 on deployments JC037/052, JC037/060, JC037/076 and JC037/083, the benthic trap was replaced by two core tubes 400 mm long × 100 mm internal diameter with a (mesh) funnel (aperture 25 mm) at one end, after the original benthic trap was lost. In 2010, a new trap rig was used comprising four traps on one rig; two benthic and two epibenthic traps set at 90° to each other. Each trap was 500 mm long × 290 mm internal diameter with a double funnel entrance (42 mm then 25.8 mm apertures) at one end, baited with a single muslin-wrapped mackerel.

The rig was launched by hand, buoyancy first, with the frame hung over the stern on a crane and released with a slip hook. Ideally the rig was left in situ for 24 h, but soak times varied widely (13–101 h) owing to ship schedule constraints and weather conditions. On retrieval of the trap, contents were fixed in either 100% ethanol or 4% buffered formaldehyde. Formaldehyde-fixed material was transferred to 80% industrial methylated spirit solution on return to the laboratory.

Authorities for scientific names are quoted in Table 2, with links to the World Register of Marine Species for up-to-date taxonomic validity of each species (Appeltans et al., 2012).

2.2. Analyses

Amphipod samples were sorted, identified to species level and counted in the laboratory. Large samples (> 10,000 specimens) were split using a Folsom Plankton Splitter (Dahiya, 1980; Griffiths et al., 1984) and two 1/16 sub-samples were used to calculate the total sample size according to the equation

$$N = 2^T \sum_{i=1}^{n} X_i/n = 2^T \overline{X}$$

where N *is* the estimated total catch, T is the number of splits, and X_i is the number of organisms in the ith sub-sample. Diversity indices were calculated on untransformed data. Species abundance data were converted to percentage composition and $\sqrt{}\sqrt{}$-transformed prior to analyses using PRIMER 6 software (Clarke and Gorley, 2006; Clarke and Warwick, 1994), to allow for low abundances and rare species occurrences and to account for the very high abundances of *Abyssorchomene abyssorum*. Group average cluster analysis was conducted on Bray and Curtis (1957) similarities. Non-metric, multi-dimensional scaling (nMDS) ordination was then applied to visualize clusters in two and three dimensions, followed by SIMPER analysis to identify characteristic species and ANOSIM to assess the significance of the cluster separation.

The BIOENV procedure (Biota and environment matching) was used to match the community patterns with environmental variables (depth, bottom temperature, salinity, oxygen saturation (from CTD data), latitude, POC flux, and primary productivity; (Abell et al., this issue). Group cluster analyses were conducted on normalized Euclidean distances, with no transformation or standardization.

3. Results

A total of 39 species from 253,306 specimens were identified at the four sampling areas over the 4-year study period: 20 entities from the north-east site, 20 from the north-west site, 26 from the south-east site and 23 from the south-west site (Table 2). Less than half (14) of the entities could be ascribed to known species, two of which were described by the authors (TH and MT; Horton and Thurston, 2011, in press) during the project. Twelve species were common to all four sampling areas, three of which were recorded in every sample and are known to be widely recorded scavenging species (*Eurythenes gryllus*, *Abyssorchomene abyssorum*, and *Abyssorchomene chevreuxi*). The most abundant species, *Abyssorchomene. abyssorum* was present at all four sampling areas and dominated all samples while its congener *A. chevreuxi* was abundant at all sites in all years but in far lower numbers. The common eurybathic scavenger species *E. gryllus* was also found at all four sampling areas and while it contributed substantially to the biomass of each catch, the numbers in each sample were relatively low (maximum of 334 specimens from the SW site). Another species, *Centromedon zoe*, was abundant in the northern sites in 2007 and 2009 but was found in much lower numbers in 2010. It was present at all but one (JC037/076) of the samples and has been found at similar depths in the Porcupine Seabight (Horton and Thurston, 2011). The ostracod *Azygocypridina imperialis*, although found at all four sampling areas, particularly characterized the NW site, occurring in very high numbers in 2009. This species was also common in epibenthic sledge hauls throughout this depth range in the NE Atlantic (Athersuch, 1980), although the present records are the first of such high numbers from baited traps.

Only two species were unique to the NE site: *Centromedon* sp. 3 and *Paracallisoma* sp. 4. Three species were unique to the NW site: *Paracallisoma* sp. 5; Eusiroid gen. and sp. nov. and *Cleonardo* sp. 1. Five species were unique to the SE site: *Tmetonyx* sp. 2; Tryphosinae indet.; *Valettiopsis longidactyla*; *Tryphosella* sp. 4 and *Tryphosella* sp. 5. Four species were unique to the SW site: *Cyphocaris bouvieri*; *Valettiopsis macrodactyla*; *Abyssorchomene distincta* and the ostracod *Metavargula* sp. All of these 14 species were rare, some being represented by single specimens, and the most abundant, *Tryphosella* sp. 5, accounted for only 0.03% of the specimens studied. In addition, three of the species were found at northern sites only (*Centromedon* sp. 2; *Paracallisoma abyssi*; *Nebalia* sp.) and three at southern stations only (*Hirondellea namarensis*; *Hirondellea* sp. 2; *Paracallisoma* sp. 2).

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Table 2
Species composition of catches from trap deployments.

Species	**JC011/98 NE**	**JC011/114 NE**	**JC037/076 NE**	**JC037/083 NE**	**JC048/020 NE**	**JC011/79 NW**	**JC037/052 NW**	**JC037/060 NW**	**JC048/008 NW**	**JC037/013 SE**	**JC048/046 SE**	**JC048/032 SW**
Lysianassoidea & related families												
Abyssorchomene abyssorum (Stebbing, 1888)	4972	3107	42,479	40,376	37,602	1965	5995	9297	46,096	3250	11,987	10,174
Abyssorchomene chevreuxi (Stebbing, 1906)	291	192	74	240	787	84	476	847	1392	26	105	422
Abyssorchomene distinctus (Birstein and Vinogradov, 1960)	0	0	0	0	0	0	0	0	0	0	0	1
Centromedon zoe Horton and Thurston, 2011	5382	1861	0	1813	111	678	28	1546	1	58	16	64
Centromedon sp. 2	42	0	0	0	2	0	0	24	0	0	0	0
Centromedon sp. 3	8	0	0	0	0	0	0	0	0	0	0	0
Cyphocaris bouvieri Chevreux, 1916	0	0	0	0	0	0	0	0	0	0	0	1
Eurythenes gryllus (Lichtenstein, 1822)	99	129	194	68	220	16	41	335	250	188	127	334
Hirondellea namarensis Horton and Thurston, in press	0	0	0	0	0	0	0	0	0	697	1289	396
Hirondellea sp. 2	0	0	0	0	0	0	0	0	0	0	5	15
Orchomene aff. *oxystoma*	298	127	0	362	72	3	0	0	0	2	0	4
Orchomene aff. *pectinata*	19	31	0	48	140	3	0	42	8	8	200	2187
Tryphosinae indet.	0	0	0	0	0	0	0	0	0	2	0	0
Scopelocheirus abyssi Oldevig, 1959	0	2	0	0	0	1	0	0	8	0	0	0
Paracallisoma alberti Chevreux, 1903	23	5	8	0	8	4	14	6	8	59	784	1886
Paracallisoma sp. 2	0	0	0	0	0	0	0	0	0	0	4	9
Paracallisoma sp. 3	0	0	0	0	0	0	3	0	0	0	16	19
Paracallisoma sp. 4	4	0	0	0	0	0	0	0	0	0	0	0
Paracallisoma sp. 5	0	0	0	0	0	1	0	0	0	0	0	0
Paracallisoma sp. 1	36	4	0	8	24	9	50	113	194	1	26	44
Paralicella caperesca Schulenberger and Barnard, 1976	2	1	0	1	0	3	2	0	8	3	0	11
Stephonyx biscayensis Chevreux, 1908	26	150	0	566	113	1	0	71	0	5	0	0
Tmetonyx sp. 1	364	837	186	305	1993	12	0	40	0	14	52	4
Tmetonyx sp. 2	0	0	0	0	0	0	0	0	0	6	0	0
Tryphosella sp. 1	11	13	0	0	0	0	0	0	0	269	241	0
Tryphosella sp. 2	0	0	2	0	0	0	0	0	0	2	119	2
Tryphosella sp. 3	0	0	8	0	0	0	0	0	0	0	4	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0	0	5	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0	0	20	60	0
Valettiopsis longidactyla Horton, 2004	0	0	0	0	0	0	0	0	0	3	0	0
Valettiopsis macrodactyla Chevreux, 1909	0	0	0	0	0	0	0	0	0	0	0	1
Non-lysianassoid families												
Cleonardo sp. 1	0	0	0	0	0	1	0	0	0	0	0	0
Euandania sp.	0	0	0	0	0	0	7	11	24	0	12	2
Eusiroid unknown gen. and sp. nov.	0	0	0	0	0	1	0	0	0	0	0	0
Hyperiopsis voringii Sars, 1885	2	0	0	0	0	0	3	24	0	0	0	2
Ostracoda												
Azygocypridina imperialis (Stebbing, 1901)	2	1	0	49	0	35	728	1214	124	0	20	2
Metavargula sp.	0	0	0	0	0	0	0	0	0	0	0	28
Vargula sp.	2	4	0	0	0	6	3	12	0	0	1	27
Leptostraca												
Nebalia sp.	7	0	0	1	0	2	1	0	0	0	0	0
Number of specimens	**11583**	**6464**	**42,951**	**43,836**	**41,072**	**2823**	**7350**	**13,582**	**48,113**	**4618**	**15,068**	**15,635**
Number of species	**18**	**15**	**7**	**11**	**11**	**17**	**12**	**15**	**11**	**19**	**19**	**23**

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Table 3
Median and inter-quartile range of diversity indices calculated for each sampling area. NE, n=5: NW, n=4; SE, n=2; SW, n=1.

Diversity index	NE			NW			SE			SW		
	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3
Species richness (S)	9.00	12.00	17.00	11.25	13.50	17.00	19.00	19.50	20.00	–	23	–
Shannon diversity (*H*′)	0.23	0.40	1.27	0.34	0.79	1.07	0.89	0.98	1.07	–	1.18	–
Pielous's Evenness (*J*′)	0.10	0.17	0.45	0.14	0.29	0.40	0.30	0.33	0.36	–	0.38	–

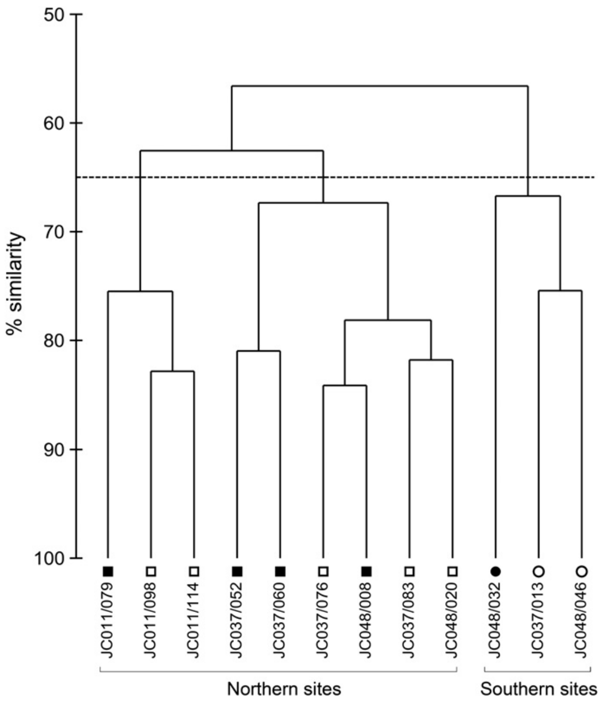

Fig. 2. Dendrogram of trap deployments, using group-average clustering from Bray–Curtis similarities. NW and NE sites indicated by closed and open squares respectively, SW and SE sites indicated by closed and open circles, respectively. Dashed line represents 65% similarity in community composition.

The north-east site although similar in composition to the north-west site, had higher abundances of species that were found at both sites (e.g. *Orchomene* aff. *oxystoma*; *Stephonyx biscayensis*; *Tmetonyx* sp. 1). The north-west site had higher abundances of only two species: *Paracallisoma* sp. 1 and the ostracod *Azygocypridina imperialis.*

3.1. *Diversity analyses*

There were no significant differences between the northern and southern stations for Pielou's Evenness Index (*J*′) and Shannon Diversity Index (H). There was a significant difference in Species Richness (S) between northern and southern stations (Fig. 3a; Table 3; Mann–Whitney *U*: $n=12$, $U=26.5$, $p=0.009$).

Multivariate analyses allowed further examination of these differences. Cluster analyses revealed three distinct groupings at the 65% similarity level (Fig. 2). Two of these groups correspond to northern and southern sites while the third group represents a cluster of three samples from 2007. ANOSIM revealed that the spatial separation was significant ($R=0.551$, $p=0.002$) when considering site as a comparative factor. A second analysis was conducted using only the data from 2009 and 2010. ANOSIM revealed that the spatial separation between northern and southern stations in 2009/10 was strongly significant ($R=0.852$, $p=0.002$).

SIMPER analysis indicated that over half of the community dissimilarity between the northern and southern sites was due to the cumulative effect of variance in abundances of five species (*Hirondellea namarensis*, 16.83%; *Paracallisoma alberti*, 12.70%, *Orchomene* aff. *pectinata*, 9.21%, *Tryphosella* sp. 1, 7.39%; *A. imperialis*, 6.18%). The first four of these species were found frequently at southern sites but were rare at northern sites while the ostracod *Azygocypridina imperialis* was far more abundant north of the CGFZ.

The BIOENV indicated that the cluster characteristics were explained equally well by the single variable latitude (°) (64.9%), and the combination of primary productivity ($\text{g C m}^{-2}\ \text{year}^{-1}$) and latitude (°).

4. Discussion

The ECOMAR sites have yielded typical bathyal deep-sea scavenging amphipod assemblages. Samples were large, with some traps containing more than 40,000 specimens. The most abundant species, *Abyssorchomene abyssorum*, dominated all trap samples with percentage compositions over 90% at the NE stations in 2009–2010. More than 25% of the species recorded were found at all of the sampling areas, supporting the view that necrophagous amphipods are widely distributed animals. The high number of lysianassoid species recorded from this study (31) was not expected, particularly as all sampling was carried out at one depth (2500 m). Deep-sea scavenging amphipods are generally thought to have low diversity and previous studies have supported this view. Thurston (1990) recorded only 15 species from a study of 44 baited traps, set over a far wider geographic and bathymetric range (3144–5940 m and from three different North Atlantic abyssal plains). De Broyer et al. (2004) recorded 26 lysianassoid species from Antarctic deep-water traps (1000–3739 m) with the majority of species being collected in shallower waters.

A significant difference in community composition is apparent between the northern and southern stations. The three groups identified at the 65% similarity levels by cluster analysis correspond to two groups of northern samples and a single group of southern stations. The northern groupings are divided by year with 2007 samples clustered separately from those species taken in 2009 and 2010. It is not clear what environmental variables may be driving differences between the years 2007 and 2009–2010, as only environmental data from 2007 are available. It is also unknown whether similar temporal variation occurred at southern sites since deployments were unsuccessful at southern sites in 2007.

Results of BIOENV suggest that latitude is the primary environmental factor responsible for the variability seen between communities north and south of the CGFZ. Other environmental factors included in the analyses (e.g. primary productivity) are coupled with latitudinal variation, and did not increase the correlation we observed. As some species are found only in the south and others only at the northern sites it is not surprising that latitudinal differences account for much of the changes in species composition. The southern group is characterized by the species

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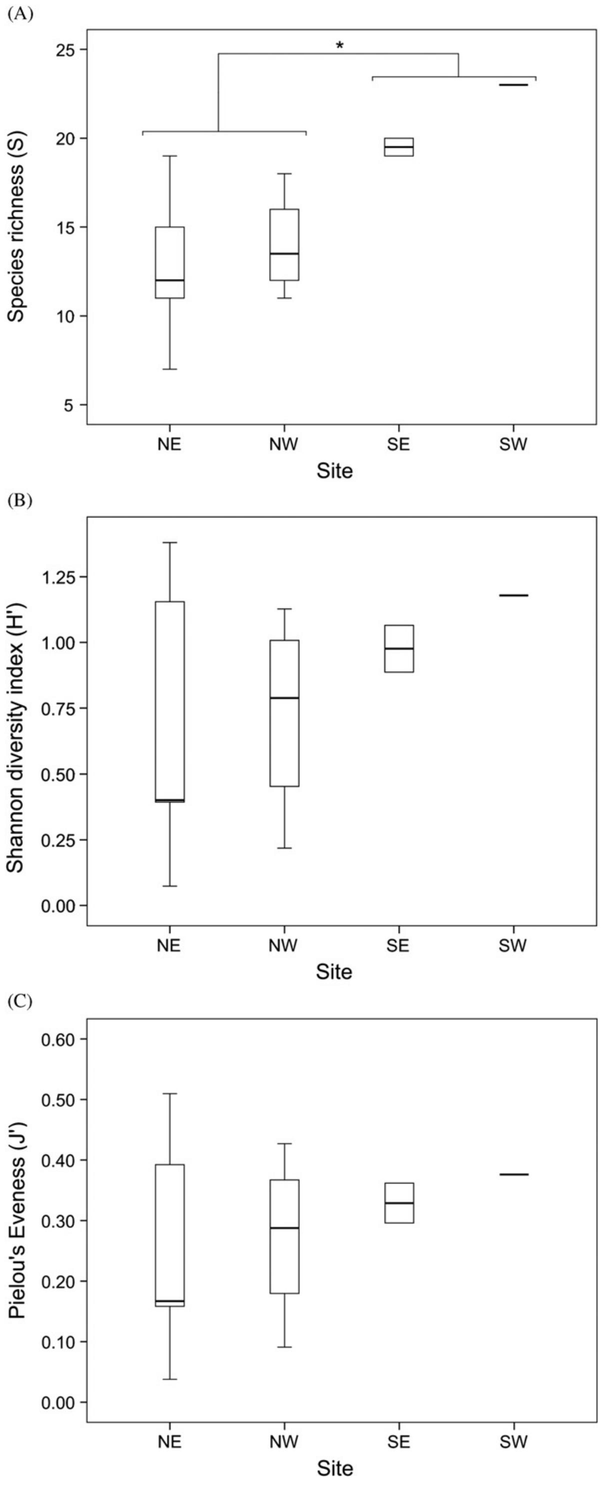

Fig. 3. Distributions of diversity indices calculated for each site (Table 3) (a) Species richness (S). *A significant difference was seen between northern and southern sampling areas (Mann–Whitney *U*: $n=12$, $U=26.5$, $p=0.009$); (b) Shannon diversity index (H'). No significant difference in distribution among sampling areas; and (c) Pielou's Evenness (J'). No significant difference in distribution among sampling areas.

Hirondellea namarensis, *Paracallisoma alberti*, *Orchomene* aff. *pectinata*, and *Tryphosella* sp. 1; which are found frequently at southern sites but rarely at northern sites while the ostracod *Azygocypridina imperialis* was far more abundant north of the CGFZ.

Apart from the presence or absence of rare species, there seem to be no substantial differences between the two northern sites. Of the 25 species found at the two northern sampling areas, 13 occurred on both sides of the MAR. The remaining species were all rare, each with less than 12 specimens collected (mostly singletons). Low representation in trap samples may result from the adventitious capture of non- or weakly necrophagous species or be indicative of under-sampling of rare species. In either case, it cannot be assumed that they are not also found at other sites. Twelve of the 39 species found in this study were recorded at all four sampling areas. Of these species, three are common and very abundant scavenger species also found elsewhere in the North Atlantic Ocean, although depth ranges appear to vary, with the most abundant species (*A. abyssorum*) and a congener (*A. chevreuxi*) found shallower and in greater abundances on the MAR than they are on the abyssal plains and continental margins (Thurston, 1990).

A. abyssorum is widely recorded in the deep-sea and commonly found at bathyal, abyssal and hadal depths (Thurston, 2000). In the North Atlantic Ocean it has been recorded from the MAR south of the Azores (Chevreux, 1903). It has been found in lower numbers on the Porcupine Abyssal Plain but is not found at depths comparable to those of the present collections on the adjacent continental margin (Desbruyeres et al., unpublished results; Thurston, 1990). *Abyssorchomene chevreuxi* has been captured at bathyal and abyssal depths but appears to have a disjunct geographical distribution, having been recorded reliably from the North Atlantic and south-west Pacific Oceans (Thurston, 1990). *Eurythenes gryllus* is the most widely distributed of all amphipods, occurring throughout the world's oceans (Stoddart and Lowry, 2004) from the surface to hadal depths (Thurston, 1990; Thurston et al., 2002) where water temperatures are below 6–7 °C. It has been postulated for many years, however, that the entity is likely to be composed of a number of cryptic species (Thurston and Bett, 1995; Thurston et al., 2002).

Differences in abundances among sites might be attributable to a number of factors, including current speeds at the trap sites, rather than actual abundances of scavengers. However, soak time and trap type were included in the BIOENV analyses and did not contribute significantly to differences in species composition at the four sampling areas. Data on swim speeds and times of first arrival at bait can be used to assess populations of scavenging fish (Priede and Merrett, 1996). Estimation of population abundances of scavenging amphipods is almost impossible since species cannot be distinguished in camera images with any certainty, with the possible exception of the large scavenging species, *E. gryllus*. Premke (2006) have attempted to use similar calculations for scavenging amphipods to estimate background populations but with little success, probably because the methodology is highly sensitive to variation in the parameters used. The inverse square law of the model can be subject to large errors when arrival times are short (King et al., 2006). Swim speeds are difficult to obtain for deep-sea species and appear to vary widely, depending on species, size and degree of excitation of individual organisms (Ide et al., 2007; Jamieson et al., 2012).

The dependence of deep benthic biomass and community structure on upper ocean processes is well established (Billett et al., 2010; Ruhl and Smith, 2004). Our data support a difference in benthic community structure in the North Atlantic, north and south of the Charlie–Gibbs Fracture Zone and the position of the

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Sub-Polar Front. Similar faunal changes at bathyal and abyssal depths have been reported for fish (Merrett, 1987), megafaunal necrophages (King et al., 2006; Thurston et al., 1995), invertebrate megabenthos (Thurston et al., 1998) and necrophagous amphipods (Christiansen, 1996). Other studies have confirmed that larger fish and cetaceans may associate with the Mid-Atlantic Ridge and frontal systems—providing elevated food supplies in these areas for scavenging organisms (Doksæter et al., 2008; Skov et al., 2008; Waring, et al., 2008). These aggregations may explain the elevated populations of *A. abyssorum*, which are not found at similar depths on the continental slopes of the eastern Atlantic (Desbruyeres et al., unpublished results). The shallower occurrence and greater abundance on the Mid-Atlantic Ridge might also reflect a lack of competition from shallower-dwelling species that occur on the continental margins. The shallowest *A. chevreuxi* is encountered in the Porcupine Seabight is 3922 m, but a single specimen of the species has been recorded at 2080 m in the Bay of Biscay (Thurston, 1990).

Most of the *Abyssorchomene* specimens captured at the north east site in 2009 and 2010 were juvenile. Very little is known of the reproductive habits of deep-sea necrophagous amphipods as brooding females do not enter traps (Ingram and Hessler, 1987; Sainte-Marie, 1991; Thurston and Bett, 1995) with the notable exception of an undescribed hadal species attributed to *Uristes* (Blankenship et al., 2006). Necrophagy by deep-sea amphipods is not a risk-free strategy (see Thurston and Bett, 1995) as individuals may be subject to predation by fish (Jamieson et al., 2011; Janßen et al., 2000; Jones et al., 1998), decapods (Jamieson et al., 2009) and other amphipods (Jamieson et al., 2012). Brood-carrying females would be particularly vulnerable to predation or cannibalism by other amphipods. Vulnerability would be increased if, as in *E. gryllus*, brooding females appear to undergo changes that result in a softened cuticle (Ingram and Hessler, 1987; Thurston and Bett, 1995). Fasting while brooding will reduce the risk of predation but the two activities may be mutually exclusive. Females of obligate necrophages such as *Paralicella* spp., in which food capacity is increased enormously by a huge ventral expansion of the peraeon, would suffer a total dislocation of the brood pouch and would be unable to retain a brood (Shulenberger and Barnard, 1976; Thurston, 1979). Although the ventral surface in *E. gryllus* and *Abyssorchomene* spp. is less extendible than in *Paralicella*, the capacity and length of the stomadaeum, which extends throughout the peraeon (Dahl, 1979; De Broyer et al., 2004), would preclude retention of eggs or hatchlings. However, very large numbers of juveniles implies that females are releasing broods in the vicinity of the trap sites as it is unlikely that such small specimens (~3.8 mm) could swim very long distances to attend baits. High proportions of juvenile *A. abyssorum* were found only at the NE site, therefore it can be speculated that either this location is a nursery ground or that there is an abundant episodic or regular food source available at this location, probably in the form of cetacean or fish carcasses. Detailed analysis of the population structure of *A. abyssorum* at the four sampling areas will be published in a separate paper (Duffy et al., this issue).

More than half of the species collected were new to science. Two described during the lifetime of the project, *Centromedon zoe* (Horton and Thurston, 2011) and *Hirondellea namarensis* (Horton and Thurston, in press), were present in high numbers and ranked among the most abundant species. There are at least 15 new species to be described from the ECOMAR samples, and particular effort is required in the genus *Paracallisoma* in which five of the seven entities collected are new species, and the genus *Tryphosella* in which all five entities collected are likely to be new species. The identification of a possible nursery ground for the species *A. abyssorum* is of critical importance at a time when exploitation of deep-sea resources such as rare-earth metal mining is just beginning on mid-ocean ridges. While little information is available to quantify the importance of scavenging amphipods in the deep-sea ecosystem, it is very probable that necrophages play a crucial role in the recycling and transport of energy. Deep-sea mining operations have the potential to bring about a detrimental effect on the North Atlantic populations of these scavengers, and the consequences of such a loss on the wider deep-sea ecosystem are at this stage unknown. Clearly, further work is needed to better understand the diversity and ecology of our mid-ocean ridges before their resources are exploited.

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Deep-sea scavenging amphipod assemblages from the submarine canyons of the Western Iberian Peninsula

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Abstract. Submarine canyons have often been identified as hotspots of secondary production with the potential to house distinct faunal assemblages and idiosyncratic ecosystems. Within these deep-sea habitats, assemblages of scavenging fauna play a vital role in reintroducing organic matter from large food falls into the wider deep-sea food chain.

Free-fall baited traps were set at different depths within three submarine canyons on the Iberian Margin. Amphipods from the traps were identified to species level and counted. Scavenging amphipod assemblages were compared at different depths within each canyon and between individual canyon systems. Using data from literature, abyssal plain assemblages were compared to submarine canyon assemblages. Samples from canyons were found to contain common abyssal plain species but in greater than expected abundances. It is proposed that this is a result of the high organic carbon input into canyon systems owing to their interception of sediment from the continental shelf and input from associated estuarine systems. Community composition differed significantly between the submarine canyons and abyssal plains. The cause of this difference cannot be attributed to one environmental variable due to the numerous inherent differences between canyons and abyssal plains.

1 Introduction

Large submarine canyons are complex, poorly understood, topographical features (Shepard and Dill, 1966). They experience heightened levels of sediment input, with active submarine canyons acting as downward conduits for matter that has been transported along the continental shelf (Vetter and Dayton, 1998). This effect is often amplified in the presence of contributory river systems (van Weering et al., 2002; Cúrdia et al., 2004). Elevated sediment input carries with it substantial quantities of organic matter (Kiriakoulakis et al., 2011), providing food for deep-sea scavengers (Sorbe, 1999). Many submarine canyons have been identified as hotspots of secondary production (Jannasch and Taylor, 1984; Gage and Tyler, 1992; Vetter, 1995; Soliman and Rowe, 2008; De Leo et al., 2010; Van Oevelen et al., 2011). One section of the Nazaré Canyon, on the Iberian Peninsula, contains an estimated biomass of megabenthic invertebrates that is 2–3 orders of magnitude greater than that found on open slopes at similar depths (Van Oevelen et al., 2011). Biomass in the Kaikoura Canyon, off the coast of New Zealand is estimated to be yet another order of magnitude greater again (De Leo et al., 2010).

Scavenging organisms are particularly important in the deep sea (Britton and Morton, 1994). In an environment where food-supply is often a limiting factor, they play a pivotal role in the degradation and redistribution of organic matter (Christiansen and Diel-Christiansen, 1993). Scavengers breakdown, disperse, and reintegrate organic carbon from food falls into the deep-sea food web via predator-prey interactions (Payne and Moore, 2006) and by faecal enrichment of sediments (Stockton and DeLaca, 1982; Jones et al., 1998).

Of all of the scavenging organisms, members of the order Amphipoda (Crustacea, Malacostraca) have been found to be some of the most abundant and successful in the deep sea (Hessler et al., 1978; De Broyer et al., 2004). Morphological evidence suggests that scavenging has evolved independently on numerous occasions within this order, with the majority of scavenging amphipods being members of the

Table 1. Trap deployments made within the Iberian Margin submarine canyons during research expeditions RRS *Discovery* 297, RRS *Charles Darwin* 179, and RRS *James Cook* 010. [1] Data from CTD casts deployed in the vicinity (<2.5 km radius) of each baited trap; [2] averaged data from Cunha et al. (2011).

Canyon	Deployment	Duration (hh : mm)	Depth (m)	Latitude	Longitude	Temp.[1] (°C)	[O$_2$][1] (μmol l^{-1})	Sal.[1]	TOC[2] (mg g^{-}1)
Nazaré	JC010/094	43 : 16	3400	39.4983	−09.9367	2.63	252.20	34.93	18.3
	CD179/56855	23 : 02	3499	39.5027	−09.9050	2.63	252.20	34.93	18.3
	D297/15734	21 : 28	3600	39.4963	−09.9648	2.63	252.20	34.93	18.3
	D297/15741	24 : 22	4286	39.5825	−10.2750	2.49	258.20	34.90	18.2
	CD179/56847	24 : 34	4403	39.5917	−10.3167	2.49	258.20	34.90	18.2
Setúbal	CD179/56817	31 : 14	3194	38.1528	−09.6000	2.79	–	34.95	13.0
	CD179/56839	24 : 12	4445	38.1095	−09.9697	2.50	–	34.90	10.6
Cascais	CD179/56837	30 : 17	4230	38.3662	−09.8834	2.46	–	34.90	11.2

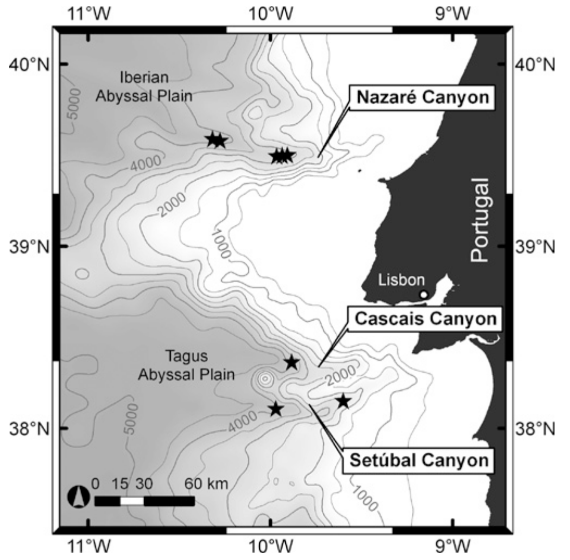

Fig. 1. Map of Iberian Peninsula submarine canyon trap deployments as part of research expeditions RRS *Discovery* 297, RRS *Charles Darwin* 179, and RRS *James Cook* 010.

super-family Lysianassoidea (Dahl, 1979; De Broyer et al., 2004; Lowry and Stoddart, 2009, 2011). Many deep-sea scavenger species have cosmopolitan distributions and there is little evidence of endemism in individual abyssal plain communities (Thurston, 1990). Some species, such as *Eurythenes gryllus* Lichtenstein, 1822 have been found in all of the World's oceans and over a wide range of depths (Christiansen et al., 1990; De Broyer et al., 2004). There is, however, a growing body of evidence to support the theory that discrete populations inhabit the Atlantic and Pacific oceans. The extent of this separation has yet to be determined with some indication that populations are on the verge of speciation (Thurston et al., 2002, and references therein).

Assemblages of scavenging amphipods in submarine canyons have been poorly studied (e.g., Soliman and Rowe, 2008) and factors affecting the composition of these communities are yet to be identified. This study aims to determine if scavenging amphipod communities in submarine canyons differ from those in other locales and identify factors that may potentially be affecting community composition and species distributions.

2 Methods

2.1 Sample collection

Three submarine canyons on the Iberian Margin, off of the west coast of Portugal, were studied; Nazaré, Setúbal, and Cascais (Fig. 1). A total of eight baited trap deployments were made, five in Nazaré Canyon, two in Setúbal, and one in Cascais. Sampling occurred on three scientific research expeditions (RRS *Discovery* 297, RRS *Charles Darwin* 179, RRS *James Cook* 010) between August 2005 and June 2007 as part of the European HERMES (Hotspot Ecosystem Research on the Margins of European Seas) Project (Table 1). Samples were collected using a basic trap design comprising of a funnelled entrance leading into a container with bait attached inside. All deployments during D297 and CD179 utilised a free-fall lander frame with one trap at the base and one a metre above. Recovery was via an iXSea acoustic release attached to the frame alongside the trap. The JC010/094 deployment used two traps placed on the seafloor and recovered using the remotely operated vehicle (ROV) Isis. All but one of the traps were baited with a single raw mackerel (*Scomber scombrus*) of approximately equal size wrapped in muslin cloth. Trap CD179/56817 was baited with smoked fish fillets. Upon recovery, the contents of all traps were

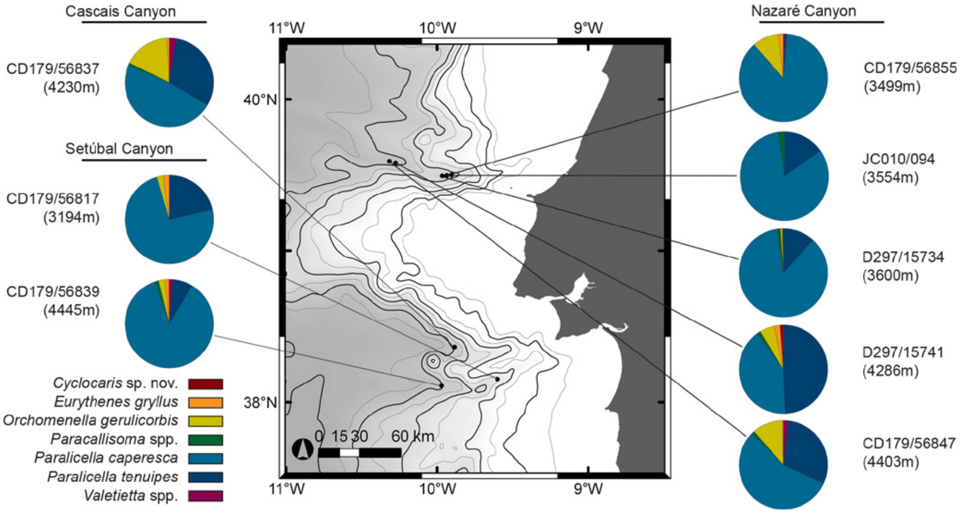

Fig. 2. Species composition of samples collected from trap deployments in submarine canyons off the Iberian Peninsula.

fixed in 4 % buffered formaldehyde-saline solution and subsequently preserved in 80 % industrial methylated spirits.

2.2 Sample analysis

All amphipods were identified to species level using morphological characteristics viewed under a stereo dissecting microscope. Following sorting, counts of each species were taken. For the purposes of this study, the contents of the two traps used in each deployment were analysed as a whole.

Abundance data were converted to percentage composition and square-root transformed. Bray-Curtis Similarity matrices were subsequently produced. A one-way analysis of similarities (ANOSIM; Clarke, 1993) was performed using PRIMER 6 (Plymouth Routines In Multivariate Ecological Research; Clarke and Gorley, 2006) statistical software to determine if community composition varied significantly between samples. A SIMPER analysis (Clarke, 1993) was used to identify which components of the community were responsible for any variability detected.

Study areas were grouped into mega habitats (e.g., canyon, abyssal plain) and macro habitats (e.g., lower canyon, middle canyon; de Stigter et al., 2007) to facilitate comparative analyses between locales (Greene et al., 1999). Samples from the Iberian submarine canyons were compared using canyon and depth as factors to test for dissimilarity between macro habitats within submarine canyons. Canyon samples were compared to published records of scavenging amphipod community composition from traps deployed in the Iberian Abyssal Plain (Thurston, 1990). Where possible data on environmental variables were obtained from CTD casts deployed in the vicinity (<2.5 km radius) and from UKORS megacores and UNSEL box cores (Table 1; Cunha et al., 2011). Temperature and total organic carbon (TOC) measurements were grouped into discrete categorical bins (temperature, $\leq 2.5\,^{\circ}$C, $>2.5\,^{\circ}$C; TOC, ≤ 15 mg g^{-1}, >15 mg g^{-1}) to facilitate subsequent factorial analysis.

The diversity of each site was measured using Simpson's Diversity Index (D; Simpson, 1949). The calculated indices were compared with those calculated for the adjacent abyssal plain using published data (Table 2; Thurston, 1990) with a Mann-Whitney U test. Evenness was measured using Pielou's Evenness Index (J'; Pielou, 1966) and compared with a Mann-Whitney U test.

3 Results

Large catches of scavenging amphipods were obtained from all but three of the deployments. During deployment D297/15734, the trap was damaged while in situ, possibly by strong currents in the canyon as recorded on the seabed lander system ROBIO (RObust BIOdiversity; OceanLab, Aberdeenshire, UK) deployed at the same time nearby (Weaver, 2005). Smoked fish was used instead of raw mackerel for deployment CD179/56817. Deployment JC010/094 was made using small traps deployed by ROV. Despite these three deployments returning smaller catches, the overall composition of the catches appeared to be unaffected, clustering with standard deployments in ordination plots (Fig. 3). Therefore, these samples were included in analysis of community structure following standardisation for sample size.

Ten species of lysianassoid amphipod were identified, representing six scavenging amphipod families (Table 3; Fig. 2). Eight of the species have been recorded previously on the abyssal plains of the northeast Atlantic (Thurston, 1990; Christiansen, 1996, unpublished data). Four species are new

Table 2. Species composition and abundance for scavenging amphipod samples collected from baited trap deployments made on the abyssal plains adjacent to the Iberian Margin submarine canyons as part of the 1981 ABYPLANE research expedition. Taken from Thurston, 1990. Species richness (S), Pielous's Eveness (J'), and Simpson's Diversity Index (D) shown.

Station	na09	na10	na11	na12	na13	na14	na15
Depth (m)	3400	3499	3600	4286	4403	3194	4445
Species richness (S)	3	6	3	5	5	6	1
Simpon's Index (D)	0.61	0.73	0.59	0.67	0.58	0.65	–
Pielou's Eveness (J')	0.82	0.82	0.84	0.75	0.68	0.71	–
Paralicella caperesca	–	26	5	11	36	58	–
Paralicella tenuipes	1	7	2	1	16	20	–
Eurythenes gryllus	5	20	10	13	4	15	1
Orchomenella gerulicorbis	2	6	–	2	4	11	–
Cyclocaris sp. nov.	–	2	–	–	–	–	–
Valetietta gracilis	–	4	–	–	–	1	–
Abyssorchomene chevreuxi	–	–	–	2	1	2	–
Total	8	65	17	29	61	107	1

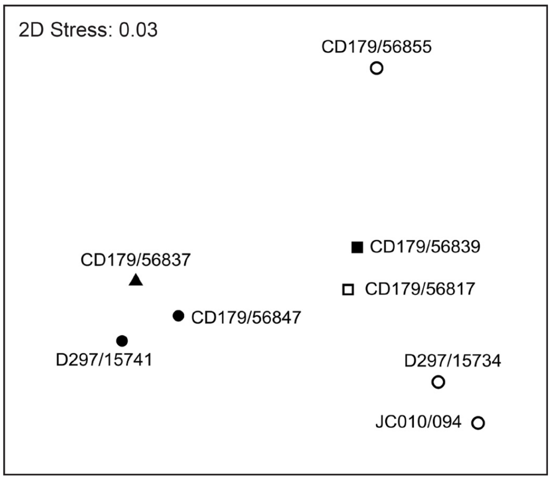

Fig. 3. MDS plot of all canyon samples. Samples coded by canyon (circles, Nazaré Canyon; squares, Setúbal Canyon; triangles, Cascais Canyon) and depth (open symbols, middle canyon; filled symbols, lower canyon). Sample number shown next to each point.

to science; *Cyclocaris* sp. nov., *Valettietta* sp. nov., and two species of *Paracallisoma*.

Paralicella caperesca Shulenberger and Barnard, 1976 was the dominant species in all but one sample. *Paralicella caperesca* and *P. tenuipes* Chevreux, 1908 accounted for between 77.7 % and 96.1 % of all scavenging amphipod specimens in each sample (Fig. 2). The prevalence of *P. tenuipes* was reduced at shallower sites. This trend was particularly apparent in Nazaré Canyon where this species dominated at the lower canyon site but represented less than 1 % of the total scavenging amphipod component of the middle canyon sites.

No significant difference in scavenging amphipod communities was observed between submarine canyons (one-way ANOSIM: $R = -0.269$, $P = 0.885$). The limited number of replicates within each canyon may be confounding this analysis but ordination plots show little clustering of points by canyon (Fig. 3). A significant difference was evident between sample sites in the middle and lower canyon (ANOSIM: $R = 0.494$, $P = 0.040$). There was no significant difference between communities based upon temperature (ANOSIM: $R = 0.124$, $P = 0.248$) or TOC of the sediments (ANOSIM: $R = -0.333$, $P = 0.971$).

The scavenging amphipod assemblages from canyons differed significantly from those of the adjacent Iberian Abyssal Plain (ANOSIM: $R = 0.219$, $P = 0.018$). SIMPER analysis showed that the majority (~72 %) of this dissimilarity was explained by differences in catches of *E. gryllus* (34.5 %), *P. caperesca* (24.8 %), and *P. tenuipes* (12.4 %).

Simpson's Diversity Index values ranged from 0.23 to 0.65 ($n = 9$, median $= 0.32$, Q1 $= 0.25$, Q3 $= 0.59$) and were generally lower than values calculated for the abyssal plain ($n = 6$, median $= 0.63$, Q1 $= 0.59$, Q3 $= 0.68$). This difference was significant (Mann-Whitney U test; $P = 0.013$). Pielou's Evenness Index showed the composition of abyssal plain samples was more evenly spread than canyon samples (Mann-Whitney U test; $P = 0.013$).

Table 3. Species composition and abundance (percentage contribution in parentheses) for scavenging amphipod component of samples collected from baited trap deployments in Iberian Margin submarine canyons (NC: Nazaré Canyon, SC: Setúbal Canyon; CC: Cascais Canyon). Species richness (S), Pielous's Eveness (J'), and Simpson's Diversity Index (D) shown.

Expedition	JC010		CD179		D297		D297		CD179		CD179		CD179		CD179	
Station	#094		#56855		#15734		#15741		#56847		#56817		#56839		#56837	
Canyon	NC		NC		NC		NC		NC		SC		SC		CC	
Depth (m)	3400		3499		3600		4286		4403		3194		4445		4230	
Species richness (S)	3		6		5		10		9		4		8		6	
Simpon's Index (D)	0.30		0.23		0.25		0.59		0.59		0.41		0.25		0.65	
Pielou's Eveness (J')	0.48		0.27		0.30		0.47		0.49		0.52		0.29		0.66	
Paralicella caperesca	38	(82.6)	889	(87.1)	259	(86.0)	1424	(40.7)	4217	(55.6)	66	(74.2)	825	(86.0)	558	(47.9)
Paralicella tenuipes	7	(15.2)	8	(0.8)	35	(11.6)	1716	(49.0)	2287	(30.1)	19	(21.3)	71	(7.4)	360	(30.9)
Eurythenes gryllus	–		18	(1.8)	–		77	(2.2)	23	(0.3)	2	(2.2)	14	(1.5)	10	(0.9)
Orchomenella gerulicorbis	–		99	(9.7)	2	(0.7)	191	(5.5)	845	(11.1)	2	(2.2)	22	(2.3)	197	(16.9)
Cyclocaris sp. nov.	–		–		1	(0.3)	40	(1.1)	3	(<0.1)	–		1	(0.1)	–	
Valetietta gracilis	–		6	(0.6)	–		3	(0.1)	134	(1.8)	–		12	(1.3)	29	(0.9)
Valetietta lobata	–		1	(0.1)	–		1	(< 0.1)	1	(1.8)	–		–		–	
Valetietta sp. nov.	–		–		–		6	(0.7)	–		–		–		–	
Paracallisoma sp. nov. 1	1	(2.2)	–		4	(1.3)	42	(1.2)	75	(1.0)	–		12	(1.3)	10	(0.9)
Paracallisoma sp. nov. 2	–		–		–		1	(< 0.1)	5	(< 0.1)	–		2	(0.2)	–	
Total	46		1021		301		3501		7590		89		959		1164	

4 Discussion

4.1 Community composition

The similarity of communities between canyons demonstrates the wide distribution of deep-sea scavenging amphipods and confirms that canyons do not restrict the movement of motile scavenging fauna. A similar trend is evident in abyssal basins, with little community variation between adjoining abyssal plains in the northeast Atlantic (Thurston, 1990).

While the scavenging amphipod species identified in canyons are largely identical to those on the adjacent abyssal plains, there is a significant difference in the composition of the assemblages in these two habitats. This difference may be caused by temporal variability, plain samples were taken more than a decade before canyon samples (Thurston, 1990). Unpublished data from the Porcupine Abyssal Plain time series indicates that temporal variability has no effect on community composition of scavenging amphipod assemblages; therefore, the difference can be confidently attributed to the different sampling locations. The results of the SIMPER analysis coupled with the significant difference in Pielous's Evenness Index suggest that the disparity in community composition is due to the reduced importance of *Paralicella* spp. and increased evenness of community composition in abyssal plain settings, including a greater representation of *E. gryllus*. A more even distribution of species results in a higher diversity index when measured using indices, such as Simpson's, despite few differences in species richness.

A similar trend of high abundances of a few dominant species in submarine canyon communities has also been observed in scavenging fish (Stefanescu et al., 1994; King et al., 2008) and various macrofauna (Paterson et al., 2011). Cunha et al. (2011) identified a comparable trend in macrofauna of Nazaré and Setúbal canyons but not in Cascais, demonstrating that complex and heterogenous nature of submarine canyons. The similarity of the assemblages in the different canyons taken together with the occurrence of species with global distributions, the mobility of amphipods (Boudrias, 2002), and the interconnectivity evident between canyons and abyssal plains (Vetter and Dayton, 1998) support the theory that the observed differences within canyons are mainly due to variation in environmental conditions, notably depth-correlated variables, rather than canyons acting as physical barriers to dispersal and species distributions.

Although community composition does not vary significantly between canyons, there is a clear difference in community composition within canyons at different depths. Within the limitations of this study, it has not been possible to establish which of the many depth-correlated variables (e.g., hydrostatic pressure, temperature, salinity, oxygen concentration, POC flux) specifically leads to the community differences seen. Temperature, salinity, and oxygen concentration varied little between canyon sites and were not found to contribute significantly toward variability in community composition when tested as individual factors. Sediment TOC, although much more variable, also had no detectable effect on community composition. It may be that hydrostatic pressure alone is responsible for these differences, however, the polar emergence of *E. gryllus* (Ainley et al., 1986), a deep-sea scavenger primarily seen at abyssal depths at mid-latitudes (Ingram and Hessler, 1983; Smith and Baldwin, 1984), suggests that temperature also plays a role in the depth distribution limitations of deep-sea scavenging amphipods (Thurston et al., 2002). A more feasible explanation is that both of these depth-correlated variables, along with other variables that correlate to depth, such as oxygen concentration, each contribute a small amount toward the community-level differences. While their individual effects are not detectable, the cumulative and interacting influences of these factors are detectable. The synergistic effect of low temperature and high pressure upon respiration has been found during laboratory tests on the deep sea lysianassoid *Stephonyx biscayensis* Chevreux, 1908 (Brown and Thatje, 2011), but the physiological limits of the species in the current study remain unknown.

The dominance in all samples of *Paralicella*, a genus commonly identified in traps deployed on the abyssal plains of the northeast Atlantic (Thurston, 1990, unpublished data), indicates that members of this taxon are highly efficient scavengers. Both *P. caperesca* and *P. tenuipes* have been identified as specialist scavengers with adaptations that allow them to monopolise food falls (Thurston, 1979). The reduced prevalence of *P. tenuipes* at shallower sites, as particularly apparent in Nazaré Canyon, indicates that the upper depth limit of this species is shallower than that of its congener.

4.2 Relative abundance

Estimating background population size based on catches from baited traps, as performed previously for scavenging fishes using baited camera data (Priede and Merrett, 1998; Sainte-Marie and Hargrave, 1987), is not possible for deep-sea scavenging amphipods, which can rarely be identified in photographs and have unknown maximum swim speeds. Despite this, the large catches found in this study can be qualitatively linked to the size of the background populations (Blankenship et al., 2006). Compared to catches from similar traps deployed on the abyssal plains of the northeastern Atlantic (Table 2; Thurston, 1990), submarine canyons house very large assemblages of scavenging amphipods.

The large background populations of deep-sea scavenging amphipods, indicated by catches from canyons sampled, can be linked to high levels of sedimentation and enhanced concentrations of associated organic matter found (Vetter and Dayton, 1998; Epping et al., 2002; Garcia et al., 2010; Masson et al., 2010). Setúbal and Cascais Canyons are fed by large river systems (Sado and Tagus Rivers, respectively; Arzola et al., 2008). The mouths of these rivers flow directly into the canyon heads. Estuarine input results in large quantities of terrigenous organic matter entering the canyon system (Cúrdia et al., 2004). The extent to which this material travels down these two canyons is thought to be limited, in comparison to Nazaré, owing to the rarity of large-scale episodic events, which are a particular feature of down-canyon sediment transport (de Stigter et al., 2011).

Nazaré Canyon has no direct link to any large river systems, yet it has been estimated to have the highest levels of organic carbon and sediment input (Masson et al., 2010; Garcia et al., 2010). Heavy metal contamination of sediments in the canyon suggests output from a number of small river systems enters the canyon (Oliveira et al., 2011), however, inputs from shelf sediments are the most likely source of organic matter input. This provides an explanation for why the catches from this canyon are particularly large compared to catches from Setúbal and Cascais canyons, with Nazaré Canyon supporting larger background populations of scavenging amphipods.

The largest catches of all canyon deployments were seen in the deepest sites of the Nazaré Canyon. The location of these sites correlates with flat terraces observed during a video survey of the canyon using the ROV Isis (Tyler et al., 2009). These terraces experience relatively weak currents, acting as depocentres for sediment and larger material. As such, these depocentres could experience more frequent settling of large food falls, in turn supporting larger populations of scavengers. An increased settling rate of large food falls provides a potential explanation for the abundant catches of the baited traps deployed in submarine canyons. The idea that these terraces are nutrient rich and high in organic matter is supported by the existence of large communities of xenophyophores (Gooday et al., 2011), single-celled protists whose presence is associated with high nutrient environments (Levin, 1991).

Input from rivers and coastal waters will undoubtedly include carcasses of large terrestrial, freshwater, and marine organisms, a food source that will be readily exploited by deep-sea scavenging amphipods. The productive waters associated with submarine canyons also make them ideal grounds for fishing (Figueiredo et al., 2001; Puig et al., 2012). An increase in food falls, via the discard of bycatch from fisheries, has a positive effect on marine scavenger abundances (Kaiser and Hiddink, 2007), increasing secondary production (Bozzano and Sarda, 2002; Furness et al., 2007). Indeed some facultative scavengers switch from a predatory foraging strategy to a scavenging one in the presence of fisheries discard (Laptikhovsky and Fetisov, 1999). The depth penetration of large carrion into the deep sea remains largely unknown as few naturally occurring food falls have been found at abyssal depths (e.g., Stockton and DeLaca, 1982; Smith and Hessler, 1987; Klages et al., 2001; Soltwedel et al., 2003), as such there is currently no evidence of increased large food-fall input into the canyons studied. It is, however, presumed that a sufficient number of large carcasses do reach abyssal depths regularly enough to support a diverse and abundant scavenging fauna.

5 Conclusions

Scavenging amphipod assemblages in submarine canyons are dominated by a few common abyssal species occurring in large numbers with no evidence for endemic canyon species. There is strong evidence that submarine canyons provide a nutrient-rich environment in which scavenging amphipods can maintain larger populations than they do on the open slope or abyssal plains at similar depths. These large scavenging amphipod populations play an important role in the recycling of concentrated inputs of organic matter, driving secondary production to orders of magnitude greater than at similar depths on the open continental slope. This study shows that depth-correlated variables are an important control on scavenging amphipod distributions with a discernible difference observed between communities at different depths within submarine canyons.

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Appendix B

Data used for synthesis

Table B.1: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 1, Christiansen, 1996; 3, Kemp et al., 2006. Study areas: ANS, Angolan shelf; ARC, Arctic Ocean.

ID	**7842_1**	**7842_2**	**7848_1**	**chrst_96_ib**	**premke_i**	**premke_ii**	**premke_iii**	**premke_iv**	**premke_v**
Programme/Cruise	**D45**	**D45**	**D45**	**Meteor10**	**PS00/01**	**PS00/01**	**PS00/01**	**PS00/01**	**PS00/01**
Date (dd/mm/yy)	**3/23/72**	**3/23/72**	**3/25/72**	**7/1/89**	**Sum00/01**	**Sum00/01**	**Sum00/01**	**Sum00/01**	**Sum00/01**
Latitude	**23.7167**	**23.7767**	**25.7733**	**59.0000**	**78.5000**	**78.8333**	**79.0667**	**79.3500**	**78.8333**
Longitude	**-17.2350**	**-17.2433**	**-15.9517**	**-20.0000**	**6.2000**	**5.8667**	**4.3167**	**2.9833**	**2.7000**
Depth (m)	**951**	**953**	**929**	**3000**	**2644**	**2524**	**2377**	**1468**	**2504**
Source	**DC**	**DC**	**DC**	**1**	**3**	**3**	**3**	**3**	**3**
Area	**ANS**	**ANS**	**ANS**	**ARC**	**ARC**	**ARC**	**ARC**	**ARC**	**ARC**
Abyssorchomene abyssorum	0	0	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0	0
Eurythenes gryllus	0	0	0	1	1	1	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	1	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	0	0	0	0
Paralicella caperesca	0	0	0	0	0	0	0	0	0
Paralicella tenuipes	0	0	0	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0	0
Stephonyx biscayensis	1	1	1	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	1	1	1	1	1
Tmetonyx similis	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0	0

Table B.2: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 3, Kemp et al., 2006; 7, Thurston, 1990, and references therein. Study areas: ARC, Arctic Ocean; AZS, Azore shelf; BIS, Biscay.

ID	**premke_vi**	**56354_1**	**56319_1**	**56347_1**	**56335_1**	**biogas_vii_na18**	**biogas_vii_na19**
Programme/Cruise	**PS00/01**	**Meteor_60_1**	**Meteor_60_2**	**Meteor_60_3**	**Meteor_60_4**	**BIOGASVII**	**BIOGASVII**
Date (dd/mm/yy)	**Sum00/01**	**11/28/93**	**11/21/03**	**11/26/03**	**11/25/03**		
Latitude	**79.1000**	**39.8362**	**40.1905**	**40.3322**	**40.3167**	**47.5633**	**47.5633**
Longitude	**4.3167**	**-26.2970**	**-26.5665**	**-26.8445**	**-26.6645**	**-9.2500**	**-9.2500**
Depth (m)	**2314**	**2876**	**2655**	**1123**	**773**	**3144**	**3150**
Source	**3**	**DC**	**DC**	**DC**	**DC**	**7**	**7**
Area	**ARC**	**AZS**	**AZS**	**AZS**	**AZS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	1	1	1	1	0	0
Abyssorchomene chevreuxi	0	1	1	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	0	0	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	1	0	0	0
Hirondellea spp.	0	1	1	0	0	0	0
Hirondellea trioculata	0	1	1	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	1	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	1	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	1	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	0
Paracallisoma spp.	0	1	1	0	0	1	0
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	0	1	1	0	0	1	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	1	0
Paralicella caperesca	0	0	0	0	0	1	0
Paralicella tenuipes	0	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0	1
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0
Tmetonyx norbiensis	1	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	1	0	1	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	1	1	0	1	0	0
Valettietta gracilis	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0

Table B.3: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay.

ID	**biogas_vii_na20**	**biogas_vii_na26**	**biogas_vii_na27**	**biogas_vii_na3_9**	**biogas_vii_na3_10**	**biogas_vii_na3_11**
Programme/Cruise	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**
Date (dd/mm/yy)						
Latitude	**47.5333**	**47.5867**	**47.5867**	**47.5083**	**47.5083**	**47.5083**
Longitude	**-8.9333**	**-9.5833**	**-9.5833**	**-8.5933**	**-8.5933**	**-8.5933**
Depth (m)	**2700**	**4090**	**4090**	**2080**	**2080**	**2080**
Source	**7**	**7**	**7**	**7**	**7**	**7**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0
Eurythenes gryllus	1	1	0	0	1	1
Hippomedon sp. 1	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	1	1
Hirondellea trioculata	0	0	0	0	1	1
Hirondellea wolfendeni	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0
Orchomene oxystoma	1	0	0	1	1	1
Orchomene pectinatus	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0
Paralicella spp.	0	1	1	0	0	0
Paralicella caperesca	0	1	1	0	0	0
Paralicella tenuipes	0	0	0	0	0	0
Parandania boecki	1	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	1	0
Tmetonyx albidus	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	1	1	1
Tryphosella pusilla	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0

Table B.4: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay.

ID	**biogas_vii_na3_12**	**biogas_vii_na9_5**	**biogas_vii_na9_6**	**biogas_vii_na9_7**	**biogas_vii_na9_8**	**biogas_vii_na19_9**
Programme/Cruise	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**
Date (dd/mm/yy)						
Latitude	**47.5083**	**47.5000**	**47.5000**	**47.5000**	**47.5000**	**47.5633**
Longitude	**-8.5933**	**-8.5833**	**-8.5833**	**-8.5833**	**-8.5833**	**-9.2500**
Depth (m)	**2080**	**2090**	**2090**	**2090**	**2090**	**3150**
Source	**7**	**7**	**7**	**7**	**7**	**7**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	0	0	0	0	0
Abyssorchomene chevreuxi	1	0	0	0	0	1
Alicella sp.	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0
Eurythenes gryllus	0	1	0	0	0	1
Hippomedon sp. 1	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0
Hirondellea spp.	1	1	1	0	1	0
Hirondellea trioculata	1	1	1	0	1	0
Hirondellea wolfendeni	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0
Orchomene oxystoma	1	1	1	1	1	0
Orchomene pectinatus	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	0
Paralicella caperesca	0	0	0	0	0	0
Paralicella tenuipes	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0
Stephonyx biscayensis	1	0	1	0	1	0
Tmetonyx albidus	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0
Tryphosella caecoides	1	1	1	1	1	0
Tryphosella pusilla	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0

Table B.5: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay.

ID	**biogas_vii_na19_10**	**biogas_vii_na19_11**	**biogas_vii_na19_12**	**biogas_vii_na28**	**biogas_vii_na29**	**biogas_vii_na30**
Programme/Cruise	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**
Date (dd/mm/yy)						
Latitude	**47.5633**	**47.5633**	**47.5633**	**47.5383**	**47.5717**	**47.5717**
Longitude	**-9.2500**	**-9.2500**	**-9.2500**	**-8.6383**	**-8.6833**	**-8.6833**
Depth (m)	**3150**	**3150**	**3150**	**2225**	**2225**	**2225**
Source	**7**	**7**	**7**	**7**	**7**	**7**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	0	0	0	0	0
Abyssorchomene chevreuxi	1	0	1	0	0	1
Alicella sp.	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0
Eurythenes gryllus	1	1	0	0	0	0
Hippomedon sp. 1	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	1	1
Hirondellea trioculata	0	0	0	0	1	1
Hirondellea wolfendeni	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	1
Orchomene pectinatus	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0
Paracallisoma spp.	1	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0
Paracallisoma alberti	1	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0
Paralicella spp.	1	0	1	0	0	0
Paralicella caperesca	1	0	1	0	0	0
Paralicella tenuipes	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	1	1
Tmetonyx albidus	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	1	1	1
Tryphosella pusilla	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0

Table B.6: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay.

ID	**biogas_vii_na31**	**biogas_vii_na32**	**biogas_vii_na33**	**biogas_vii_na36**	**biogas_vii_na37**	**biogas_vii_na38**
Programme/Cruise	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**
Date (dd/mm/yy)						
Latitude	**47.5717**	**47.5717**	**47.5717**	**47.5717**	**47.5717**	**47.5717**
Longitude	**-8.6833**	**-8.6833**	**-8.6833**	**-8.6833**	**-8.6833**	**-8.6833**
Depth (m)	**2225**	**2225**	**2225**	**2225**	**2225**	**2225**
Source	**7**	**7**	**7**	**7**	**7**	**7**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0
Eurythenes gryllus	0	1	0	0	0	0
Hippomedon sp. 1	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0
Hirondellea spp.	0	0	0	1	1	1
Hirondellea trioculata	0	0	0	1	1	1
Hirondellea wolfendeni	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	1
Orchomene pectinatus	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	0
Paralicella caperesca	0	0	0	0	0	0
Paralicella tenuipes	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0
Tryphosella caecoides	1	1	1	1	1	1
Tryphosella pusilla	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0

Table B.7: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay.

ID	**biogas_vii_na39**	**biogas_vii_na40**	**biogas_vii_na41**	**biogas_ix_na42**	**biogas_ix_na43**	**biogas_ix_na45**
Programme/Cruise	**BIOGASVII**	**BIOGASVII**	**BIOGASVII**	**BIOGASIX**	**BIOGASIX**	**BIOGASIX**
Date (dd/mm/yy)						
Latitude	**47.5717**	**47.5717**	**47.5717**	**47.5263**	**47.5270**	**47.5280**
Longitude	**-8.6833**	**-8.6833**	**-8.6833**	**-9.0708**	**-9.0703**	**-9.0725**
Depth (m)	**2225**	**2225**	**2225**	**2718**	**2780**	**2730**
Source	**7**	**7**	**7**	**7**	**7**	**7**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	1	0	0
Alicella sp.	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0
Eurythenes gryllus	0	0	0	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0
Hirondellea spp.	1	1	1	0	0	0
Hirondellea trioculata	1	1	1	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0
Orchomene oxystoma	0	1	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	0
Paralicella caperesca	0	0	0	0	0	0
Paralicella tenuipes	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0
Tryphosella caecoides	1	1	1	1	0	0
Tryphosella pusilla	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0

Table B.8: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay.

ID	**biogas_ix_na46**	**biogas_ix_pa01**	**biogas_ix_pa02**	**biogas_ix_pa03**	**biogas_ix_pa04**	**biogas_ix_pa05**
Programme/Cruise	**BIOGASIX**	**BIOGASIX**	**BIOGASIX**	**BIOGASIX**	**BIOGASIX**	**BIOGASIX**
Date (dd/mm/yy)						
Latitude	**47.5270**	**47.3000**	**47.5255**	**47.5262**	**47.5245**	**47.5270**
Longitude	**-9.0672**	**-9.0833**	**-9.0900**	**-9.0703**	**-9.0703**	**-9.0700**
Depth (m)	**2715**	**2730**	**2720**	**2797**	**2732**	**2750**
Source	**7**	**7**	**7**	**7**	**7**	**7**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	0
Paralicella caperesca	0	0	0	0	0	0
Paralicella tenuipes	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0

Table B.9: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay.

ID	**biogas_ix_pa06**	**biogas_ix_pa07**	**biogas_x_pa08**	**biogas_x_na48**	**biogas_x_na49**	**biogas_x_na50**
Programme/Cruise	**BIOGASIX**	**BIOGASIX**	**BIOGASX**	**BIOGASX**	**BIOGASX**	**BIOGASX**
Date (dd/mm/yy)						
Latitude	**47.5270**	**47.5270**	**47.5912**	**47.5522**	**47.5522**	**47.5522**
Longitude	**-9.0750**	**-9.0672**	**-9.6595**	**-9.6095**	**-9.5952**	**-9.5945**
Depth (m)	**2770**	**2710**	**4250**	**4260**	**4250**	**4250**
Source	**7**	**7**	**7**	**7**	**7**	**7**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**
Abyssorchomene abyssorum	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	1	1	1	1
Alicella sp.	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	0	0
Hippomedon sp. 1	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0
Paralicella spp.	0	0	1	1	0	1
Paralicella caperesca	0	0	1	1	0	1
Paralicella tenuipes	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0

TABLE B.10: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 7, Thurston, 1990, and references therein. Study areas: BIS, Biscay; CVP, Cape Verde Abyssal Plain.

ID	**biogas_xi_na53**	**biogas_xi_na54**	**biogas_xi_na55**	**ecogas_na56**	**ecogas_na57**	**12600_41**	**12600_44**
Programme/Cruise	**BIOGASXI**	**BIOGASXI**	**BIOGASXI**	**ECOGAS**	**ECOGAS**	**D204**	**D204**
Date (dd/mm/yy)						**10/8/93**	**10/9/93**
Latitude	**46.5495**	**47.6123**	**47.6090**	**47.5553**	**47.5552**	**21.0767**	**21.0867**
Longitude	**-10.3625**	**-9.5928**	**-9.5903**	**-8.6798**	**-8.6858**	**-31.1933**	**-31.1100**
Depth (m)	**4700**	**4200**	**4200**	**2190**	**2195**	**4615**	**4540**
Source	**7**	**7**	**7**	**7**	**7**	**DC**	**DC**
Area	**BIS**	**BIS**	**BIS**	**BIS**	**BIS**	**CVP**	**CVP**
Abyssorchomene abyssorum	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	1	0	1	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	1
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	0	1	1	0
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	1	1	0	0
Hirondellea trioculata	0	0	0	1	1	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	1	1
Orchomene oxystoma	0	0	0	0	0	0	1
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	1	1
Paracallisoma spp.	0	0	1	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	1	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	1	0	1	0	0	1	1
Paralicella caperesca	1	0	1	0	0	0	1
Paralicella tenuipes	1	0	1	0	0	1	1
Parandania boecki	0	0	0	0	1	0	0
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	1	1	0	0
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	1	1	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	1	1
Valettietta lobata	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	1

Table B.11: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 7, Thurston, 1990, and references therein. Study areas: CVP, Cape Verde Abyssal Plain.

ID	**12600_46**	**12600_51**	**12600_60**	**seabed2_na06**	**seabed2_na07**	**seabed2_na08**	**seabed2_na10**
Programme/Cruise	**D204**	**D204**	**D204**	**SEABED2**	**SEABED3**	**SEABED4**	**SEABED5**
Date (dd/mm/yy)	**10/10/93**	**10/12/93**	**10/14/93**	**11/7/80**	**11/7/80**	**11/7/80**	**11/8/80**
Latitude	**21.0203**	**21.0733**	**21.0855**	**24.8495**	**24.8483**	**24.8498**	**24.9137**
Longitude	**-31.2167**	**-31.1198**	**-31.2160**	**-24.9317**	**-24.9323**	**-24.9323**	**-25.0283**
Depth (m)	**4555**	**4582**	**4569**	**5190**	**5190**	**5190**	**5200**
Source	**DC**	**DC**	**DC**	**7**	**7**	**7**	**7**
Area	**CVP**	**CVP**	**CVP**	**CVP**	**CVP**	**CVP**	**CVP**
Abyssorchomene abyssorum	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	1	0	0	1	0	1	1
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	0	1	0	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	1	0	0
Hirondellea trioculata	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	1	1	1
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	1	0	1	0	0	0	0
Orchomenella gerulicorbis	1	0	0	0	0	0	1
Paracallisoma spp.	0	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	1	0	1	1	1	1	1
Paralicella caperesca	1	0	1	0	1	1	1
Paralicella tenuipes	1	0	1	1	1	0	1
Parandania boecki	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0
Valettietta gracilis	1	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	1	0	0	0	0	0	0

Table B.12: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: CVP, Cape Verde Abyssal Plain, DAP, Demerara Abyssal Plain

ID	**seabed2_na11**	**seabed2_na12**	**seabed2_na13**	**seabed2_na14**	**demeraby_na01**	**demeraby_na03**	**demeraby_na04**
Programme/Cruise	**SEABED6**	**SEABED7**	**SEABED8**	**SEABED9**	**DEMERABY**	**DEMERABY**	**DEMERABY**
Date (dd/mm/yy)	**11/16/80**	**11/16/80**	**11/17/80**	**11/17/80**	**9/11/80**	**9/20/80**	**9/24/80**
Latitude	**19.2402**	**19.2402**	**19.2402**	**19.2402**	**8.1337**	**10.4275**	**10.3572**
Longitude	**-29.7845**	**-29.7845**	**-29.8228**	**-29.8228**	**-49.0330**	**-46.8010**	**-46.7338**
Depth (m)	**4945**	**4973**	**4942**	**4942**	**4430**	**4850**	**4850**
Source	**7**	**7**	**7**	**7**	**7**	**7**	**7**
Area	**CVP**	**CVP**	**CVP**	**CVP**	**DAP**	**DAP**	**DAP**
Abyssorchomene abyssorum	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0
Alicella sp.	0	0	1	1	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	1	1	1	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0
Normanion spp.	1	1	1	1	0	0	0
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	1	1	1	1	1
Orchomene oxystoma	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0	0
Orchomenella gerulicorbis	1	1	1	1	1	1	1
Paracallisoma spp.	0	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	1	1	1	1	1	1	1
Paralicella caperesca	0	1	1	1	1	1	1
Paralicella tenuipes	1	1	1	1	1	1	1
Parandania boecki	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	1	0	1
Scopelocheirid Gen nov.	0	0	0	0	0	0	1

Table B.13: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 7, Thurston, 1990, and references therein. Study areas: DAP, Demerara Abyssal Plain; FSC, Faroe-Shetland Channel.

ID	**demeraby_na05**	**raeanne_h**	**raeanne_m**	**raeanne_g**	**53759_1**	**53768_1**	**53778_1**	**53799_1**	**53809_1**	**53817_1**
Programme/Cruise	**DEMERABY**	**serpent**	**serpent**	**serpent**	**537**	**537**	**537**	**537**	**538**	**538**
Date (dd/mm/yy)	**9/27/80**									
Latitude	**10.3767**	**67.0468**	**64.0166**	**66.1480**	**60.9915**	**61.1288**	**60.8968**	**61.4442**	**61.5399**	**61.4135**
Longitude	**-46.8170**	**7.0589**	**5.2791**	**3.9401**	**2.4986**	**2.7037**	**2.3683**	**1.5258**	**1.1503**	**1.9530**
Depth (m)	**4830**	**1248**	**928**	**1380**	**498**	**781**	**289**	**508**	**294**	**775**
Source	**7**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**DAP**	**FSC**	**FSC**	**FSC**	**FSC**	**FSC**	**FSC**	**FSC**	**FSC**	**FSC**
Abyssorchomene abyssorum	0	0	0	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	1	0	0	0	1	0	0	0	1
Anonyx nugax	0	1	1	1	0	1	0	0	0	1
Anonyx ochoticus	0	0	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	1	0	0	0	0	0	0	0	0
Centromedon productus	0	1	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	1	0	0	0	1	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	0	1	0	0	0	0
Hippomedon sp. 1	0	1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0	0	0
Onisimus affinis	0	1	0	0	0	0	0	0	0	0
Onisimus leucopis	0	1	1	1	0	0	0	0	0	0
Onisimus sextonae	0	1	1	1	0	0	0	0	0	0
Orchomene amblyops	0	1	1	0	0	1	0	0	0	1
Orchomene cavimanus	0	0	0	0	0	0	0	0	0	0
Orchomene distincta	1	0	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	1	0	1	0	0	0	1
Orchomene sp. 1	0	0	0	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	1	0	0	0	1
Orchomenella gerulicorbis	0	0	0	0	0	0	0	0	0	0
Paracallisoma spp.	0	1	1	1	0	0	0	0	0	0
Paracallisoma abyssi	0	1	1	1	0	0	0	0	0	0
Paracallisoma alberti	0	1	0	1	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	0	0	0	0	0
Paralicella caperesca	0	0	0	0	0	0	0	0	0	0
Paralicella tenuipes	0	0	0	0	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	1	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	1	1	1	1	1
Tmetonyx norbiensis	0	0	0	1	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	1	1	0	1	0	0
Tmetonyx sp. 3	0	1	1	1	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	1	1	0	1	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	1	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	1	1	0	1	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	1	0	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0	0	0

Table B.14: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 6, Thurston, 1979; 7, Thurston, 1990, and references therein. Study areas: FSC, Faroe-Shetland Channel; HAP, Horseshoe Abyssal Plain; IAP, Iberian Abyssal Plain.

ID	**53826_1**	**53979_1**	**57060_1**	**57077_1**	**57101_1**	**thurston_1979_9629**	**abyplane_na09**	**abyplane_na10**
Programme/Cruise	**538**	**539**	**570**	**570**	**570**	**D088**	**ABYPLANE**	**ABYPLANE**
Date (dd/mm/yy)						**10/26/77**	**6/8/81**	**6/8/81**
Latitude	**61.3006**	**61.4787**	**62.6527**	**62.2608**	**61.5766**	**37.7917**	**39.9300**	**39.9300**
Longitude	**2.4971**	**2.7943**	**1.2328**	**0.3211**	**0.4911**	**-13.2167**	**-15.1083**	**-15.1083**
Depth (m)	**1069**	**1396**	**1611**	**888**	**198**	**4588**	**5270**	**5270**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**6**	**7**	**7**
Area	**FSC**	**FSC**	**FSC**	**FSC**	**FSC**	**HAP**	**IAP**	**IAP**
Abyssorchomene abyssorum	0	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	1	0	0
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	1	0	0	1	1	0	0	0
Anonyx nugax	1	1	1	1	0	0	0	0
Anonyx ochoticus	1	0	0	1	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	1	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	1	0	1
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	0	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	1	1	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	0	1	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	1	1	1
Paracallisoma spp.	0	1	1	0	0	1	0	0
Paracallisoma abyssi	0	0	1	0	0	0	0	0
Paracallisoma alberti	0	1	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	1	1	1
Paralicella caperesca	0	0	0	0	0	1	0	1
Paralicella tenuipes	0	0	0	0	0	1	1	1
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	1	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	1	1	0	0	1	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	1	1	1	1	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	1	1	1	1	0	0	0	0
Tmetonyx sp. 5	0	0	0	1	0	0	0	0
Tmetonyx sp. 6	0	0	0	1	0	0	0	0
Tmetonyx sp. 7	0	0	1	1	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	1	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0	1
Valettietta lobata	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0

Table B.15: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 7, Thurston, 1990, and references therein. Study areas: IAP, Iberian Abyssal Plain; ISC, Iberian Submarine Canyons.

ID	**abyplane_na11**	**abyplane_na12**	**abyplane_na13**	**abyplane_na14**	**abyplane_na15**	**56837_1**	**56847_1**
Programme/Cruise	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**	**D568**	**D568**
Date (dd/mm/yy)	**6/10/81**	**6/10/81**	**6/12/81**	**6/12/81**	**6/13/81**	**5/2/06**	**5/7/06**
Latitude	**42.8617**	**42.8617**	**42.9933**	**42.9933**	**42.9967**	**38.3662**	**39.5917**
Longitude	**-15.9117**	**-15.9117**	**-14.1417**	**-14.1417**	**-14.1033**	**-9.8834**	**-10.3167**
Depth (m)	**4380**	**4380**	**5260**	**5260**	**5260**	**4230**	**4403**
Source	**7**	**7**	**7**	**7**	**7**	**DC**	**DC**
Area	**IAP**	**IAP**	**IAP**	**IAP**	**IAP**	**ISC**	**ISC**
Abyssorchomene abyssorum	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	1	1	1	0	0	0
Alicella sp.	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	1
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0	0
Orchomenella gerulicorbis	0	1	1	1	0	1	1
Paracallisoma spp.	0	0	0	0	0	1	1
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	1
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	1	1
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	1	1	1	1	0	1	1
Paralicella caperesca	1	1	1	1	0	1	1
Paralicella tenuipes	1	1	1	1	0	1	1
Parandania boecki	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	1	0	1	1
Valettietta lobata	0	0	0	0	0	0	1
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0

Table B.16: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: ISC, Iberian Submarine Canyons; MAP, Madeira Abyssal Plain.

ID	**56839_1**	**56855_1**	**15734_1**	**15741_1**	**56817_1**	**jc10_94_a1**	**jc10_94_a2**	**12174_20**
Programme/Cruise	**D568**	**D568**	**CD157**	**CD157**	**D568**	**JC10**	**JC10**	**D194**
Date (dd/mm/yy)	**5/4/06**	**5/11/06**	**8/1/05**	**8/4/05**	**4/25/06**	**6/14/07**	**6/14/07**	**8/18/90**
Latitude	**38.1095**	**39.5027**	**39.4963**	**39.5825**	**38.1528**	**39.4993**	**39.4993**	**31.1267**
Longitude	**-9.9697**	**-9.9050**	**-9.9648**	**-10.2750**	**-9.6000**	**-9.9350**	**-9.9350**	**-21.1667**
Depth (m)	**4445**	**3499**	**3600**	**4286**	**3194**	**3554**	**3554**	**4941**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**ISC**	**ISC**	**ISC**	**ISC**	**ISC**	**ISC**	**ISC**	**MAP**
Abyssorchomene abyssorum	0	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	1	0	1	1	0	0	0	1
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	0	1	1	0	0	1
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0	0	0
Orchomenella gerulicorbis	1	1	1	1	1	0	0	1
Paracallisoma spp.	1	0	1	1	0	0	1	0
Paracallisoma abyssi	0	0	0	0	0	0	0	0
Paracallisoma alberti	1	0	0	1	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	1	0	1	1	0	0	1	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0	0
Paralicella spp.	1	1	1	1	1	1	1	1
Paralicella caperesca	1	1	1	1	1	1	1	1
Paralicella tenuipes	1	1	1	1	1	1	1	1
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	1	1	0	1	0	0	0	1
Valettietta lobata	0	1	0	1	0	0	0	0
Valettietta sp. 1	0	0	0	1	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	1

Table B.17: Data used for synthesis analysis. Sources: 7, Thurston, 1990, and references therein. Study areas: MAP, Madeira Abyssal Plain.

ID	**abyplane_na01**	**abyplane_na02**	**abyplane_na03**	**abyplane_na04**	**abyplane_na05**	**abyplane_na06**	**abyplane_na07**
Programme/Cruise	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**	**ABYPLANE**
Date (dd/mm/yy)	**5/20/81**	**5/21/81**	**5/21/81**	**5/22/81**	**5/22/81**	**5/23/81**	**5/23/81**
Latitude	**36.8233**	**35.0050**	**35.0050**	**34.9317**	**34.9367**	**32.9683**	**32.9683**
Longitude	**-19.1650**	**-21.4717**	**-21.4717**	**-21.4267**	**-21.4267**	**-22.0050**	**-22.0050**
Depth (m)	**4960**	**5100**	**5100**	**5140**	**5140**	**5230**	**5230**
Source	**7**	**7**	**7**	**7**	**7**	**7**	**7**
Area	**MAP**	**MAP**	**MAP**	**MAP**	**MAP**	**MAP**	**MAP**
Abyssorchomene abyssorum	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	1	0	1	0	1
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	0	1	1	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0
Hirondellea spp.	0	1	0	1	0	0	0
Hirondellea trioculata	0	1	0	1	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	1	1	0	1
Paracallisoma spp.	0	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	0	1	1	1	1	0	1
Paralicella caperesca	0	1	1	0	1	0	1
Paralicella tenuipes	0	1	0	1	1	0	1
Parandania boecki	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0

Table B.18: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 1, Christiansen, 1996. Study areas: MAP, Madeira Abyssal Plain; MAR, Mid-Atlantic Ridge.

ID	**chrst_96_map**	**JC011_98**	**JC011_114**	**JC037_076**	**JC037_083**	**JC048_020**	**JC011_79**	**JC037_052**
Programme/Cruise	**Meteor12**	**JC11**	**JC11**	**JC37**	**JC37**	**JC48**	**JC11**	**JC37**
Date (dd/mm/yy)	**6/1/90**	**8/9/07**	**8/12/07**	**8/31/09**	**9/2/09**	**6/8/10**	**8/5/07**	**8/25/09**
Latitude	**34.0000**	**54.0680**	**54.0385**	**53.9823**	**54.0385**	**54.0658**	**53.9407**	**53.9887**
Longitude	**-20.0000**	**-34.1572**	**-34.1600**	**-34.0490**	**-34.1590**	**-34.1520**	**-36.1927**	**-36.1353**
Depth (m)	**5100**	**2500**	**2453**	**2552**	**2452**	**2505**	**2564**	**2570**
Source	**1**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**MAP**	**MAR**	**MAR**	**MAR**	**MAR**	**MAR**	**MAR**	**MAR**
Abyssorchomene abyssorum	0	1	1	1	1	1	1	1
Abyssorchomene chevreuxi	0	1	1	1	1	1	1	1
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	1	1	0	1	1	1	1
Centromedon sp. 1	0	1	0	0	0	1	0	0
Centromedon sp. 2	0	1	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	1	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	0	1	1	0	1	1	1	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	1	1	0	1	1	1	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	1	0	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	0	0
Paracallisoma spp.	0	1	1	0	1	1	1	1
Paracallisoma abyssi	0	0	1	0	0	0	1	0
Paracallisoma alberti	0	1	1	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	1	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	1	1	0	1	1	1	1
Paracentromedon sp. 1	0	0	0	0	0	0	0	0
Paralicella spp.	1	1	1	0	1	0	1	1
Paralicella caperesca	0	1	1	0	1	0	1	1
Paralicella tenuipes	0	0	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	1	1	0	1	1	0	1
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	1	1	1	0	1	1	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	1	1	0	1	0	0	0
Tryphosella sp. 3	0	0	0	1	0	0	0	0
Tryphosella sp. 4	0	0	0	1	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0

Table B.19: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK. Study areas: MAR, Mid-Atlantic Ridge; MET, Meteor Seamount.

ID	**JC037_060**	**JC048_008**	**JC037_013**	**JC037_018**	**JC037_025**	**JC048_046**	**JC048_032**	**56375_1**
Programme/Cruise	**JC37**	**JC48**	**JC37**	**JC37**	**JC37**	**JC48**	**JC48**	**Meteor_60_5**
Date (dd/mm/yy)	**8/27/09**	**6/2/10**	**8/8/09**	**8/10/09**	**8/17/09**	**6/23/10**	**6/16/10**	**12/4/03**
Latitude	**53.9743**	**53.9887**	**49.0333**	**49.0200**	**49.0372**	**49.0335**	**48.7890**	**33.8150**
Longitude	**-36.1033**	**-36.1345**	**-27.7240**	**-27.7005**	**-27.8943**	**-27.7240**	**-28.6408**	**-14.3657**
Depth (m)	**2340**	**2628**	**2501**	**2500**	**1830**	**2507**	**2448**	**210**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**MAR**	**MAR**	**MAR**	**MAR**	**MAR**	**MAR**	**MAR**	**MET**
Abyssorchomene abyssorum	1	1	1	1	1	1	1	1
Abyssorchomene chevreuxi	1	1	1	1	1	1	1	0
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	1	1	1	1	0	1	1	0
Centromedon sp. 1	1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	1	0
Eurythenes gryllus	1	1	1	1	1	1	1	0
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	1	1	1	1	1	1
Hirondellea trioculata	0	0	0	0	0	0	0	1
Hirondellea wolfendeni	0	0	1	1	1	1	1	0
Hirondellea sp. 1	0	0	0	0	1	0	0	0
Hirondellea sp. 2	0	0	0	0	1	1	1	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	1	0	1	0	1	1	1	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	1	0
Orchomene oxystoma	0	0	1	1	1	1	1	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	1	0	0	0
Orchomene sp. 2	0	0	0	0	0	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	0	0
Paracallisoma spp.	1	1	1	1	0	1	1	0
Paracallisoma abyssi	0	1	0	0	0	0	0	0
Paracallisoma alberti	1	1	1	0	0	1	1	0
Paracallisoma 'kojack'	0	0	0	0	0	0	1	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	1	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	1	0
Paracallisosoma sp. 4	1	1	0	1	0	1	1	0
Paracentromedon sp. 1	0	0	0	0	0	0	0	0
Paralicella spp.	0	1	0	0	0	0	1	0
Paralicella caperesca	0	1	0	0	0	0	1	0
Paralicella tenuipes	0	0	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	1	0	1	1	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	1	0	1	1	1	1	1	0
Tmetonyx sp. 10	0	0	1	0	0	1	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	1	1	1	1	1	0
Tryphosella sp. 3	0	0	0	0	1	1	0	0
Tryphosella sp. 4	0	0	0	0	0	1	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	1	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	1	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0

Table B.20: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK. Study areas: PAP, Porcupine Abyssal Plain.

ID	**12930_55**	**12930_7**	**12930_71**	**12930_83**	**12930_96**	**13077_35**	**13077_4**	**13077_71**
Programme/Cruise	**D222**	**D222**	**D222**	**D222**	**D222**	**D226**	**D226**	**D226**
Date (dd/mm/yy)	**9/11/96**	**9/1/96**	**9/14/96**	**9/18/96**	**9/21/96**	**3/19/97**	**3/14/97**	**3/24/97**
Latitude	**48.7510**	**48.9217**	**48.7738**	**48.9353**	**48.8957**	**48.9683**	**48.9303**	**48.8335**
Longitude	**-16.5550**	**-16.9335**	**-16.4722**	**-16.5922**	**-16.2993**	**-16.4155**	**-16.5875**	**-16.2995**
Depth (m)	**4837**	**4839**	**4836**	**4839**	**4838**	**4845**	**4844**	**4840**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**
Abyssorchomene abyssorum	0	0	0	0	0	1	1	1
Abyssorchomene chevreuxi	0	0	0	0	0	1	1	1
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	1	1	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	0	0	1	1	0	1	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	1	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	1	0	0	1	0
Orchomenella gerulicorbis	0	0	0	0	0	1	1	1
Paracallisoma spp.	0	0	0	0	0	1	1	1
Paracallisoma abyssi	0	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	1	1
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	1	1	0
Paralicella spp.	0	0	1	1	0	1	1	1
Paralicella caperesca	0	0	1	0	0	1	1	1
Paralicella tenuipes	0	0	1	0	0	1	1	1
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	1	1	1
Valettietta lobata	0	1	0	0	0	1	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0

Table B.21: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK. Study areas: PAP, Porcupine Abyssal Plain.

ID	**13077_92**	**13077_99**	**13078_14**	**13078_22**	**13078_3**	**13078_35**	**13200_31**	**13200_42**
Programme/Cruise	**D226**	**D226**	**D226**	**D226**	**D226**	**D226**	**D229**	**D229**
Date (dd/mm/yy)	**3/27/97**	**3/28/97**	**4/1/97**	**4/3/97**	**3/29/97**	**4/6/97**	**7/11/97**	**7/13/97**
Latitude	**48.8250**	**48.8093**	**48.7531**	**48.9083**	**48.7832**	**48.9097**	**48.8132**	**48.9135**
Longitude	**-16.3495**	**-16.3400**	**-16.5847**	**-16.5627**	**-16.3682**	**-16.5793**	**-16.3905**	**-16.5822**
Depth (m)	**4844**	**4846**	**4845**	**4842**	**4842**	**4843**	**4842**	**4844**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**
Abyssorchomene abyssorum	0	0	0	1	0	0	0	0
Abyssorchomene chevreuxi	1	0	0	1	0	0	1	1
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	1	0	1	1	1	0	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	1	0	1	0	1	0	1	1
Orchomenella gerulicorbis	1	0	0	1	0	0	0	0
Paracallisoma spp.	1	0	1	1	1	0	1	1
Paracallisoma abyssi	0	0	0	0	0	0	0	0
Paracallisoma alberti	1	0	1	1	1	0	1	1
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	1	0	0	0	1	0	0	0
Paralicella spp.	1	0	1	1	1	0	1	1
Paralicella caperesca	1	0	1	1	1	0	1	1
Paralicella tenuipes	1	0	1	1	1	0	1	1
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	1	0	0	0	1	0	0	1
Valettietta lobata	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0

Table B.22: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK. Study areas: PAP, Porcupine Abyssal Plain.

Programme/Cruise	**D229**	**D229**	**522**	**522**	**524**	**527**	**527**	**527**
Date (dd/mm/yy)	**7/15/97**	**7/20/97**	**6/23/85**	**6/23/85**	**12/8/86**	**5/15/91**	**5/21/91**	**5/22/91**
Latitude	**48.9113**	**48.7825**	**48.8398**	**48.8337**	**49.1817**	**48.8033**	**48.7850**	**48.7850**
Longitude	**-16.5927**	**-16.5012**	**-16.4918**	**-16.5070**	**-16.2783**	**-16.4150**	**-16.4267**	**-16.4267**
Depth (m)	**4847**	**4845**	**4805**	**4542**	**4849**	**4840**	**4844**	**4844**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**
Abyssorchomene abyssorum	0	0	0	1	1	0	0	0
Abyssorchomene chevreuxi	0	0	0	1	1	0	0	0
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	1	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	1	1	1	0	0
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	1	0	1	0	0	1	0	0
Orchomenella gerulicorbis	0	0	0	1	0	0	0	0
Paracallisoma spp.	0	0	0	1	1	1	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	1	1	1	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	1	0	0	0	0
Paralicella spp.	1	0	1	1	1	1	0	0
Paralicella caperesca	1	0	0	1	1	1	0	0
Paralicella tenuipes	1	0	0	1	1	1	0	0
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	1	1	0	0	0
Valettietta lobata	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0

Table B.23: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK. Study areas: PAP, Porcupine Abyssal Plain; PSB, Porcupine Seabight.

ID	**52701_35**	**53201_18**	**53201_25**	**53201_35**	**53205_4**	**chrst_96_bt**	**50909_**	**51103_1**
Programme/Cruise	**527**	**C111**	**C111**	**532**	**C111**	**Meteor10**	**509**	**511**
Date (dd/mm/yy)	**5/22/91**	**4/12/94**	**4/14/94**	**4/16/94**	**4/20/94**	**7/1/89**	**11/10/80**	**5/21/81**
Latitude	**48.8083**	**48.7900**	**48.8178**	**48.9000**	**48.8542**	**47.0000**	**49.8972**	**51.7533**
Longitude	**-16.3933**	**-16.5698**	**-16.5172**	**-16.3400**	**-16.4403**	**-20.0000**	**-13.9117**	**-13.1317**
Depth (m)	**4843**	**4846**	**4844**	**4844**	**4844**	**4000**	**3905**	**1005**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**1**	**DC**	**DC**
Area	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PAP**	**PSB**	**PSB**
Abyssorchomene abyssorum	1	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	1	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	1	0	1	1	0	0
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	0
Hirondellea trioculata	0	0	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	1	1	0	0	0	1	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0	0
Paralicella spp.	1	1	1	0	1	1	0	0
Paralicella caperesca	1	1	1	0	0	0	0	0
Paralicella tenuipes	1	1	1	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	1	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	1	0	0	0	0	0	0	0

Table B.24: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK. Study areas: PSB, Porcupine Seabight.

ID	**51105_1**	**51110_2**	**52007_2**	**52024_2**	**52025_2**	**52217_2**	**52338_**	**52518_**
Programme/Cruise	**511**	**511**	**520**	**520**	**520**	**522**	**523**	**525**
Date (dd/mm/yy)	**5/22/81**	**5/27/81**	**8/17/84**	**8/23/84**	**8/25/84**	**6/26/85**	**7/28/86**	**6/18/87**
Latitude	**51.0317**	**50.1600**	**50.3785**	**50.3807**	**50.7492**	**50.7492**	**49.3400**	**47.5167**
Longitude	**-13.0767**	**-13.5283**	**-12.6787**	**-12.7193**	**-11.3320**	**-12.9310**	**-13.1000**	**-8.3333**
Depth (m)	**2000**	**2910**	**2445**	**2456**	**940**	**1481**	**1679**	**2008**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**
Abyssorchomene abyssorum	0	0	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	0	0	0	0	0	0
Alicella sp.	0	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0	0
Eurythenes gryllus	0	0	0	0	0	0	1	1
Hippomedon sp. 1	0	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0	0
Hirondellea spp.	0	0	0	0	0	0	0	1
Hirondellea trioculata	0	0	0	0	0	0	0	1
Hirondellea wolfendeni	0	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0	0
Orchomene oxystoma	0	0	0	0	0	0	1	1
Orchomene pectinatus	0	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	0	0	1	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	0	0
Paracallisoma spp.	0	0	0	0	0	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0	0
Paralicella spp.	0	0	0	0	0	0	0	0
Paralicella caperesca	0	0	0	0	0	0	0	0
Paralicella tenuipes	0	0	0	0	0	0	0	0
Parandania boecki	0	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	1	1	0
Tmetonyx norbiensis	0	0	0	0	0	0	0	0
Tmetonyx similis	0	0	0	0	0	0	1	1
Tmetonyx sp. 1	0	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	1	0
Tryphosella sp. 1	0	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	0	0	0	0	0	0

Table B.25: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK. Study areas: PSB, Porcupine Seabight.

ID	**52520_**	**52522_**	**52806_**	**52811_**	**52815_**	**52838_**	**53203_1**
Programme/Cruise	**525**	**525**	**528(challenger94)**	**528(challenger94)**	**528(challenger94)**	**528(challenger94)**	**C111**
Date (dd/mm/yy)	**6/21/87**	**6/22/87**	**8/2/92**	**8/5/92**	**8/6/92**	**8/15/92**	**4/17/94**
Latitude	**47.5167**	**47.5167**	**50.1967**	**50.5533**	**49.7117**	**49.5700**	**49.7233**
Longitude	**-8.3333**	**-8.3333**	**-14.6850**	**-14.3933**	**-13.3500**	**-11.8933**	**-13.2900**
Depth (m)	**2008**	**2013**	**3976**	**1690**	**2000**	**1005**	**2050**
Source	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**	**DC**
Area	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**
Abyssorchomene abyssorum	0	0	1	0	0	0	1
Abyssorchomene chevreuxi	0	0	0	0	0	0	0
Alicella sp.	0	0	1	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	1	0	0	0	0	1
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0
Hirondellea spp.	1	1	0	0	0	0	1
Hirondellea trioculata	1	1	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0
Normanion spp.	0	0	1	0	1	0	0
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0
Orchomene oxystoma	1	1	0	0	0	0	1
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	0	0	0	1	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	0
Paracallisoma spp.	1	0	0	1	0	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	1	0	0	0	0	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	0	0	1	0	0	0	0
Paralicella caperesca	0	0	1	0	0	0	0
Paralicella tenuipes	0	0	1	0	0	0	0
Parandania boecki	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	0	0	0	0	1	1	1
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	1	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0
Tmetonyx similis	1	1	0	1	1	0	1
Tmetonyx sp. 1	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	1	1	0	0	0	0	0
Tryphosella sp. 1	0	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0
Lyss. Gen. nov.	0	0	0	0	0	0	0
Scopelocheirid Gen nov.	0	0	1	0	0	0	0

Table B.26: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 2, Jones et al., 1998; 3, Kemp et al., 2006; 4, Lampitt et al., 1983. Study areas: PSB, Porcupine Seabight.

ID	**53404_1**	**9752_2**	**9756_8**	**kemp_et_al_d2**	**lampitt_1983_ft**	**lampitt_1983_st_btm**	**jones1998_1**
Programme/Cruise	**C113**	**D92**	**D92**	**D260**	**D97**	**C51215**	**C134**
Date (dd/mm/yy)	**7/8/94**	**4/7/79**	**4/13/79**	**8/29/01**	**4/13/78**	**9/27/81**	**8/8/97**
Latitude	**49.7159**	**51.3033**	**49.8933**	**49.9833**	**49.9067**	**49.8783**	**49.9983**
Longitude	**-13.2704**	**-11.7283**	**-13.9117**	**-13.5497**	**-13.9383**	**-14.1383**	**-14.3183**
Depth (m)	**2017**	**1020**	**3852**	**2710**	**3852**	**4009**	**4000**
Source	**DC**	**DC**	**4**	**3**	**4**	**4**	**2**
Area	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**	**PSB**
Abyssorchomene abyssorum	1	0	0	0	0	0	0
Abyssorchomene chevreuxi	0	0	1	0	1	1	1
Alicella sp.	0	0	0	0	0	0	0
Anonyx lilljeborgii	0	0	0	0	0	0	0
Anonyx nugax	0	0	0	0	0	0	0
Anonyx ochoticus	0	0	0	0	0	0	0
Caeconyx caeculus	0	0	0	0	0	0	0
Centromedon productus	0	0	0	0	0	0	0
Centromedon zoe	0	0	0	0	0	0	0
Centromedon sp. 1	0	0	0	0	0	0	0
Centromedon sp. 2	0	0	0	0	0	0	0
Cyclocaris guilemi	0	0	0	0	0	0	0
Cyclocaris sp. 1	0	0	0	0	0	0	0
Cyphocaris bouvieri	0	0	0	0	0	0	0
Eurythenes gryllus	1	0	1	1	1	0	1
Hippomedon sp. 1	0	0	0	0	0	0	0
Hippomedon sp. 2	0	0	0	0	0	0	0
Hirondellea spp.	1	0	0	0	0	0	0
Hirondellea trioculata	1	0	0	0	0	0	0
Hirondellea wolfendeni	0	0	0	0	0	0	0
Hirondellea sp. 1	0	0	0	0	0	0	0
Hirondellea sp. 2	0	0	0	0	0	0	0
Hirondellea sp. 3	0	0	0	0	0	0	0
Normanion spp.	0	0	0	0	0	0	0
Onisimus affinis	0	0	0	0	0	0	0
Onisimus leucopis	0	0	0	0	0	0	0
Onisimus sextonae	0	0	0	0	0	0	0
Orchomene amblyops	0	0	0	0	0	0	0
Orchomene cavimanus	0	0	0	0	0	0	0
Orchomene distincta	0	0	0	0	0	0	0
Orchomene oxystoma	1	0	0	0	0	0	0
Orchomene pectinatus	0	0	0	0	0	0	0
Orchomene sp. 1	0	0	0	0	0	0	0
Orchomene sp. 2	0	1	0	1	0	0	0
Orchomenella gerulicorbis	0	0	0	0	0	0	1
Paracallisoma spp.	0	0	1	0	1	0	0
Paracallisoma abyssi	0	0	0	0	0	0	0
Paracallisoma alberti	0	0	1	0	1	0	0
Paracallisoma 'kojack'	0	0	0	0	0	0	0
Paracallisoma sp. 1	0	0	0	0	0	0	0
Paracallisoma sp. 2	0	0	0	0	0	0	0
Paracallisoma sp. 3	0	0	0	0	0	0	0
Paracallisosoma sp. 4	0	0	0	0	0	0	0
Paracentromedon sp. 1	0	0	0	0	0	0	0
Paralicella spp.	0	0	1	0	1	1	1
Paralicella caperesca	0	0	1	0	1	1	1
Paralicella tenuipes	0	0	1	0	0	1	1
Parandania boecki	0	0	0	0	0	0	0
Scopelocherius hopei	0	0	0	0	0	0	0
Stephonyx biscayensis	1	1	0	0	0	0	0
Tmetonyx albidus	0	0	0	0	0	0	0
Tmetonyx cicada	0	0	0	0	0	0	0
Tmetonyx norbiensis	0	0	0	0	0	0	0
Tmetonyx similis	1	0	0	0	0	0	0
Tmetonyx sp. 1	0	0	0	0	0	0	0
Tmetonyx sp. 2	0	0	0	0	0	0	0
Tmetonyx sp. 3	0	0	0	0	0	0	0
Tmetonyx sp. 4	0	0	0	0	0	0	0
Tmetonyx sp. 5	0	0	0	0	0	0	0
Tmetonyx sp. 6	0	0	0	0	0	0	0
Tmetonyx sp. 7	0	0	0	0	0	0	0
Tmetonyx sp. 8	0	0	0	0	0	0	0
Tmetonyx sp. 9	0	0	0	0	0	0	0
Tmetonyx sp. 10	0	0	0	0	0	0	0
Tryphosella caecoides	0	0	0	0	0	0	0
Tryphosella pusilla	0	0	0	0	0	0	0
Tryphosella sp. 5	0	0	0	0	0	0	0
Tryphosella sp. 1	1	0	0	0	0	0	0
Tryphosella sp. 2	0	0	0	0	0	0	0
Tryphosella sp. 3	0	0	0	0	0	0	0
Tryphosella sp. 4	0	0	0	0	0	0	0
Uristes sp.	0	0	0	0	0	0	0
Valettietta gracilis	0	0	0	0	0	0	0
Valettietta lobata	0	0	0	0	0	0	0
Valettietta sp. 1	0	0	0	0	0	0	0
Valettietta sp. 2	0	0	0	0	0	0	0
Valettiopsis macrodactyla	0	0	0	0	0	0	0

Table B.27: Data used for synthesis analysis. Sources: DC, Discovery Collection, National Oceanography Centre, Southampton, UK; 2, Jones et al., 1998. Study areas: PSB, Porcupine Seabight.

ID	**jones1998_2**	**jones1998_3**	**8978_b**
Programme/Cruise	**C134**	**D222a**	**D77**
Date (dd/mm/yy)	**8/11/97**	**7/30/96**	**8/6/76**
Latitude	**50.0017**	**48.6017**	**31.4933**
Longitude	**-14.3217**	**-16.1667**	**-10.6917**
Depth (m)	**4000**	**4800**	**925**
Source	**2**	**2**	**DC**
Area	**PSB**	**PSB**	**SES**
Abyssorchomene abyssorum	0	1	0
Abyssorchomene chevreuxi	1	0	0
Alicella sp.	0	0	0
Anonyx lilljeborgii	0	0	0
Anonyx nugax	0	0	0
Anonyx ochoticus	0	0	0
Caeconyx caeculus	0	0	0
Centromedon productus	0	0	0
Centromedon zoe	0	0	0
Centromedon sp. 1	0	0	0
Centromedon sp. 2	0	0	0
Cyclocaris guilemi	0	0	0
Cyclocaris sp. 1	0	0	0
Cyphocaris bouvieri	0	0	0
Eurythenes gryllus	1	1	0
Hippomedon sp. 1	0	0	0
Hippomedon sp. 2	0	0	0
Hirondellea spp.	0	0	0
Hirondellea trioculata	0	0	0
Hirondellea wolfendeni	0	0	0
Hirondellea sp. 1	0	0	0
Hirondellea sp. 2	0	0	0
Hirondellea sp. 3	0	0	0
Normanion spp.	0	0	0
Onisimus affinis	0	0	0
Onisimus leucopis	0	0	0
Onisimus sextonae	0	0	0
Orchomene amblyops	0	0	0
Orchomene cavimanus	0	0	0
Orchomene distincta	0	0	0
Orchomene oxystoma	0	0	0
Orchomene pectinatus	0	0	0
Orchomene sp. 1	0	0	0
Orchomene sp. 2	0	0	0
Orchomenella gerulicorbis	1	1	0
Paracallisoma spp.	0	0	0
Paracallisoma abyssi	0	0	0
Paracallisoma alberti	0	0	0
Paracallisoma 'kojack'	0	0	0
Paracallisoma sp. 1	0	0	0
Paracallisoma sp. 2	0	0	0
Paracallisoma sp. 3	0	0	0
Paracallisosoma sp. 4	0	0	0
Paracentromedon sp. 1	0	0	0
Paralicella spp.	1	1	0
Paralicella caperesca	1	0	0
Paralicella tenuipes	1	1	0
Parandania boecki	0	0	0
Scopelocherius hopei	0	0	0
Stephonyx biscayensis	0	0	1
Tmetonyx albidus	0	0	0
Tmetonyx cicada	0	0	1
Tmetonyx norbiensis	0	0	0
Tmetonyx similis	0	0	0
Tmetonyx sp. 1	0	0	0
Tmetonyx sp. 2	0	0	0
Tmetonyx sp. 3	0	0	0
Tmetonyx sp. 4	0	0	0
Tmetonyx sp. 5	0	0	0
Tmetonyx sp. 6	0	0	0
Tmetonyx sp. 7	0	0	0
Tmetonyx sp. 8	0	0	0
Tmetonyx sp. 9	0	0	0
Tmetonyx sp. 10	0	0	0
Tryphosella caecoides	0	0	0
Tryphosella pusilla	0	0	0
Tryphosella sp. 5	0	0	0
Tryphosella sp. 1	0	0	0
Tryphosella sp. 2	0	0	0
Tryphosella sp. 3	0	0	0
Tryphosella sp. 4	0	0	0
Uristes sp.	0	0	0
Valettietta gracilis	0	1	0
Valettietta lobata	0	0	0
Valettietta sp. 1	0	0	0
Valettietta sp. 2	0	0	0
Valettiopsis macrodactyla	0	0	0
Lyss. Gen. nov.	0	0	0
Scopelocheirid Gen nov.	0	0	0

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