Vertical Distribution of Mesozooplankton in Polar Waters: Evidence for Foray Behaviour and its Implications

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Abstract

The biological carbon pump (BCP) helps regulate the Earth’s carbon cycles through exporting carbon from the ocean surface to the interior, where it may be stored for millennia. Zooplankton play an important role within the BCP, transporting carbon to depth-through a combination of their diel and seasonal vertical migrations and the rates at which they respire, produce faecal pellets and die. There remains much uncertainty around the timing and extent of these vertical movements. In this thesis, I examine the contribution that copepods (abundant crustacean zooplankton) make to the BCP, focussing on the Polar Regions, where the BCP is especially intense.

Most commonly, diel vertical migration (DVM) is considered to comprise zooplankters feeding in surface layers during the night and residing in deeper waters during the day, principally to minimise visual predation. My analysis of depth stratified nets showed that Southern Ocean copepods do not always undertake synchronised DVM, but distribute themselves through the water column both day and night, suggesting the existence of a multitude of different migration patterns.

Through deploying a novel motorised upward downward looking net (MUDL), I further revealed that, in populations of copepods such as *Oithona spp.,* both upward and downward migrations take place simultaneously, indicating that individuals make vertical forays regularly over the daily cycle.

Beyond visual predator avoidance, DVM may also be advantageous in slowing metabolic rate and reducing energy expenditure when occupying deeper cooler layers during the non-feeding periods. In Arctic *Metridia longa*, I found that the metabolic response to be sex dependent, with males in the near surface layers having a significantly higher respiration rate than those caught at depth, but females showing no difference between the two strata.

Overall, I illustrate that patterns of vertical migration within copepods are complex and need to be considered in more detail to fully assess their contribution to the BCP.

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Chapter 1: Introduction

1.1 Biological Carbon Pump

The oceans play a vital role in the global climate system, from heat redistribution, weather formation and absorption of atmospheric carbon dioxide (CO_2) (Figure 1.1) (Bigg et al., 2003). Atmospheric CO_2 has increased rapidly from ~227 parts per million (ppm) in 1750 (Joos & Spahni, 2008) to 405 (± 0.1) ppm in 2017 (Dlugokencky & Tans, 2018). Currently CO_2 emissions are dominated by the burning of fossil fuels, however other anthropogenic activities such as deforestation and land-use change activities also play a role (Le Quéré et al., 2018). These anthropogenic emissions add to a natural carbon cycle in which carbon is circulated between the atmosphere, oceans and terrestrial biosphere (Archer et al., 2009; Le Quéré et al., 2018). Once absorbed, some of this carbon remains out of contact from the atmosphere for decadal to millennial timescales (Boyd et al., 2019). The oceanic CO_2 reservoir is thought to be 50 times greater than the atmospheric reservoir (Falkowski et al., 2000) with ~30 % of anthropogenic CO_2 produced since industrial times being absorbed within them (Stocker et al., 2013). Recent assessments estimate that, globally, oceans absorbed 2.4 ± 0.5 petagrams of carbon every year (Pg C yr^{-1}) between 2008 and 2017 (Le Quéré et al., 2018). The absorption and subsequent sequestration (long-term storage of carbon) aids in the regulation of atmospheric CO_2 by reducing the rate of the increase in atmospheric carbon dioxide , playing a major role in climate regulation.

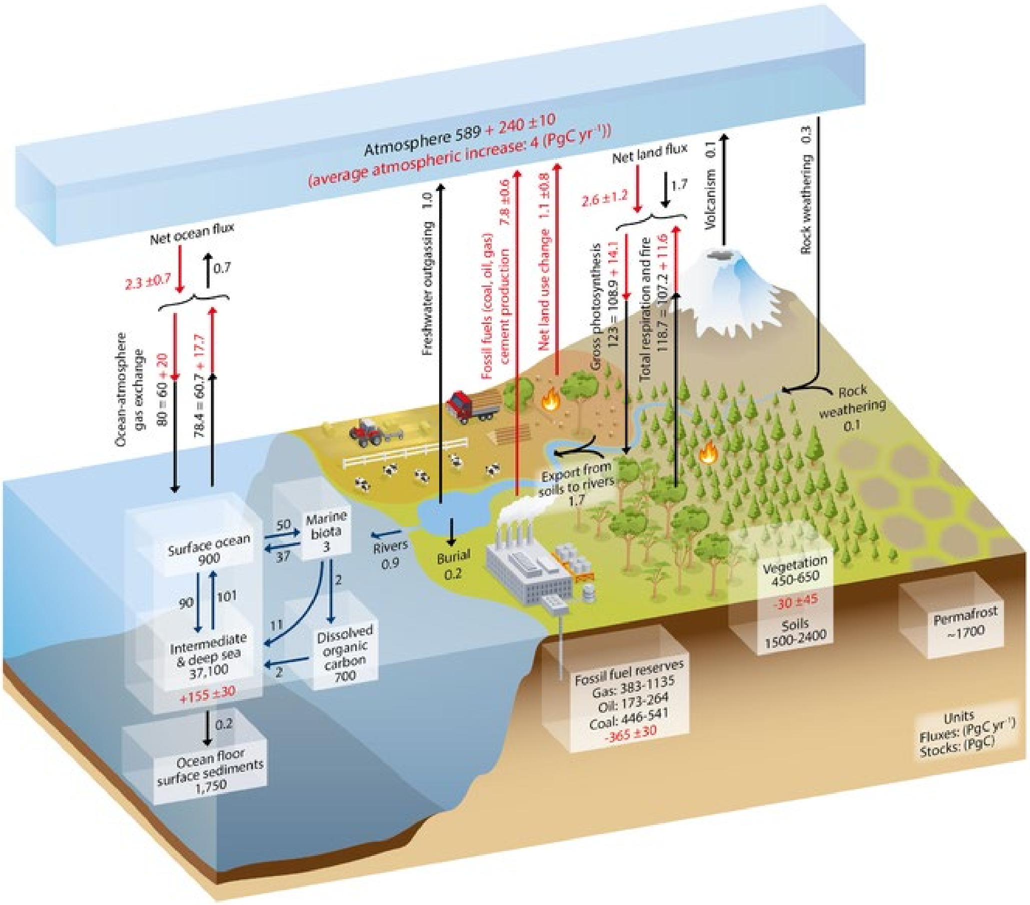


Figure 1. 1: Schematic of global carbon cycles taken from Stocker et al., (2013), showing global carbon reservoirs. Numbers within boxes represent carbon stored within reservoirs in Pg C. Arrows represent fluxes between reservoirs in Pg C yr^{-1}. Black numbers and arrows show natural reservoirs and exchanges during the pre-industrial period and red numbers for reservoirs and fluxes indicate annual anthropogenic perturbations to the global carbon cycle, with the numbers for reservoirs giving total perturbations and the numbers for fluxes giving annual perturbations between 2000 and 2009.

Uptake of CO_2 by the ocean is controlled by a number of processes, which can be grouped into two established mechanisms: the biological carbon pump (BCP) and the solubility pump (Volk & Hoffert, 1985). Within these pumps are a number of processes (Figure 1.2) including the lipid pump, mesopelagic migrant pump (Boyd et al., 2019)(Figure 1.3) and microbial carbon pump (Legendre et al., 2015). Together, these pumps create a gradient within the global ocean, in which dissolved inorganic carbon (DIC) concentrations are greater in the deep water compared to shallow waters (Volk and Hoffert, 1985). Once carbon reaches deep oceanic waters, it remains there for significantly long time periods, helping prevent reabsorption into the atmosphere. The solubility (or solution) pump is driven by physical processes relying on carbon dioxide dissolving into the surface layers of the ocean, delivering cold, dense water rich in DIC to depths (Boyd et al., 2019). Due to the increased solubility of CO_2 at cold temperatures, this pump is strongest at high latitudes and areas of deep-water formation (Boyd et al., 2019; Volk & Hoffert, 1985). The BCP consists of organic carbon pumps and the carbonate counter pump, which are driven, in part, by biological processes and are thought to account for ~90 % of the vertical DIC gradient (Sarmiento and Gruber, 2006). Models have predicted that, without the BCP, atmospheric pCO_2 would be twice as high (Maier-Reimer et al., 1996). The organic carbon pump is the process connecting photosynthetic carbon fixation in surface waters with mid-water biota sustenance and carbon storage in the ocean interior (Boyd et al., 2019; Buesseler et al., 2007). Dissolved CO_2 in surface waters is converted through photosynthesis to organic carbon, which is then exported through a sequence of biological interactions to deeper water (Longhurst and Harrison, 1989; Legendre et al., 2015) (Figure 1.2). Approximately half of all primary production takes place in the ocean (Chisholm, 2000), with ~ 52 Pg C yr^{-1} produced by oceanic phytoplankton (Westberry et al., 2008). It is thought that ~10 Pg C of this is exported to deeper ocean layers each year by the BCP (Buesseler & Boyd, 2009), via processes such as gravitational sinking, and direct particle injection into deeper layers by pelagic organisms (Boyd et al., 2019). The carbonate pump removes carbon from surface layers through bioprecipitation of calcium carbonate ($CaCO_3$) (Manno et al., 2018). However, this pump also counteracts the reduction of pCO_2 as the production of calcium carbonate by calcareous phytoplankton and zooplankton (mainly in the surface layers) releases pCO_2, counteracting the DIC gradient generated by the organic carbon pump (Legendre et al., 2015; Manno et al., 2018; Volk & Hoffert, 1985).

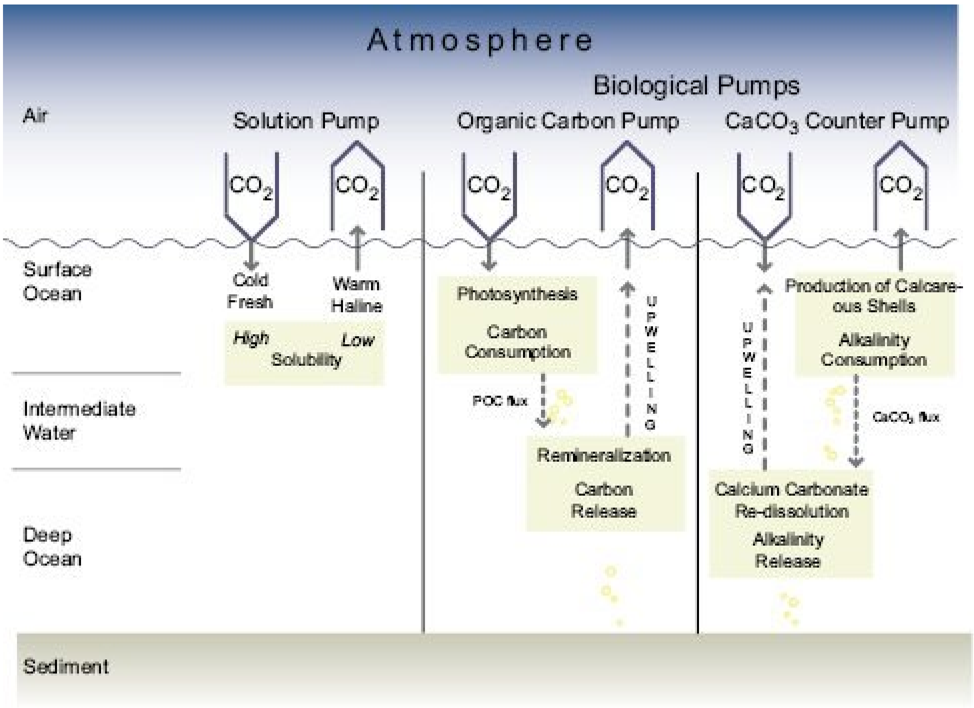


Figure 1. 2: Schematic of the three main ocean carbon pumps governing the regulation of atmospheric CO_2 by the ocean (image from Heinze et al., 1991).

A dominant component of the biological carbon pump is the transport of particles to depth, also referred to as the particle injection pump (PIP) (Boyd et al., 2019) (Figure 1.3). PIP processes all transport particles from the surface layers to greater depths potentially reaching sequestration depths. The biological gravitational pump is the process in which particulate organic carbon (POC) export occurs through gravitational sinking. The POC is often in the form of detritus of both phytoplankton and zooplankton origin.

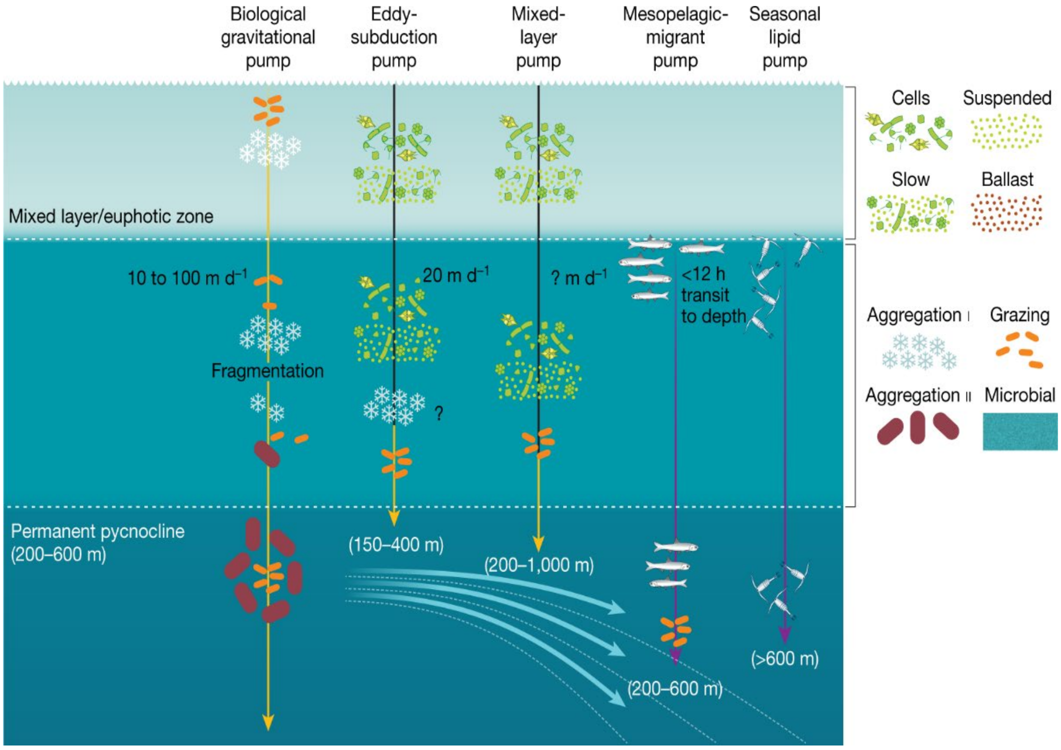


Figure 1. 3: Schematic of particle injection pumps, showing mechanisms in which carbon may be transported through the water column. The box on the upper right indicates particle type. Line colour denotes drawdown mechanism; yellow arrows represent gravitational sinking, black lines show physically mediated transport and purple lines signify biologically mediated transport (active flux) which forms part of the biological carbon pump. Image from Boyd et al., 2019

The eddy subduction pump is the process in which organic particles get trapped within eddies and frontal systems across a variety of spatial scales. These particles are then entrained and have been found to augment the sinking carbon flux (Omand et al., 2015). While this pump contributes to the sinking of particles, it is not likely to be detectable in typical carbon export measurements such as sediment traps, making it difficult to quantify (Stukel et al., 2018). However, this pump may be a significant source of carbon entering the deeper water, with Stukel and Ducklow (2017) estimating that 23 % of the carbon transported by the BCP in the Southern Ocean came from vertical mixing and subduction. In studies combining *in situ* measurements with Lagrangian particle tracking models, Stukel et al., (2018) found that in the California Current ecosystem particle subduction could contribute up to 90 % of the sinking particles. While this pump may contribute to the sinking of carbon, it was also found that subducted particles were often remineralised at depths shallower than 150 m, whereas ~ 50 % of the POC exported through the biological gravitation pump was remineralised below 500m (Stukel et al., 2018), suggesting that subducted particles may not play a large role in carbon sequestration.

The mixed layer pump operates on an annual cycle and requires seasonal stratification of the water column. In this pump, particles and dissolved organic matter accumulate within the mixed layer during the growing season of spring and summer. The mixed layer deepens in winter, such that these particles reach greater depths (Figure 1.4). When stratification takes place during warmer periods, some of these particles are trapped in the interior of the oceans below the warm productive surface layers (Boyd et al., 2019). This pump is thought to be more active in high latitudes due to seasonal variability in the mixed layer depth (Boyd et al., 2019), with the mixed layer pump contributing 23 % of the fast sinking particles in these areas (Dall'Olmo et al., 2016).

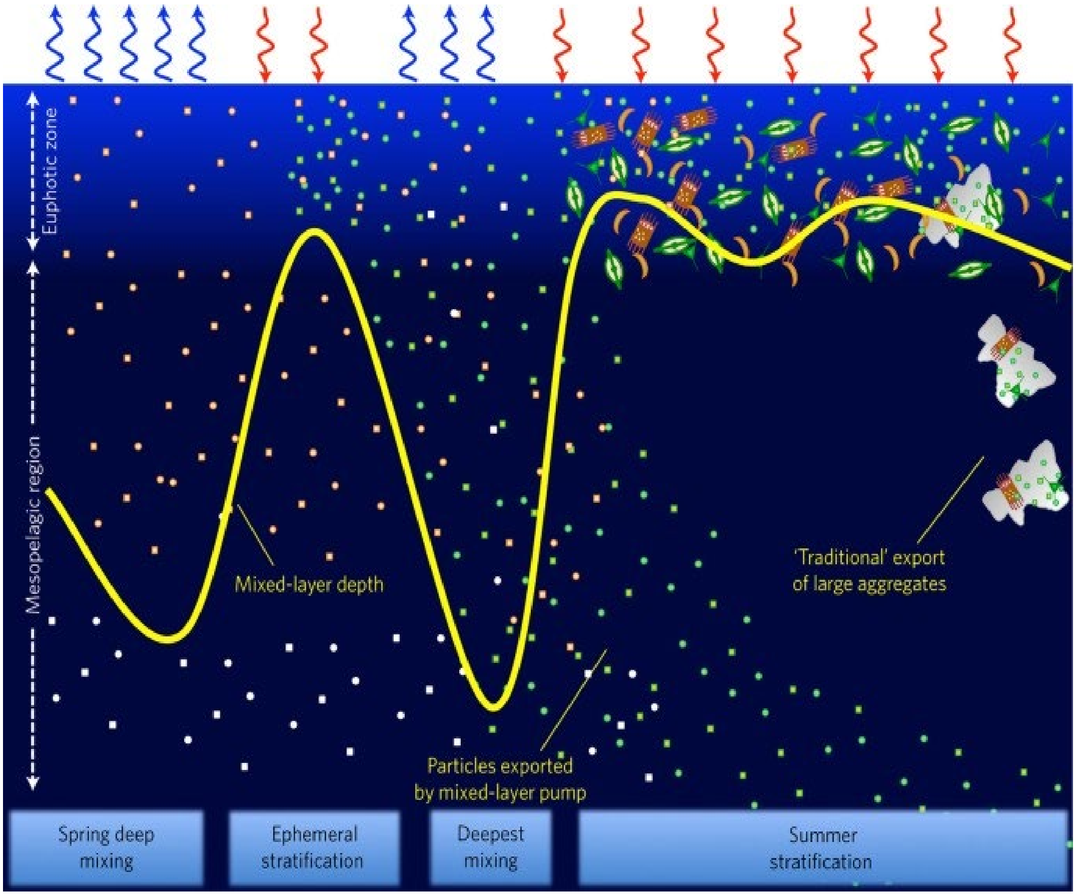


Figure 1. 4 : Conceptual diagram of the mixed layer pump. The yellow line shows the location of the mixed layer throughout an annual cycle, deepening as air temperatures cool and heat is lost from the ocean, as shown by blue arrows, and stratification weakens. At this point, particles are able to reach deeper depths. When air temperatures are warmer and heat enters the ocean, as denoted by red arrows, stratification intensifies and the mixed layer shallows. Any particles that had previously sunk below this depth will remain trapped and be more likely to reach sequestration depths. Image from Dall'Olmo et al., (2016).

Gravitational sinking of organic matter (including dead plankton, aggregates of matter [marine snow], zooplankton faecal pellets and moults of organisms) and physical mixing dominate the BCP. However, the BCP is also driven by the activity of pelagic biota and is therefore influenced by the vertical biomass gradient of this biota as well as their movements within the water column (Figure 1.5). Pelagic biomass decreases by an order of magnitude for every kilometre of depth (Longhurst &Harrison, 1989), meaning organic matter interactions with biota decrease with depth. Buesseler and Boyd, (2009) estimated that the BCP is responsible for exporting over 10 Pg of carbon from surface waters. However, the BCP can be inefficient, as most exported carbon is remineralised before reaching depths of 1000m, the depth at which carbon is considered to be sequestered (Turner, 2015). This remineralisation results in less than 1 % of particulate organic matter produced within the euphotic zone reaching sequestration depths (Libes, 2009; Longhurst et al., 1990). At depth, sequestered carbon is consumed and respired by organisms such as heterotrophic zooplankton and microbes (Legendre et al., 2015). This process converts carbon into DIC at depths greater than 1000 m, where it can remain for long time periods (Legendre et al., 2015). The strength of the BCP is influenced by a number of factors, including seasonality and latitude (Lutz et al., 2007), variations in remineralisation depths (Kwon et al., 2009), zooplankton communities (Legendre & Rivkin, 2002), nutrient availability (Takeda, 1998) and physical processes such as variations in the mixing of water masses (Hauck et al., 2013).

The transport of carbon within the oceans is also facilitated by the microbial loop. Often overlooked, this loop sits beside the BCP and aids in carbon sequestration. It operates in a similar manner to the classic food chain, with primary producers fixing carbon through photosynthesis and subsequent assimilation of these organisms through a number of processes into higher trophic levels within the loop (Figure 1. 5). The role the microbial loop plays in the carbon cycle is highly variant over space and time, but is of particular importance in oligotrophic areas (Fenchel, 2008), where it has greater dominance. This is because it utilises dissolved nutrients and minerals more effectively than larger plankton (Kiørboe, 1993). While the carbon sequestration via the microbial loop is thought to be a fraction of that sequestered through the biological carbon pump, bacteria have been found to account for 50 % of the primary productivity sink (Anderson & Ducklow, 2001) and therefore must be acknowledged when examining processes within the carbon cycle.

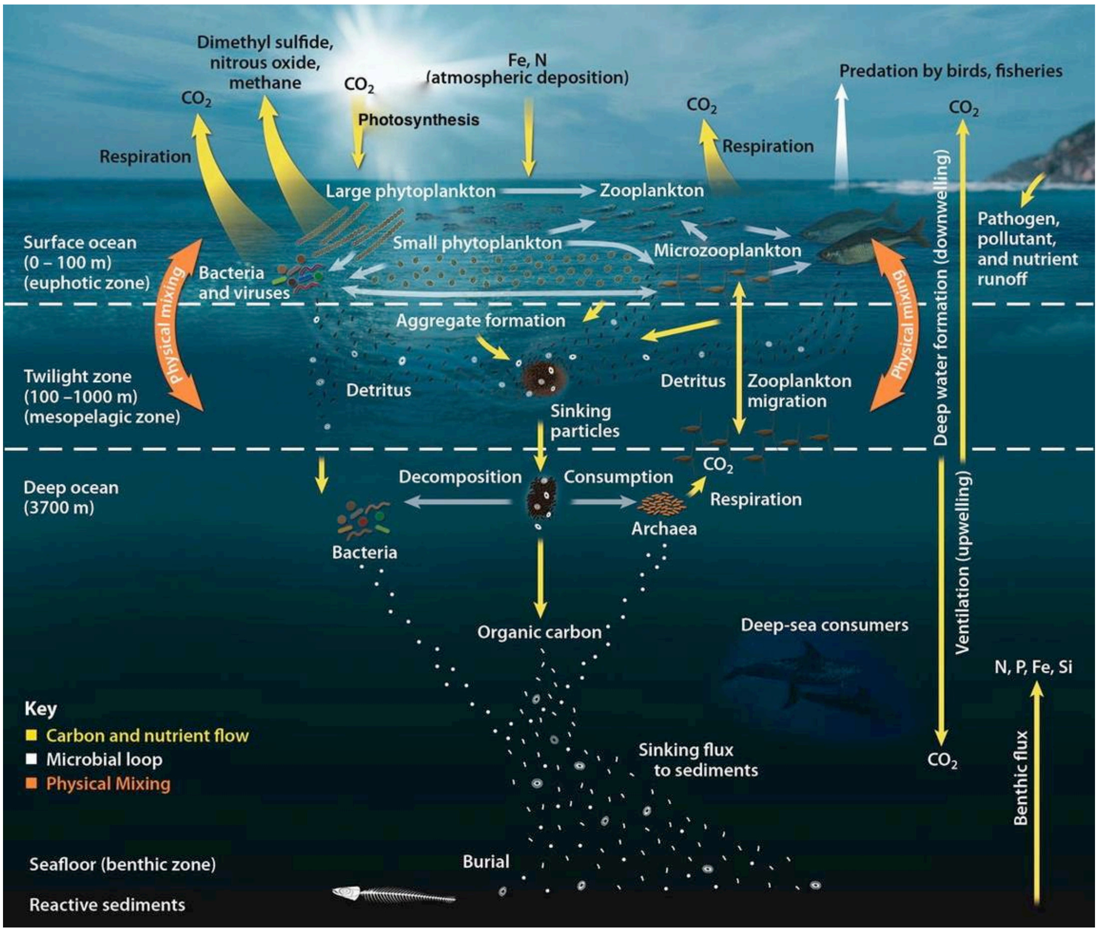


Figure 1. 5: Image showing the carbon cycle within the ocean. Arrows represent the movement of carbon with arrow colour signifying mechanisms. White arrows show the mechanisms and processes taking place within the microbial loop, which contribute to the wider biological carbon pump (Image credit: U.S. DOE, 2008).

1.2 The Role of Zooplankton in Carbon Transportation

Pelagic food webs are vital in the carbon cycle, moving CO_2 from the surface to deeper layers of the oceans, with zooplankton playing a pivotal role in transferring carbon from primary producers to higher trophic levels and in recycling carbon and nutrients into dissolved matter (Steinberg & Landry, 2017). Phytoplankton fix carbon in the upper layers through photosynthesis. The carbon pump then transports POC and dissolved organic carbon (DOC) to depth through passive sinking and deposition, respiration and excretion from vertically migrating animals, also known as the mesopelagic migrant pump (Figure 1.4) (Schnetzer & Steinberg, 2002; Turner, 2002). Zooplankton-mediated processes are some of the principal mechanisms regulating the quantity and cycling of DOC (Hansell & Carlson, 2014). DOC can be released via a number of routes including sloppy feeding (where not all food is taken or ingested), excretion, respiration, egestion and release of faecal pellets. POC can be released from zooplankton in the form of faecal pellets, mucous feeding webs, molts and carcasses (Steinberg & Landry, 2017). Zooplankton faecal pellets are commonly reported as a major component of particulate organic carbon within sediment traps (Riser et al., 2007; 2008). The faecal pellets of zooplankton are thought to make a large contribution to the downward flux of POC (Turner, 2002) with predictions ranging from <1 % to more than 90 % of the total oceanic POC (Wallace et al., 2013). The total contribution that faecal pellets make to the sinking POC flux is often reported as under 40 % (Turner, 2015), however, this may be an underestimate since faecal pellets become degraded in sediment traps causing difficulties in accurately assessing faecal pellet flux. Faecal pellets are made up of partly digested or undigested matter and are able to sink rapidly due to their density being higher than that of water (Wallace et al., 2013). However, a number of factors, including plankton size, distribution, abundance, community composition and the presence of coprophagous zooplankton that feed on faecal pellets, may affect the sinking of these pellets. It is thought that zooplankton size and species composition have a great impact upon the carbon sequestration rate from sinking faecal pellets due to differences in pellet size and density. Faecal pellets from copepods and euphausiids are thought to sink at rates of tens to hundreds of metres a day (e.g. Yoon et al., 2001) while those produced from salps can sink over 1000 metres per day (Phillips et al., 2009). Many other factors can also affect the carbon flux from faecal pellets, with most pellets undergoing degradation as they sink. A number of processes including bacterial degradation (Tang, 2005; Thor et al., 2003), fragmentation (Poulsen & Kiørboe, 2005), ingestion and repackaging by mesopelagic consumers (Steinberg et al., 2008; Wilson et al., 2008) can cause this. Physical features also cause pellet degradation including water density discontinuities causing pellets to remain within certain layers (Alldredge et al., 1987) and eddies causing degradation or retention of pellets (Goldthwait & Steinberg, 2008; Shatova et al., 2012).

1.2.1 The Biological Carbon Pump and Vertical Migrations

Vertical migrations carried out by zooplankton are also an important component of the Biological Carbon Pump (BCP). Termed the mesopelagic migrator pump (Figure 1.3), zooplankton transport carbon through their vertical movements within the water column. This pump has been widely acknowledged for some time with Banse (1964) concluding that: “the flux of material by vertical migrators was of greater importance to deep-sea organisms than sinking material or heterotrophic production from dissolved organic matter”. In support of this, a number of studies focussing on benthic biomass have reported that the estimates of the carbon these areas were receiving from passive sinking alone would not support the levels of biomass observed (Christiansen et al., 2001; Tseitlin, 1999; Wiebe et al., 1976). Furthermore, Fellows et al., (1981) and Karl & Knauer (1984) mentioned that there was an unexplained increase in carbon in the waters below the euphotic zone for which zooplankton migration was thought to be responsible. Zooplankton transport ingested carbon from the surface layers to their daytime residence depths below the euphotic zone where it is released through respiration, excretion and egestion (Steinberg & Landry, 2017). This flux has been coined active flux in order to distinguish these processes from the passive sinking of matter that also contribute to the BCP.

The release of faecal pellets through vertical migrations at depth increases the chance of the carbon being transported to deeper layers and eventually becoming sequestered. However, for this to be the case, a number of conditions must be met. Firstly, the organism’s migration needs to be faster than the natural sinking rates of faecal pellets. Secondly, gut retention times have to be longer than the time taken to migrate to depth. Finally, migrations need to reach relatively deep and faecal pellets must be relatively large and dense (Pearre, 2003). This pattern tends to be seen in pelagic organisms such as calanoid copepods and euphausiids (Pearre, 2003). To date, the majority of studies aiming to assess the extent to which active flux plays a role in carbon sequestration have used gut passage times (GPT). These studies aim calculate how long after feeding will faecal pellets be produced. Once this time has been established, an estimate of where the plankton are likely to be in their migration is made. A number of studies have reported that many plankton species with strong migration patterns have a long enough GPT time to allow active flux to occur (Schnetzer & Steinberg, 2002; Smith & Lane, 1988). Atkinson et al., (1996) showed that gut evacuation rates (a proxy for the rate at which food is digested) were negatively correlated with migration distances, meaning that transport of carbon is likely to increase if the organisms have a greater migration. However, this assumption relies on plankton undertaking downward migration immediately after feeding.

Active transport of carbon by zooplankton can also take place over longer time periods. A number of zooplankton species overwinter in a dormant state known as diapause, with this behaviour being particularly common in large copepods inhabiting high latitudes. Whilst in this state they reside in deeper layers between 600 m and 1400 m (Jónasdóttir et al., 2015), where they catabolize carbon rich lipids that were accumulated over summer and, in doing so, transport carbon below the pycnocline. This process is known as the lipid–pump (Figure 1.3) (Boyd et al., 2019). The strength of this pump is currently unknown due to the difficulties in sampling high latitude areas throughout winter where the lipid pump will be strongest. However, Jónasdóttir et al., (2015) showed that, in the North Atlantic, seasonal migration of *Calanus finmarchicus* resulted in 1-4 g C m^{-2} yr^{-1} being exported, which is thought to be equivalent to the volume of sinking POC at depths of 600-1400 m. Within the Arctic Ocean, large *Calanus* spp. are thought to transport 31 g C m^{-2} yr^{-1} below 100 m, the equivalent of 85-132 % of sinking POC at this depth as a result of respiration of their large lipid sacs throughout winter (Darnis & Fortier, 2012).

1.2.2 Respiratory Flux

Another way in which zooplankton may contribute to the BCP through the interaction between vertical migration (VM) and respiration. Approximately 50 % of absorbed carbon is thought to be lost through respiration in mesozooplankton (Steinberg & Landry, 2017). Through respiring at depth, zooplankton release carbon below the mixed layer. Global mesozooplankton respiration is estimated to account for 17-32 % of global primary productivity (Steinberg & Landry, 2017). In an early study looking into respiratory flux, Longhurst et al., (1990) used respiration measurements obtained from incubation experiments combined with measures of migrant biomass across seven stations in the Atlantic Ocean to compute how much carbon may be transported through migrant respiration. These measures were then used to parameterise a conservative model which predicted that respiratory carbon flux at the sampled stations ranged from 20 to 430 mg C m^{-2} d^{-1}, equating to 13-58 % of total particulate sinking matter. From these values it was estimated that respiratory flux of diel migrants could enhance the carbon flux by up to 20 % between 50˚N and 50˚S (Longhurst et al., 1990).

Steinberg et al., (2000) suggest that respiratory flux by migrating zooplankton may provide a vital source of carbon when mixing does not occur in the water column due to stratification. When measuring respiration and excretion rates of migrating zooplankton within the North Atlantic, it was found that respiratory carbon equated to 10 %, on average, of body carbon content each day. Further to this, these authors report that migratory CO_2 flux was three times higher than the DOC flux, indicating that in this case respiration was a greater source of carbon than egestion. When combining respiratory flux with DOC, these active transport mechanism accounted for 71.4 % of the mean sinking POC at 300 m and supplied 37 % of the organic mineralised carbon found between 300 and 600 m (Steinberg et al., 2000). Ariza et al., (2015) followed a similar approach to assess the contribution of respiratory carbon to the subtropical Atlantic Ocean. In that study respiration was measured in zooplankton caught within the upper 200m of the water column and sinking particles were collected from 150 m. It was found that, at this depth, respiratory carbon accounted for 53 % of the total carbon flux (Ariza et al., 2015). While the estimates of the contribution respiratory flux make to the BCP vary, it is apparent that this often overlooked aspect of zooplankton behaviour may make a significant contribution to the BCP.

1.3 Vertical Migrations in Zooplankton

Diel vertical migration (DVM) is a well-known phenomenon, encompassing a range of animals, taking place in all aquatic environments (Ringelberg, 1995) with the first written accounts dating back to the early 19th century (Bayly, 1986; Pearre, 2003). By the middle of the 20th century, DVM was a well-accepted phenomenon, with Hutchinson (1967) stating "No serious modern worker doubts the reality of diurnal migration". These early references were referring to 'normal' or 'traditional' DVM, which is currently thought to be the most common daily migration pattern. In traditional DVM, there is an upward migration at dusk to feed in surface waters and a downward migration at dawn to spend the day in deeper waters. Cushing (1951) and Hardy (1953) put forward a criterion that DVM could only be inferred from stratified samples where the deep daytime mode disappeared and a shallow night time mode appeared. While this may be the most commonly reported form of DVM, it is not the only one. A number of examples of reverse migrations have been recorded (Pearre, 2003). These range from female *Psuedocalanus sp*. in Dabob Bay (Ohman et al., 1983) to basking sharks in the English Channel and Clyde Sea (Sims et al., 2005). Alongside a variety of vertical migration (VM) patterns (Hays et al., 2001), the amplitude and timings of migrations appear to vary with species, life stage, location and season (e.g. Pearre, 1973, 2003; Sims et al., 2005). A number of studies (e.g. Lampert, 1989; Sims et al., 2005) have aimed to establish the reasons behind this phenomenon but the full range of causes are far from fully understood (Bormans et al., 1999; Huntley, 1985). Ultimately, both physical and biological factors influence this behaviour to various extents (Lagergren et al., 2008).

Cushing (1951) hypothesised a five-phase pattern of "normal" DVM. This pattern comprises of: (1) The ascent towards the surface at dusk; (2) a sinking behaviour at, or just before midnight (termed 'midnight sinking'); (3) a 'dawn rise' where the zooplankton rise to shallow waters again just before dawn; (4) descent back to deeper layers when light begins to penetrate the water and (5) a resting position at variable depths for the day. It was noted that not all of these phases were present in all species, e.g. midnight sinking or the dawn rise may be absent. However, Cushing (1951) proposed that all zooplankton would follow a variant of this DVM pattern. Midnight sinking had been proposed a few decades earlier when Michael (1911) proposed the idea that chaetognaths follow their daytime isolumes when undertaking their migrations, but upon nearing the surface during times of low light they would become disorientated and spread out within the water column. This theory was applied to other plankton by Russell, (1927). At this time, the mechanisms behind the behaviour were unknown. Cushing (1951) proposed that midnight sinking was due to a slowing in swimming in response to the darkness. However, many studies have reported that zooplankton will continue to swim upwards in darkness and will reach their minimum depths just before dawn (Clarke, 1933; Worthington, 1931), disputing the theory that darkness causes midnight sinking. An alternative theory was proposed by Pearre (1970, 1973, 1979), who considered that midnight sinking may be a result of early feeders returning to deep water once they had reached satiation and that dawn risers were either late migrators or early feeders that had sufficiently digested their dusk feed enough to begin feeding again. This theory of plankton feeding then descending to deeper layers once satiated is now known as the saturation hypothesis or satiation sinking. In support of this theory, Pearre (1979) argued that if midnight sinking was a result of low light, migrations would be synchronous as all migrators would experience the same light levels at the same time, providing they were at similar points in the water column, whereas, if sinking was caused by satiation, the migrations would be asynchronous. Pearre (1979) further argued that asynchronous migrations would result in a bimodal vertical distribution as has often been observed.

Since Pearre (1979), a number of studies have considered the asynchronicity found within VMs (e.g. Cottier et al., 2006; Morozov et al., 2011; Pierson et al., 2009). Cottier et al., (2006) found that once DVM had been taken into account shorter migrations, termed forays, were taking place throughout the day and night, leading to asynchronous patterns within plankton layers. Modelling studies have also taken this into consideration and there are now a few studies considering a foray type behaviour (e.g. Morozov et al., 2011, Wallace et al., 2013). These models examine this behaviour over shorter timescales than the DVM cycle and simulations suggest that differential feeding behaviour within populations (i.e. some individuals feeding whilst others digest), lead to unsynchronised forays. Field studies are now attempting to investigate this foray behaviour (e.g. Morozov et al., 2011; Pierson et al., 2009). Pierson et al., (2009) described the development and deployment of a specialised zooplankton trap (see section 1.7.2) that successfully captured zooplankton migrating upwards and downwards simultaneously. These novel nets allowed foray behaviour and asynchrony to be resolved within the *Metridia* copepod population of Dabob Bay, East Pacific coast.

1.4 Why Do Plankton Undertake Vertical Migrations?

DVM is generally thought to be coordinated by a number of proximal cues, with the most recognised being light (Andersen & Nival, 1991). Zusser, (1958) stated that light was a true signal due to the observations that all species migrate upwards in a short time period. Many have proposed that light intensity is the signal required to initiate migrations (e.g. Frank & Widder, 1975; Michael, 1911; Onsrud & Kaartvedt, 1998; Pearre, 1973; Russell, 1927; Swift & Forward Jr, 1988; Young & Watt, 1993), while others argue that it is the rate of change in light intensity that signals the start of the migration (e.g. Clarke, 1930; Dice, 1914; Haney et al., 1990; Kikuchi, 1930; Moore, 1909, 1950; Ringelberg, 1694, 1999; Stearns & Forward, 1984). The disparity in the supposed role that light plays in vertical migration (VM) reflects the fact that there are a several competing hypotheses about what coordinates and drives VM behaviour, which I will explore further below.

1.4.1 Predator-Evasion

The predator-evasion hypothesis is the most commonly cited driver for DVM (Hays, 2003). After reviewing various VM hypotheses, Lampert (1993) came to the conclusion that predator avoidance was the most reasonable explanation. The premise for this hypothesis is that plankton are prey for a variety of visual predators. Therefore, these organisms feed in the surface layers at night, when light levels are low, in order to minimise the risk of predation. There is a wealth of evidence to support this theory (Zaret & Suffern, 1976). One particularly illustrative example is that provided by Gliwicz (1986) who examined the migration patterns of the copepods, *Cyclops* within the lakes of the Tatra Mountains. These lakes provide a suitable and relatively unique study site due to their impenetrable drainage streams and lack of waterways between them, preventing any transfer of fish. The majority of the lakes in this area are naturally free of fish, however, a number of lakes were stocked with Char towards the end of the 19th century and a few other lakes have been stocked more recently (Gliwicz, 1986). Since the lakes were stocked, plankton that were unable to develop a migratory pattern have gone extinct (Gliwicz, 1986). Gliwicz (1986) used net samples to determine the presence of DVM in *Cyclops* in lakes with no fish, lakes stocked in the 19th century and lakes stocked more recently. Across all lakes, the mean depth of *Cyclops* was higher at midnight than noon. However, this pattern was only significant in lakes containing fish, which supports the predator avoidance hypothesis. Furthermore, the greatest DVM signal was found in lakes in which fish had been present the longest. Tarling et al., (2002) also found migrations that could be linked to predator presence. These authors found that the copepod *C. finmarchicus* migrated downwards when krill migrated into the surface layers, potentially providing evidence of downward migration driven by predator avoidance.

Nevertheless, this hypothesis does not explain why DVM should take place in communities dominated by chemical- or vibration-sensing predators (such as chaetognaths and chaoboridae larvae), where prevailing light levels should be less important to predation risk (Pearre, 2003). Pearre (1970, 1973) found that most of the chaetognath, *Sagitta elegans* population undertook DVM but continued to feed throughout the day, suggesting that DVM would not be a predator avoidance strategy for their prey. However, those that did remain in the surface layers ceased feeding, suggesting that prey remaining in surface layers would be less likely to be predated on and therefore DVM may be not be predator avoidance strategy for these prey. However, it was proposed that this cessation of feeding by *S. elegans* may be a strategy in which they avoid being prey for higher predators. *S. elegans* are transparent and feeding may make them more visible to predators through prey being visible within them. Transparent copepods have also been studied (e.g. Atkinson et al., 1992; Dagg et al., 1989) and similar conclusions reached. Pearre (2003) proposed that being transparent and less active may be adaptations to decrease visual predation, which may provide an alternative strategy to VM.

1.4.2 Light-Avoidance

Light-avoidance may be another driver of DVM. Light may be harmful to zooplankton, particularly short wave UV light (Williamson et al., 2011) which can damage cell membranes, DNA, and a number of other biochemicals, in turn leading to high mortality rates (Williamson et al., 1999). UV radiance is at its highest near the surface during the daytime. A small number of field experiments have been carried out to investigate whether UV is driving VM behaviour. Leech et al., (2005) looked into the depth distributions of plankton as a result of UV levels in three lakes. They found that species with a low UV tolerance, such as *Daphnia*, had a greater response to UV with their daytime depths being greatest in lakes with highest UV. However, this theory is not without its critics. UV light is absorbed in the upper parts of the water column, with only 10 % of the surface UV being detected at 25 m below the surface in clear marine waters (Fleischmann, 1989). Therefore, UV sensitive plankton would only need to migrate to depths of between 50 and 100 m rather than the deeper depths they are found at during the daytime. Another criticism is that areas of high UV are likely to have high transparency and chlorophyll production will be able to occur at greater depths, meaning that migrations do not need to be to the shallow depths that may be required in other places. Assuming migration lengths are consistent, this is likely to lead to the plankton inhabiting deeper waters during the daytime. No evidence of deeper daytime residence in plankton in areas of high UV has been reported thus far.

1.4.3 Density and Buoyancy

One of the earliest hypothesised drivers of DVM was that the density and buoyancy of plankton changed over the diel cycle. When investigating the DVM pattern of *Daphnia pulex,* Eyden (1923) found that, after feeding, *Daphnia* had an increased density. It was proposed that this density increase played a role in the dawn descent. This hypothesis was tested in other *Daphnia* species by Dodson et al., (1997), who reported that higher sinking rates were found in *Daphnia* in high-food environments compared to low-food environments. Hence, feeding during the night increases density and leads to descending at dawn. This phenomenon of increased density after feeding has also been reported in the ostracod, *Cyprdina sinuosa* (Arashkevich, 1977) and the copepod, *Calanus plumchrus* (Yayanos et al., 1978), showing that this may be a widespread phenomenon. It has been argued by a number of authors that these density changes may be beneficial to migrating organisms, as by using the gut contents to increase density, the energy required to migrate downwards is reduced and an increased buoyancy when the stomach is empty reduces the energy requirements of migrating upwards (e.g. Angel, 1985; Yayanos et al., 1978). Krause & Radach (1989) took this argument further and proposed that some plankton, *C. finmarchicus* in particular, fed on dense particles throughout the night, in order to decrease their buoyancy, and produced wax esters during the day to increase buoyancy, driving DVM. Cervetto et al., (1995) also thought that this mechanism may be present in *Acartia tonsa*.

1.4.4 Starvation Hypothesis

McLaren (1963) suggested that DVM may conserve energy through feeding in warm food-rich waters during the night and sinking to cooler waters during the day. In a further work, McLaren (1974) added that copepods growing at lower temperatures will reach larger sizes and, therefore, would have a greater fecundity. However, as was noted by Kerfoot (1985), increased fecundity will not compensate for a slower rate of growth due to the cooler temperatures. Many attempts have been made to provide evidence for this hypothesis; however, these have been unsuccessful to date (Lampert, 1993). A modified version of this idea is the starvation avoidance hypothesis. Geller (1986) proposed that plankton may stay in an area of high food availability if the food source is abundant, however, when the food supply is less predictable, plankton will migrate to cooler waters to minimise energy losses. While residing in cooler, deeper waters, forays would have to be made to avoid starvation, leading to DVM behaviour. This pattern of behaviour was observed in *Daphnia* in Lake Constance (Geller, 1986), but has yet to be found in any marine environment.

1.4.5 Hunger/Satiation Hypothesis

Consideration of the hunger/satiation hypothesis was rejuvenated by the review of Pearre (2003). The hypothesis is that organisms are driven to surface waters by hunger and once satiated will migrate downwards in order to digest their food. Pearre (2003) argues that if enough sampling is carried out then it may be possible to find individuals containing food from surface layers deep within the water column before any light signal could have triggered a downwards movement. This is then interpreted as the downward movement being triggered by feeding and satiation.

Gauld (1953) thought that *Calanus finmarchicus* were adhering to this theory due to the presence of green-pigmented guts in copepods caught from deep within the water column during the day. He proposed that this indicated that the copepods had fed in the near surface waters recently. However, he was not able to detect any migration from stratified net sampling, leading to the suggestion that the copepods were migrating to the food-rich layers at all times, driven by hunger. Harris, (1998) found that *Calanus helgolandicus* in the English Channel migrated upwards through the chlorophyll maximum on their evening ascent, before dropping below after midnight and then returned to the surface for a period before beginning their dawn descent. Gut chlorophyll levels increased in the shallow waters during the evening and before dawn with a decrease in between. In the deeper water, gut chlorophyll levels did not increase until after midnight, corresponding with the first descent. This pattern of midnight sinking was not triggered by light, suggesting that hunger and satiation are the main triggers.

Other authors have linked VM patterns to hunger; near South Georgia, Atkinson et al., (1992a) found gut pigments in deep residing copepods to increase throughout the night , concluding that individuals sank to this layer from feeding at the surface. These authors also found that the maximum phaeopigment concentration per copepod was found to be beneath the layer in which copepods were at their highest population density. Both observations implied that individuals sank once satiated. Zagorodnyaya (1975) found that the *Pseudocalanus elongates* in the deepest layer sampled contained food at 02:00 and 03:00 h. The layer sampled was too deep for grazing to be occurring, therefore the copepods must have fed in shallow waters prior to sinking to this depth before dawn, suggesting that light did not trigger descent. Lopez and Huntley (1995) found that the gut pigment levels of *Metridia gerlachei* were highest in individuals found in shallower waters despite deeper layers having greater densities of *M. gerlachei*. This was interpreted as the copepods making forays into the surface waters to feed and returning as soon as possible. Mackas and Bohrer (1976), Nicolajsen et al., (1983)and Tang et al., (1994) all used gut pigments to trace copepod feeding and VM and found evidence of downwards movement after feeding.

Angel (1986) put forward the idea that, if hunger and satiation were drivers of VM, then food quality and availability would influence VM behaviour. A variation of this had already been investigated by Hardy and Gunther (1935), who found that the amount of time copepods spent in the food-rich surface layers was inversely proportional to food abundance. It was suggested that this was due to copepods leaving the surface layers once satiated, and satiation was reached sooner in areas of greater food abundance. Wilson and Roff (1973) reported that the mean day depth of migrating crustaceans was correlated with chlorophyll abundance rather than light. Pearre (2003) makes a compelling case citing many studies to show that food abundance does appear to influence migrations. These studies include experimentally manipulated mesocosm studies that show that, when food abundance was reduced, mean depths also decreased (Skjoldal et al., 1983), along with observational studies from various locations supporting this theory (e.g. Atkinson et al., 1992; Dagg, 1985; Daro, 1985; Durbin et al., 1995; Kouassi et al., 2001; Runge & Ingram, 1991).

Adopting a hunger satiation VM behaviour does also present some difficulties. Hardy and Gunther (1935) and Isaacs et al., (1974) point out that, by sinking when satiated, plankton are reducing their time in food abundant regions and move into deeper strata with prevailing currents that may advect them away from these productive environments. Dagg (1985) also mentions that, if phytoplankton is poor in quality or quantity, hunger will drive zooplankters to migrate to, and stay in, areas where predation may be high, leading to a higher level of zooplankton depletions than would be expected.

1.4.6 Resource Related Hypothesis

The resource related hypothesis states that plankton will migrate vertically just before dusk to feed on phytoplankton due to the quality of phytoplankton being higher at this time. Photosynthesis can only occur during the daytime, with losses to phytoplankton biomass occurring at night through grazing and other physiological processes such as respiration. Phytoplankton biomass and quality are therefore highest at dusk when the switch from photosynthesis to respiration has not yet happened. This hypothesis also assumes that migrating plankton will feed at an elevated rate at dusk due to day-time starvation. If plankton are able to gain from elevated feeding on high-quality phytoplankton, then it may be energetically advantageous to migrate to depth during the day to minimise losses from respiration as migrating will require less energy than respiring at warmer temperatures. This hypothesis predicts that zooplankton reach the surface and begin feeding before darkness. To date, few have investigated this hypothesis. Enright & Honegger (1977) sampled marine copepods and found that they migrated to surface waters before dusk in one of the three series sampled, thereby concluding that other factors must also be at play.

More recently, gut fluorescent techniques have shown that copepods that migrate early do not start feeding until after dusk, refuting this hypothesis (Dagg et al., 1989).

1.4.7 Habitat Choice hypothesis

The habitat choice hypothesis states that prey organisms should choose to occupy a place that maximises their food intake while minimising their risk of predation, taking into account the various hunting strategies that are found within marine organisms (Fossheim & Primicerio, 2008). It predicts that herbivores should be found in surface layers due to this being the area where foraging effort can be optimised (Lima, 2002), while higher trophic level predators should be in areas of optimal foraging for their prey (Sih, 1998). However, if patches with low food abundance offer refuge from predators, then a disproportionate number of prey are likely to be found in these areas, while prey in areas of high food abundance is decreased (Fossheim & Primicerio, 2008). Organisms usually display differing vulnerabilities to predation and are therefore expected to have different habitat choices, with resistant prey occupying areas of greater food abundance (Fossheim & Primicerio, 2008). Following this, vulnerable prey species are expected to occupy the deeper parts of the water column where food availability is relatively low, leading to partitioning of species throughout the water column (Fossheim & Primicerio, 2008; Primicerio, 2005). Fossheim and Primicerio (2008) investigated this theory in waters off the coast of North Norway. For this study, it was assumed that body size would affect vulnerability to predators and food requirements (Woodward et al., 2005). The authors found that small prey were found at greater depths, suggesting that their increased vulnerability to predators and lower food requirements did influence their habitat choice. Analysis of net samples also showed that the predators of small zooplankton were in areas that had a prey abundance suitable for the small zooplankters, consistent with this hypothesis.

1.4.8 Dispersal

Vertical migration may be a way of dispersing and moving to other areas. Firstly, phytoplankton is not uniform but has a patchy distribution in the surface layers (Leising, 2001), therefore zooplankton may wish to move to new feeding grounds. Secondly, dispersal may be desirable for reproduction and colonisation. Hardy, (1953) put forward the idea that migrating organisms can be transported greater distances than those that do not migrate vertically. Migrating zooplankton may be able to take advantage of the currents found at different strata within the water column for transport to another area. This may be of particular importance in places with strong upwelling or estuaries where there is a strong vertical stratification (Pierson et al., 2009). In these areas, the vertical distribution of the plankton will affect their horizontal transport (Pierson et al., 2009), potentially allowing them to move to more favourable areas.

1.4.9 Growth Strategy

Vertical migration is thought to occur partly as a result of the need to feed. However, a number of authors have suggested that this may not be the case. Neverman and Wurtsbaugh (1994) reported that juvenile *Cottus extensus* migrated but adults did not, despite both age-groups feeding benthically. This suggests that the juveniles were not migrating to feed but for some other purpose. Clarke (1978) also suggests that fish off the coast of Hawaii appeared to migrate to surface waters at night but fed at depth during the day. Both these studies propose that this migration may be to increase the speed of metabolism in warmer waters, in turn increasing growth rates. Williamson et al., (1996) looked at 3 herbivorous invertebrates in a freshwater lake and found that there was no single depth at which the invertebrates gathered despite the chlorophyll maximum being at 5 m. This distribution through the water column, including at depths shallower that 5 m, was thought to indicate that the invertebrates were not migrating to feed but possibly to increase thermal stimulation of reproduction. The idea that VM is driven by something other than feeding is not widely accepted as many migrators occupy depths well below their food source within the daytime. Therefore, these organisms must migrate to feed. The counter-arguments for this hypothesis are as follows: (1) Phytoplankton have patchy distributions and are often in microlayers (Leising, 2001); (2) it is not possible to know how long an individual has spent at any one depth and it is possible that they were moving to another area when caught (Sameoto, 1984); (3) many marine zooplankton are now thought to graze at depths above the chlorophyll maximum, preferring to be at the depth at which the potential for chlorophyll production is greatest (Harris, 1988; Longhurst & Harrison, 1989; Roman et al., 1986).

1.5 Unsynchronised vertical migration

Traditionally VM is thought to follow a diel cycle with the population moving upwards *en masse* at dusk and downwards at dawn. However, as has already been highlighted above, this may not always be the case. It is likely that a varying proportion of individuals within populations are carrying out VMs at different times, leading to unsynchronised migrations. The hunger/satiation and midnight sinking hypotheses suggest that zooplankton are not feeding continuously throughout the night, but make shorter foraging trips, or forays, into the phytoplankton rich layers (Leising et al., 2005). Foray behaviour is thought to confer an advantage as it allows the time spent in the upper layers to be spent feeding, while digestion occurs in deeper layers where mortality arising from predation will be lower (Leising et al., 2005). Detecting foray behaviour is, however, difficult due to the limitations in detecting and tracking individuals over extended times (Pearre, 2003).

Gatten and Sargent (1973) found that *C. finmarchicus* caught at depths had greater lipid contents than those caught in shallower waters. From this they hypothesised that these copepods did not migrate synchronously, but those that needed to replenish their stores would migrate up to feed when required. Hays et al., (2001) also found that the *Metridia pacifica* found at the surface had low volumes of carbon relative to their nitrogen content (C:N ratio) and low lipid reserves. Whereas those that remained deeper were found to have higher lipid reserves and C:N ratios, also suggesting that copepods migrate to the surface as individuals when they need to feed, rather than migrate *en masse*. These authors suggested that individual VM was influenced by body condition, with those with larger reserves not risking migrating to the surface to feed. Leising et al., (2005) used adult female *Calanus pacificus* to build a model to determine whether foray behaviour would be advantageous. The model resulted in a large advantage being seen in the form of higher feeding success and lower mortality rates when foray behaviour was modelled, compared to random movements throughout the upper water column.

1.6 Foray Behaviour and the BCP

Foray behaviour is not well understood, and the association of this behaviour with the carbon flux is poorly resolved. Wallace et al., (2013) modelled how different vertical migration behaviours may affect faecal pellet export. The model was parameterised with reported values of chlorophyll and the rate of faecal pellet production as a function of food and was run under three scenarios: (1) no vertical migration, (2) foray behaviour and (3) synchronised DVM. It was found that the behavioural differences had a strong influence on the distribution of faecal pellets. In particular, foray behaviour enhanced the active flux of carbon to depth since 90 % of the faecal pellets produced in the standard foray-type simulation were below the export depth of 30m.

While foray behaviour has been reported in a number of zooplankton species (e.g. Pearre, 2003; Pierson et al., 2013, 2009; Tarling & Johnson, 2006) few have investigated the influence foray behaviour may have on the BCP in the field. Tarling and Johnson (2006) found that, under laboratory conditions, a number of *Euphausia superba* suspended swimming in response to satiation. When modelled, it was predicted this behavioural response could result in an 8 % increase in carbon export when compared to *E. superba* undertaking 'traditional' DVM behaviour. Tarling and Thorpe (2017) also suggest that foray behaviour in *E. superba* may increase carbon flux of swarming krill due to satiated krill sinking to the bottom of the swarm to defecate, thereby avoiding faecal pellet degradation by the remainder of the swarm and increasing the chance of faecal pellet export.

1.7 Tracking VM

1.7.1 Gut content analysis and Detection by Tracers

It is often assumed that if an organism contains the remains of prey that are not found at the depth at which the organism was found then VM has taken place by either the prey or predator (Pearre, 2003). Evidence for this often comes from phytoplankton cells or pigments being present in organisms captured below the euphotic zone, an area too deep for photosynthesis (e.g. Gauld, 1953). Building up profiles of gut content analysis of zooplankton captured with stratified nets over diel cycles can be used to determine when vertical movements are taking place (Pierson et al., 2009).

However, predators at depths below the prey may have otherwise fed on fast-sinking aggregates (marine-snow) (Pearre, 2003). These aggregates often contain plankton remains, which may explain the presence of these remains in organisms inhabiting deeper areas. A number of studies have attributed the presence of phytoplankton in the gut of deep dwelling species to in situ feeding on sinking aggregates. Nemoto (1972) thought that the presence of phytoplankton in the gut contents of *Megacalanus princeps* was due to feeding on either sinking faecal pellets or a deep-sea phytoplankton that was unknown. Harding (1974) also found diatoms and dinoflagellates in the guts of the copepods *M.*

princeps caught from 1000m and *Pleuromamma abdominalis* at 3000m. The presence of these surface organisms within the copepod gut tracts was attributed to in situ feeding on sinking cells as neither species were caught in depths shallower than 1000 m. While *Pleuromamma abdominalis* is known to migrate, Harding (1974) considered that the depth was great enough to attribute the presence of the diatoms and dinoflagellates to feeding on sinking particles.

1.7.2 Net methodologies

Vertical migration behaviour has been studied using a range of methods since the 19th century (Pearre, 2003). Initially, DVM was observed by surface samples, collected by nets, showing an increase in abundance of plankton in the surface layers during the night (Bayly, 1986; Pearre, 2003). This method of surface-only sampling is still in use today (e.g. Steinberg et al., 2000). These studies are often limited to one depth over a small area at sporadic intervals due to constraints on equipment and time and may not produce results at the resolution required to study DVM or foray behaviours.

One way of studying plankton over larger temporal and spatial sales is to use a Continuous Plankton Recorder (CPR). The CPR method involves a device being towed behind ships of opportunity. This device operates by water entering the front and being filtered onto a band of silk that travels slowly across the device entrance. The speed at which the silk is passed across the entrance is proportional to the speed of the ship in order to maintain an approximate ratio of 10 cm of silk per 10 nautical miles. Movement of the silk is achieved via a small impellor mounted at the back of the device, which also powers a caste system. This system brings together the silk on which plankton have been caught with a covering silk which are then pressed together and wound into a storage area containing formaldehyde for plankton preservation (Reid et al., 2003). Making use of ships of opportunity allows sampling to place over larger spatial and temporal ranges than would be possible by other net techniques during field campaigns. A number of studies have used CPR data to look into DVM over large spatial scales (e.g. Beare & McKenzie, 1999; Hays, 1995, 2003; Hays et al., 1995). However, these methods do not look at patterns in plankton at depth. Franz (1910) (as cited in Pearre, 2003) pointed out that a decrease in plankton being caught in the surface layers during the day did not necessarily represent DVM. He argued that the decrease in plankton may be due to light aided avoidance of the nets. This is known to be the case for a variety of migratory species (Fleminger & Clutter, 1965). However, early multi-depth studies (e.g. Michael, 1911 as cited in Pearre, 2003) appear to confirm that a decreased catch in plankton in shallow water during the day time was accompanied by an increase in plankton at depth. The parallel increase of plankton at depth and decrease in shallow water during the daytime suggests that DVM is occurring in line with the criterion set out by Cushing (1951) and Hardy (1953).

Many authors investigating VM are now using multi-nets. These nets comprise of a number of nets that can be opened and closed on command, examples of which are the Multiple Opening and Closing Net with Environmental Sensing System (MOCNESS)(Biological Environmental Sampling System, Inc.) and the Multinet system (Hydrobios) (Wiebe et al., 1985). Both of these systems are lowered into the water column to their maximum depths and individual nets are opened and closed in sequence during hauling. This method allows stratified net sampling to occur as each net can be opened and closed at known depths, enabling the vertical distribution of organisms within the water column to be resolved. However, this methodology gives a presence at depth at any one instant rather than the direct tracking of the vertical movement of plankters.

It is now thought that plankton may make repeated forays into the surface layers of a potentially substantial vertical amplitude over shorter time periods than would be present in traditional DVM (Pierson et al., 2009). However, this is difficult to visualise with the methods mentioned above. Pierson et al., (2009) attempted to tackle this by using traps to capture simultaneously plankton migrating upwards and downwards. These authors designed a new plankton trap based on zooplankton nets. A number of prototype devices were constructed, using nylon or netting to connect the opening of the trap to a narrowing section entering the cod end (Figure 1.6) (Pierson et al., 2009).

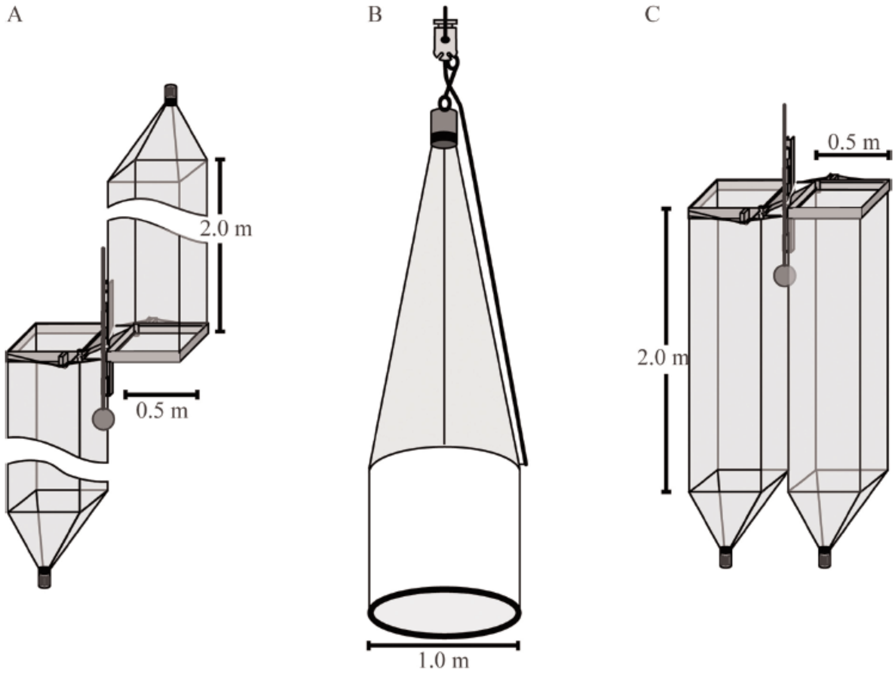


Figure 1. 6: Nets deployed by Pierson et al. (2009) in Dabob Bay, 2006. A) Bi-directional Z trap initially deployed to trap plankton moving in both upwards and downwards directions simultaneously. B) Plummet net used to trap plankton travelling upwards. C) Revised Z trap deployed to capture downwards travelling plankton. Image from Pierson et al. (2009)

All traps had a mechanism by which they could be deployed in the closed position preventing any plankton from being caught during deployment. They were then opened upon reaching a set depth and left to trap zooplankton at the desired depth. Nets were closed before recovery to ensure no plankton were caught as the net was dragged through the water and no trapped plankton were lost. The Z net was opened and closed via two moveable arms on adjacent sides of the opening. The initial arm to open the net was operated mechanically via a messenger system, while the second arm was operated acoustically in order to reseal the net opening. After the net had been closed, the weighted cod end of the downward facing net was released, in turn pulling the net below the frame to prevent flushing on retrieval. However, the acoustic release did not perform as well as desired and the Z net was modified only to look upwards (Figure 1.6c). This was then deployed at the same time as the plummet net (Figure 1.6b) to trap plankton migrating up and down simultaneously. The plummet net was deployed with a nylon cap covering the opening to avoid any plankton being caught on deployment. This cap was held on by elastic around the edge of the net opening. A weight was attached to the centre of this cap and was connected to the edge of the opening by a retrieval line. The nylon cap was removed by quickly raising the net up to a target depth after deployment to a greater depth, causing the flushing of water to force the cap off. These nets were successful in catching zooplankton migrating in both directions. However, fewer plankton appeared to be caught in downward facing than the upward facing traps. It was thought that this could be due to plankton coming into contact with the net and migrating back downward out of the trap (Pierson et al., 2009). Another limitation of these nets is that they could not be used in moderately high winds, with nets moving by up to 3 m in winds of less than 8 m s^{-1}, potentially altering the trapping rates of zooplankton (Pierson et al., 2009). Nevertheless, these nets represented an important step in the field of detecting foray behaviour, with Pierson et al., (2009) able to demonstrate vertical movements within the plankton community across all deployments. However, this study was limited to the sheltered waters of Dabob Bay, USA. The next step is to determine whether foray behaviour is prevalent in open ocean environments, which necessitates overcoming some of the design limitations reported by Pierson et al., (2009).

1.8 High Latitude Regions

1.8.1 Southern Ocean

The Southern Ocean (SO), defined as Ocean South of 50 ˚S, plays a major role within the global uptake and sequestration of CO_2 and is thought to be responsible for absorbing up to 20 % of the global oceanic CO_2 uptake, despite covering only 10 % of the global ocean (Takahashi et al., 2002). Deep-water formation is driven by cold temperatures along the Antarctic continental shelf (Broecker et al., 1998; Clark et al., 2002), while surface ice formation then results in salty water which has the potential to sink and sequester large volumes of CO_2. This area is characterised by a number of frontal currents, making up the Antarctic Circumpolar Current (ACC). The ACC is made up of three main fronts; the sub-Antarctic Front (SAF), the Polar Front (PF) and the Southern ACC Front (SACCF) (Figure 1.7). The fronts mark a transition from comparatively warmer water to the north to cooler Antarctic water to the south and represent changes in water masses with differing physical properties that exert a strong influence on the biogeography of the SO. The ACC moves in an eastern direction continuously around the Antarctic continent, transporting deep, dense bottom water northwards (Talley et al., 2011). This circulation of water at depth and vertical mixing means that much of the SO is rich in nutrients, but limitations in the availability of iron results in areas of low primary productivity (de Baar et al., 1995; Martin, 1990).

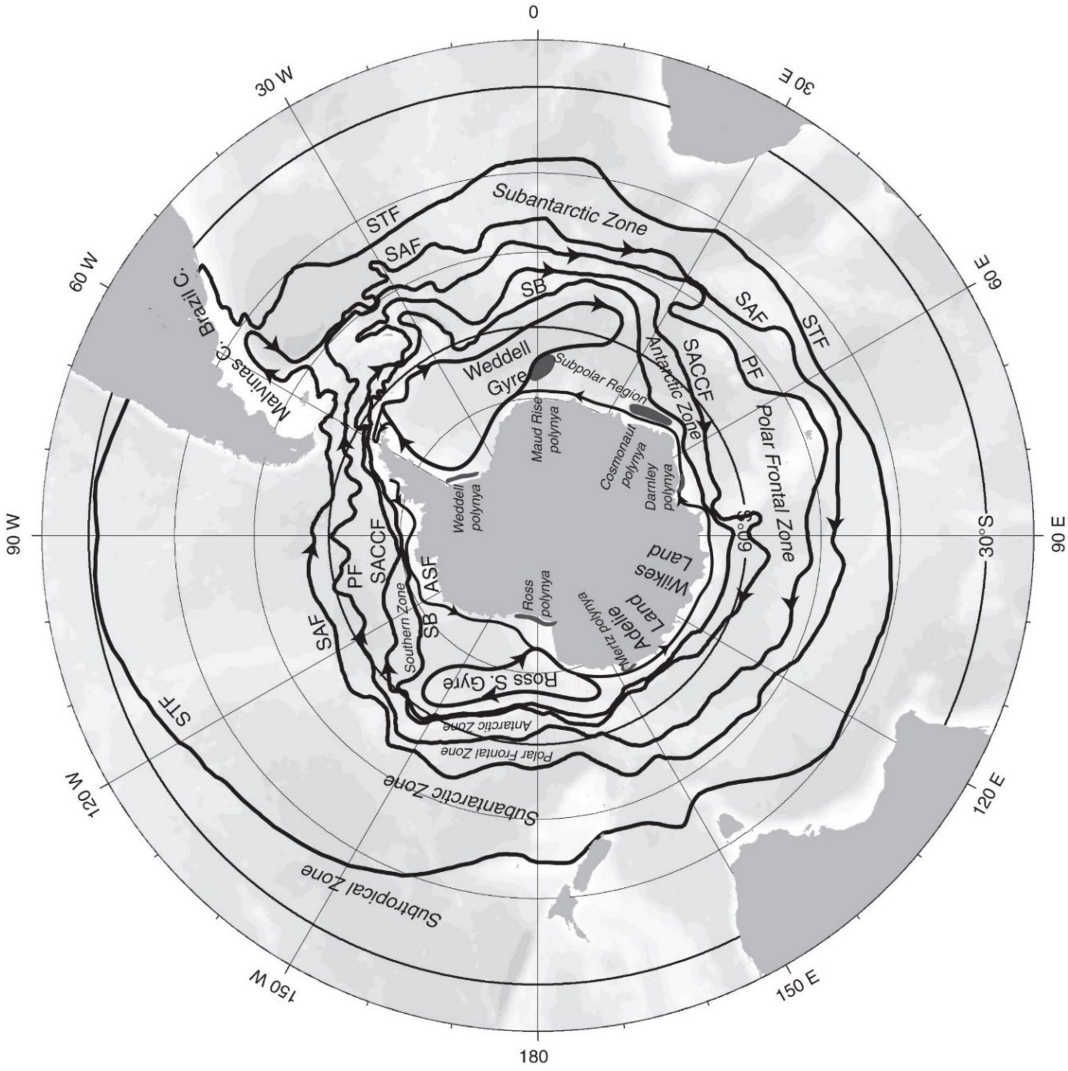


Figure 1. 7: Southern Ocean frontal features and land masses. Frontal locations as found by Orsi et al. (1995). STF = Sub-Tropical Front; SAF = Sub-Antarctic Front; PF = Polar Front; SB =Southern Boundary; SACCF = Southern Antarctic Circumpolar Current Front; ASF = Antarctic Slope Front. Image taken from Talley et al., (2011).

Nevertheless, there are regions of high primary productivity within the SO. The SO is characterised by seasonal winter-pack ice that can reach as far north as 60 °S but varies interannually (Talley et al., 2011). Sea-ice can provide refuge for a number of organisms and can be a highly productive habitat (Kattner et al., 2004). Ice algae is thought to be important for supporting the development of post-larval krill through the winter (Quetin & Ross, 1991) as well as maintaining a large macrozooplankton community (Flores et al., 2011). The seasonal melting of sea ice results in a period of high productivity due to the release of ice-algae, depositions of iron and increases in light stimulating ice-edge algal blooms (Korb et al., 2005). The primary productivity from these ice edge blooms can reach up to 2 mg C m^{-2} d^{-1} (Korb et al., 2005). Further to this, in the South Atlantic sector of the SO, the ACC is channelled through Drake Passage and flows over complex bathymetry around island arcs, resulting in turbulence and small scale hydrographic features (Garabato et al., 2004). These cause upwelling to occur, bringing nutrients from depth to the surface and combines with iron input from islands to stimulate primary production in certain areas (Garabato et al., 2004; Venables et al., 2012). One such area is in the northern part of the Scotia Sea. Here the ACC encounters the South Georgia and South Sandwich Islands, resulting in iron input downstream of the islands. As a result, iron fertilisation occurs and extended summer blooms can be found, with annual primary productivity reaching 40 mg C m^{-2} (Whitehouse et al., 1996) and high levels of atmospheric CO_2 drawdown (Jones et al., 2012).

1.8.2 The Scotia Sea

An area of focus within this thesis is the Scotia Sea, a region in the south western Atlantic sector of the Southern Ocean, to the west of islands that make up the Scotia Arc. This area lies to the south of the Drake Passage and is bounded by undersea ridges and islands to the south, east and west, leading to dynamic oceanic features (Korb et al., 2004; Thorpe et al., 2002). The predominant current in the region is that associated with the SACCF which travels through the Drake Passage before reaching South Georgia, at the eastern end of the North Scotia Ridge (Thorpe et al., 2002) (Figure 1.8). Phytoplankton blooms in this region are long lasting (Korb et al., 2012), with the resident mesozooplankton reaching levels of biomass that are six times higher than the average for the region (Atkinson, 1996; Pakhomov et al., 1997; Ward & Shreeve, 1995). Furthermore, a number of frontal features, such as the SACCF, APF and the marginal Ice-Zone (MIZ) increase the diversity of oceanographic regimes in the region leading to the formation of regions with contrasting levels of primary productivity (Korb & Whitehouse, 2004). These differing productivity regimes lead to different zooplankton communities which have been classified into different ‘bioregions’ based on both ecological and physical features (Ward et al., 2012b).

This region of the Scotia Sea, surrounding South Georgia, has been comparatively well studied due to its abundant krill fisheries and associated higher predators. Sampling programmes started in the early 20th century when a need for information regarding whale stocks was required and led to the Discovery Investigations (Kemp & Hardy, 1929). Since then, programmes such as BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) (El-Sayed, 1994), the British Antarctic Survey's (BAS) Western-core Box time series, which includes deployment of biogeochemical moorings, and BAS's DISCOVERY 2010 programme, a multidisciplinary effort to understand the Southern Ocean in greater detail (Tarling et al., 2012), have been carried out.

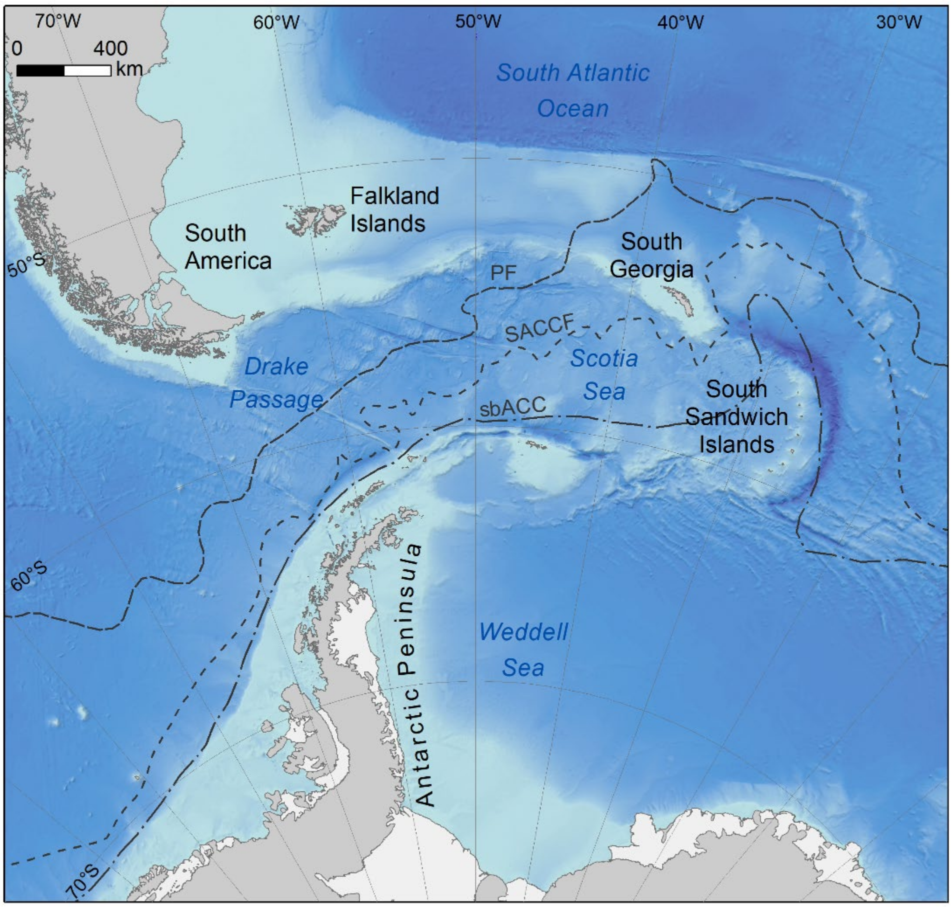


Figure 1. 8: Map of the Scotia Sea and surroundings showing the locations of dominant features. Dashed lines show the positions of the Polar Front (PF), Southern Antarctic Circumpolar Current Front (SACCF) and the southern boundary of the Antarctic Circumpolar Current (sbACC).

1.8.2.1 Zooplankton of the Scotia Sea

The SACCF is an important and dynamic feature for the ecology of the Southern Ocean. Currents associated with this front acts as a conveyor belt for the transportation of plankton from areas such as the Antarctic Peninsula to places such as South Georgia

(Hofmann et al., 1998; Hofmann & Murphy, 2004; Murphy et al., 1988; Thorpe et al., 2004). The zooplankton of the Scotia Sea have been relatively well studied, resulting in a large body of literature describing community structures, compositions and seasonal changes (Constable et al., 2014). These communities are principally partitioned by frontal zones such as the Sub-Antarctic Front (SAF) and Polar Front (PF) (Ward et al., 2002, 2003), with further distinct differences between on-and off-shelf communities (Ward & Shreeve, 1999). These frontal structures have also been found to be associated with high zooplankton abundance and diversity (Ward et al., 2003), potentially as a result of the turbulent mixing that occurs where frontal currents meet, causing upwelling of nutrients. The zooplankton community in the northern part of the Scotia Sea is mainly dominated by small euphausiids and copepods (Ward et al., 1995). However, the exception to this is the South Georgia region, where the plankton community is dominated by Antarctic krill (*Euphasia superba*) (Brierley et al., 2006) as it is in the southern Scotia Sea (Ward et al., 2012b). This South Georgia krill population is not self-sustaining and relies on SACCF-associated currents to replenish the population (Brierley et al., 2006). Acoustic surveys within this area have shown that the krill population is highly variable between years (Brierley et al., 1998; Fielding et al., 2014), in part due to the variability in the positioning of the SACCF (Thorpe et al., 2002). Despite the dominance of Antarctic krill in the South Georgia region, calanoid copepods can still make a large contribution to community productivity, with species such as *Calanoides acutus* attaining a level of secondary production in the region equivalent to that of Antarctic krill (Shreeve et al., 2005). Furthermore, smaller sac spawning species, such as *Oithona similis*, can be highly abundant in the region and may remain productive year round (Ward & Hirst, 2007).

1.8.3 Arctic Ocean

The Arctic Ocean plays a disproportionate role in carbon sequestration (Bates & Mathis, 2009), with an estimated uptake of 0.166 Pg of carbon annually, equating to approximately 10 % of the global ocean carbon uptake (MacGilchrist et al., 2014). However, in contrast to the Southern Ocean, the Arctic Ocean is an ocean surrounded by landmasses and is strongly influenced by warmer waters to the south as well as seasonal sea ice formation (Caroll & Caroll, 2009). Water masses can enter and exit the Arctic Ocean through four main gateways; Bering, Davis, and Fram Strait, and the Barents Sea Opening (Beszczynska-Möller et al., 2011), with the Fram Strait being the deepest of these (Thiede et al., 1990). Further to this, approximately 53 % of the Arctic Ocean lies above shallow continental shelves (Bates and Mathis, 2009), influencing the hydrography of the area. Within the

Upper Arctic Ocean there are two main cold water circulations, the Beaufort gyre and the Transpolar current (Gregor et al., 1998). The Beaufort Gyre is a clockwise gyre situated to the north of Alaska, the Canadian Archipelago and eastern Russia (Gregor et al., 1998) (Figure 1.9). The Transpolar drift is located to the east of the Beaufort Gyre and flows from the Laptev Sea and East Siberia across the Arctic Ocean and into the Fram Strait (Gregor et al., 1998). Water masses from the Atlantic flow in through the Barents Sea, whilst Pacific water is brought in through the Bering Strait (Gregor et al., 1998).

Figure 1. 9:- Schematic of Arctic Ocean currents taken from AMAP 1998 (Gregor et al., 1998). Arrows represent current directions with blue arrows signifying cold Arctic water and red arrows denoting warmer water currents originating from temperate areas.

These inflows bring nutrient rich water into the area and support high rates of primary productivity within the Arctic Ocean (Bates & Mathis, 2009). Seasonal sea ice forms in winter, completely covering the Arctic Ocean. This ice is made up of both thick multi-year ice in the central basin and thinner seasonal ice over continental shelves and peripheral areas (Bates & Mathis, 2009). The thinner seasonal ice melts during the summer causing the ice edge to retreat polewards. Due to the convergence of water masses, upwelling caused by storms and nutrient rich water coming in from other oceans, primary production can be high within the Arctic Ocean. In regions just outside of the ice zone, phytoplankton blooms can be spatially extensive, reaching over 100 km, and are able to fix up to 2.0 mg C mg^{-1} chl a hour^{-1} showing the potential for carbon sequestration within the region (Arrigo et al., 2012). At the ice edge, seasonal blooms occur as a result of the increase in light, nutrient influx from ice melt and small scale turbulence (Niebauer, 1991).

The Fram Strait cover the area of the Arctic Ocean from Greenland to Svalbard. This marks the transition from Atlantic water to the south and Arctic water to the north and is made up of a number of water masses. To the east, the West Spitsbergen Current (WSC) flows northwards up the west coast of Norway to the west of Svalbard, where it enters the Arctic Ocean (Rudels et al., 2005). As the WSC moves northwards, water is cooled and freshened by sea ice melt and glacial inputs from the continental shelves (Rudels et al., 2005). The WSC splits into three around Svalbard, with one branch flowing further north along the edge of Svalbard, one flowing west along the northern and western edges of the Yermack plateau and the third travelling westwards through the Fram Strait before being re-circulated in the return Atlantic Current (RAC) (Beszczynska-Möller et al., 2012). In the western part of the Fram Strait, a cooler, fresher water mass flows southward in the form of the East Greenland Current (EGC) (Rudels et al., 2002). These eastern and western currents are separated by the East Greenland Polar Front (EGPF), causing variable seasonal sea ice formation in the marginal ice zone (MIZ) (Bergmann et al., 2016). These currents result in the Fram Strait exhibiting a range of regimes, with the western section being regularly covered in sea ice whilst the south eastern section is ice free (Bergmann et al., 2016).

1.8.3.1 Zooplankton of the Fram Strait

These differences across the region have a strong influence on the biology within the Fram Strait (Hirche et al., 1991; Svensen et al., 2011). The zooplankton community within the Fram Strait is dominated by copepods, with the vast majority of the copepod biomass being comprised of calanoid copepods (Hirche et al., 1991). Hirche et al., (1991) identified four subregions within the Fram Strait based on biological and physical characteristics: a spring bloom subregion with abundant diatoms; a pack-ice region dominated by dinflagellates; a marginal ice zone region with mainly autotrophic production and an open ocean region where *Phaeocystis pouchetii* dominates. Copepods thrived most in the spring bloom region. The copepods inhabiting the east of the Fram Strait, off the coast of Norway, have been the most extensively studied (Smith, 1988). Here it has been found that *Calanus finmarchicus* comprises 40-80 % of the total annual biomass (Smith, 1988). However, other species including *Pseudocalanus* spp., *Metridia spp., Microcalanus pusillus, Acartia spp*. and *Oithona similis* are also highly abundant (Wiborg, 1954). In areas influenced by Arctic water, *Calanus hyperboreus* and *Calanus glacialis* are also important contributors to the biomass (Grainger, 1963; Kosobokova, 1978). However, the copepod community composition within the Arctic Ocean is highly variable over the seasonal cycle as well as spatial locations. Many calanoid copepods within the Arctic exhibit diapause behaviour, where they sink to deeper layers and become less active, using internal energy stores over the winter months when primary production is reduced. As a result of this behaviour, other non-diapausing copepods, such as *Metridia spp*. and *Oithona spp*. may play a greater role within the surface community during the winter months.

1.9 Asynchronous Migrations at High Latitudes

Areas in which DVM does not fit consistently with the traditional view of vertical migrations include high latitudes. These regions are often defined as those waters with latitudes north of 60˚N and further south than 60˚S, however this is arbitrary and does not encompass all polar ecosystems (Wielgolaski & Inouye, 2003). High latitude regions have great seasonal variabilities in their day-night cycle, with extended periods of daylight in summer and darkness in winter [I define high latitude areas as polar and subpolar areas where polar species are present and there is great seasonal variation in day length]. The upward migration of DVM is typically associated with the onset of dusk, therefore, in regions where dusk (or dawn) does not occur for certain periods of the year, or there is very little time of darkness, zooplankton may have little choice but to feed and possibly carry out VM during daylight. It is also possible that zooplankton may permanently occupy the surface layers during the wintertime polar night if predator avoidance is the main driver of DVM. However, that also assumes that there is phytoplankton prey available during that period, which may not be the case given primary productivity will be negligible during the polar night, as opposed to being extremely high in the midnight sun period.

To date, it is unclear as to whether DVM is carried out continuously throughout an annual cycle in these regions. Some studies investigating DVM over annual cycles have deployed acoustic Doppler current profilers (ADCPs) to detect mass plankton movements. Using this technique, traditional DVM has been reported to be present throughout much of the year (February to November) in plankton populations of the Ross, Lazarev and Wedell seas in the Southern Ocean but ceases in the summer months (December to January) (Cisewski & Strass, 2016; Cisewski et al., 2010; Picco et al., 2017). A similar pattern has been reported for the Arctic with ACDPs detecting synchronous migrations throughout winter but the pattern breaking down during the period of extended daylight (Cottier et al., 2006; Wallace et al., 2010). However, ADCPs are limited in their detection of zooplankton since these instruments rely on a strong signal coming from a large mass of plankton. If asynchronous migration is occurring, the acoustic signal from smaller bodies of plankton may not be detected and would be reported as a lack of vertical migration. Cottier et al.,(2006) also made use of the vertical velocity profile gleaned from ADCP data in an Arctic fjord. These authors found that, during the summer months when no displacement was detected, the vertical velocities showed a continuous net movement downwards. This downward vertical velocity was interpreted as asynchronous migrations taking place throughout the summer.

In order to complement ADCP data, net samples are also being used to detect DVM within these regions. These studies vary in their findings with DVM behaviour differing with location, species and sampling methods. Blachowiak-Samolyk et al., (2006) used a multiple plankton sampler to break the water column within marginal ice zone of the Barents Sea into 5 layers: 0-10 m, 10-30 m, 30-50 m,50-100 m and 100 m-sea bed. This sampling resolution found that, during a period of midnight sun, herbivorous copepods tended to remain in the upper 50 m throughout a 24 hour period while omnivorous copepods were concentrated in deeper waters. This lack of vertical movement in either group suggests that, in line with ADCP studies, traditional DVM was not occurring in the copepod species sampled. This cessation of DVM was also reported by Conroy et al., (2020) along the Western Antarctic Peninsula (WAP). In that study, using day and night depth-stratified tows from 2009-2017 and epipelagic net tows dating from 1993-2017, it was found that some plankton species altered their DVM behaviours during the austral summer. These authors found that the copepod *Metridia gerlachei*, the salp *Salpa thompsoni*, the pteropod *Limacina helicina antarctica* and ostracods all displayed consistent traditional DVM behaviour throughout the austral summer moving between epipelagic and mesopelagic zones. Further to this, the migration lengths of *M. gerlachei* and ostracods were found to increase as day length shortened, suggesting that DVM is less pronounced during the summer months. A number of other organisms also exhibited DVM behaviour; however, there was less consistency, with only slight increases in abundances seen in the epipelagic at night, which were hyperiid amphipods, gymnosome pteropods and *Tomopteris* species of polychaetes. Within the epipelagic zone, a number of organisms were found to carry out shallow vertical migrations. *Calanoides acutus* and *Rhincalanus gigas* migrated from 50-100m during the day to above 50 m at night, with the euphausiids *Thysanoessa macrura* and *Euphasia crystallorophias* also remaining within the epipelagic zone whilst carrying out DVM (Conroy et al., 2020). These shallow migrations are likely to be missed with ADCP data or net sampling with larger vertical resolutions and may account for the lack of DVM reported in other studies of these species (e.g. Huntley & Escritor, 1991). While Conroy et al.,(2020) report a number of species retaining DVM throughout the summer, absence of DVM was found in a number of other species. These species included the copepod *Calanus propinquus*, which was found to remain in the upper 50m throughout day and night sampling, and the euphausiid *E. superba,* which was found to have similar abundances in day and night 0-120 m oblique hauls. The lack of migrations in these species suggests that vertical migrations might be taking place asynchronously. Conroy et al., (2020) proposed that feeding types and environmental characteristics play a role in the vertical distribution of plankton species, with carnivorous feeding taking place in the mesopelagic zone. Seasonal migrations were also thought to play a role within the distributions they report. Relatively high abundances of the herbivorous copepod *C. acutus* in the mesopelagic zone was believed to be the result of adults remaining in diapause having not yet migrated upwards for the summer. The findings of Conroy et al., (2020) provide one of the most extensive overviews of DVM in a high latitude region; however, the study demonstrates the complexity of this behaviour and highlights the necessity of furthering our understanding of it.

1.10 Why are copepods important in the BCP?

Copepods are dominant within the zooplankton community, potentially contributing 60-80 % to global zooplankton biomass (Longhurst, 1985). Copepods are small crustaceans which range from 0.5 mm to 1 cm in size and are ubiquitous across all oceans, with over 11 500 species currently known (Humes, 1994). In general, copepods follow the same basic body plan with a tapered trunk comprised of a thorax and abdomen (Barnes, 1987) (Figure 1.10), often referred to as the prosome and urosome, respectively. Both the thorax and abdomen are segmented with the head fused to the thorax. Antennae are often present and protrude from the head which typically contains one naupliar eye (Barnes, 1987). Six pairs of appendages are present on the thorax with the first being modified into maxillipeds for feeding and the remainder used for locomotion (Barnes, 1987). However, the vastness in the number of species and abundance means that many copepods deviate slightly from this basic plan. Nevertheless, copepods form an integral part of the marine ecosystem, occupying a wide range of trophic levels and fulfilling a number of ecological functions. These functions include the removal of carbon from surface layers, the decomposition of sinking detrital matter and provision of a food source for a variety of predators from piscivorous fish (Turner, 2004) to large megafauna.

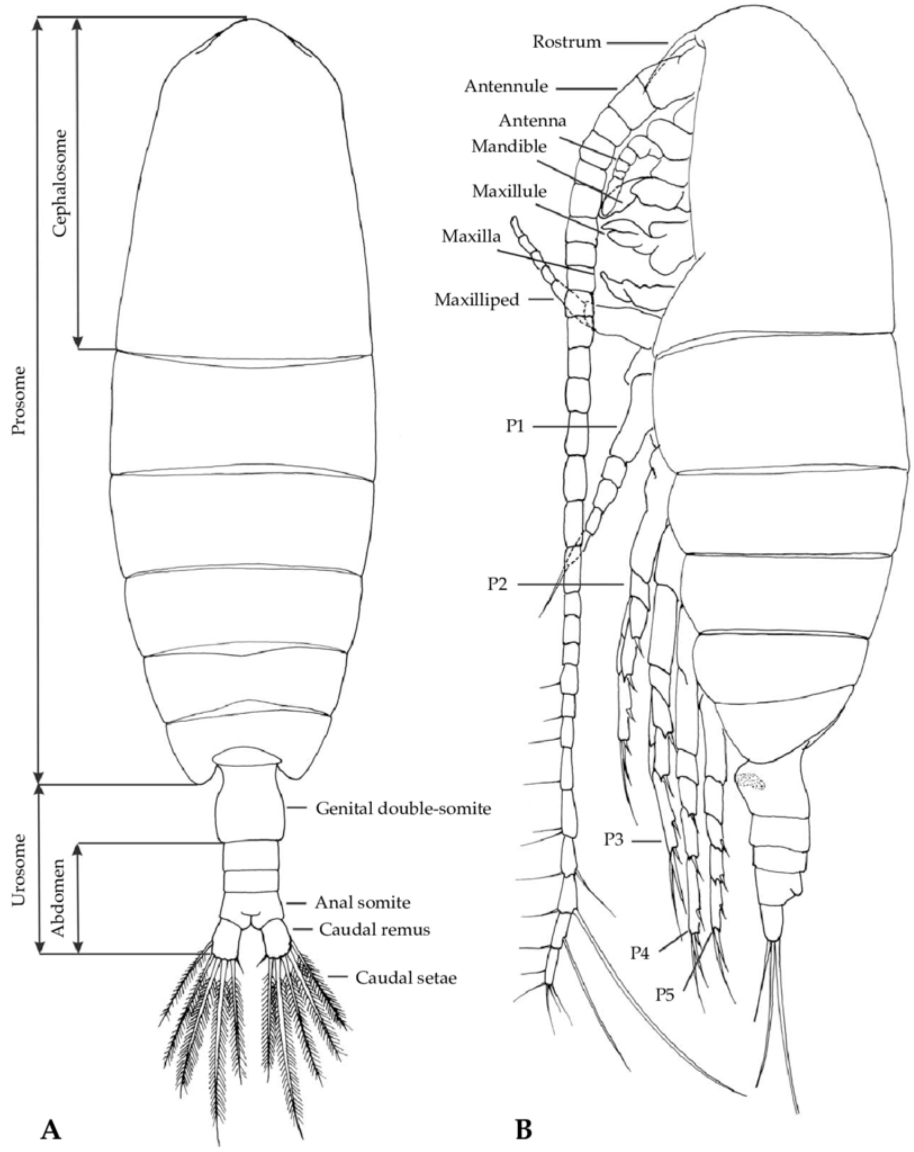


Figure 1. 10: Diagram of a typical copepod showing body plan encompassing prosome, urosome and appendages. Image from (Soh, 2013).

Copepods are a major component of the biological carbon pump. Many are grazers, feeding on phytoplankton at the surface, ingesting carbon fixed by photosynthetic plankton. As vertical migrators, they play a vital role in carbon sequestration. However, copepods also recycle carbon within shallow layers through breaking up sinking particulate material before it reaches sequestration depths (Gonzalez & Smetacek, 1994). A number of copepod species are coprophagous, feeding on sinking matter such as faecal pellets, detritus and marine snow (Gonzalez & Smetacek, 1994; Wassmànn, 1997). The combination of their feeding behaviour, VM behaviour and high abundance, particularly in the Polar Regions makes them an ideal organism to investigate the role of zooplankton in the BCP.

1.11 The Biomass Spectrum

One way in which carbon flux through ecosystems can be viewed is through the biomass spectral theory. This theory uses the premise that energy is transferred through the food web via a number of physiological and ecological processes including predation, mortality and egestion (Sprules & Barth, 2016). When exploring these processes, many studies are limited to a single species, however, in aquatic systems, a size-based approach may be better due to many predators opting to prey on organisms that can be swallowed whole (Sprules and Barth, 2016). Therefore, relationships of relative body-sizes of prey and predators are important when investigating the energy efficiency of a community (Heneghan et al., 2016). In addition, many ecological and physiological processes, such as metabolic rate, growth efficiency and diet, correspond to body size, making size a good representation of the organisms within a community (Kerr & Dickie, 2001) as well as a global index that may be related to the productive capacity of an ecosystem (Platt & Denman, 1977). Of note, early studies found that size was a greater factor than species when examining transfer efficiency of energy (Kerr & Dickie, 2001), suggesting that, while other interactions should not be completely ignored, body size may be more important than the trophic level of organisms when assessing energy transfer.

A number of studies have been carried out examining size-dependent processes (e.g. Atkinson et al., 2020; Sheldon et al., 1972; Sprules et al., 1991; Tarling et al., 2012). Sheldon (1969) looked at particle size using a coulter counter and demonstrated that the pattern of biomass resulting from the particles analysed was uniform through equal logarithmic intervals. This observation and presentation of data has since become known as the biomass spectrum (Sprules and Barth, 2016). Sheldon et al., (1972) extended this work by investigating whether this theory would hold true for planktonic particles over a variety of geographical regions. It was found that, while there was a great variation in the biomass spectral shape, once organised by location, there was a roughly equal biomass of particles through logarithmic size classes. Following this early work, a number of studies supporting this theory have been carried out (e.g. Dickie et al., 1987; Sprules & Munawar, 1986; William Sprules et al., 1991). Gaedke (1992) used a multitude of techniques to determine the abundance and size of eight taxa from bacteria to crustaceans in a meso-autotrophic lake. This study found three distinct biomass peaks, which corresponded to the major taxa within the lake, but the biomass across all size classes remained similar with a difference of less than 1.5 orders of magnitude. Sprules and Goyke (1994) carried out studies assessing whether the theory would hold when fish were added and ascertained that, within a lake system, distinctive biomass peaks could be seen and matched to corresponding trophic groups, lending further support to the biomass spectrum theory. From these few examples, it would appear that biomass spectra have a similar pattern of peaks and troughs across a wide variety of communities. An additional complexity within the zooplankton community is their fast growth rates and diverse range of body shapes, sizes and tissue composition. Many zooplankters also go through a number of life stages over short time periods. Therefore, zooplankton may perform different trophic roles during their lifecycles (Cushing, 1975; Pope et al.; 1994 Tarling et al., 2012), making their trophic level assessment difficult. However, Anderson et al., (2016) found that body size was a good determinant of trophic level. Thus, size-based studies can be used to help determine trophic structures within food webs (Blanchard et al., 2017), allowing potential predators and prey to be determined (Cohen et al., 1993).

A common approach to the size-based analysis is to normalise the data by dividing the total biomass within a log size interval by the width of the interval, known as the normalised biomass spectrum (Platt & Denman, 1977). This corrects for any distortion that arises in the biomass spectrum due to log intervals not scaling in proportion with body size, as well as standardising the data (Sprules and Barth, 2016). When the normalised data are plotted against the log individual size, a regression slope can be seen (Figure 1.11), indicating the relative contribution of different sized animals to the total biomass (Rodhouse et al., 1994). In most cases, this regression slope is negative, often with a value close to -1 (Sprules and Barth, 2016). Steep negative regression slopes indicate that biomass is lost as size increases, while shallow slopes indicate an accumulation of biomass in larger animals (Rodhouse et al., 1994; Tarling et al., 2012). In recent years, there has been a proliferation in models building upon the size spectral approach, aiming to understand how energy is transferred through ecosystems. This assists in improving our understanding of ecosystem functioning and energy flux, which is critical to inform models and increase their realism (Blanchard et al., 2017).

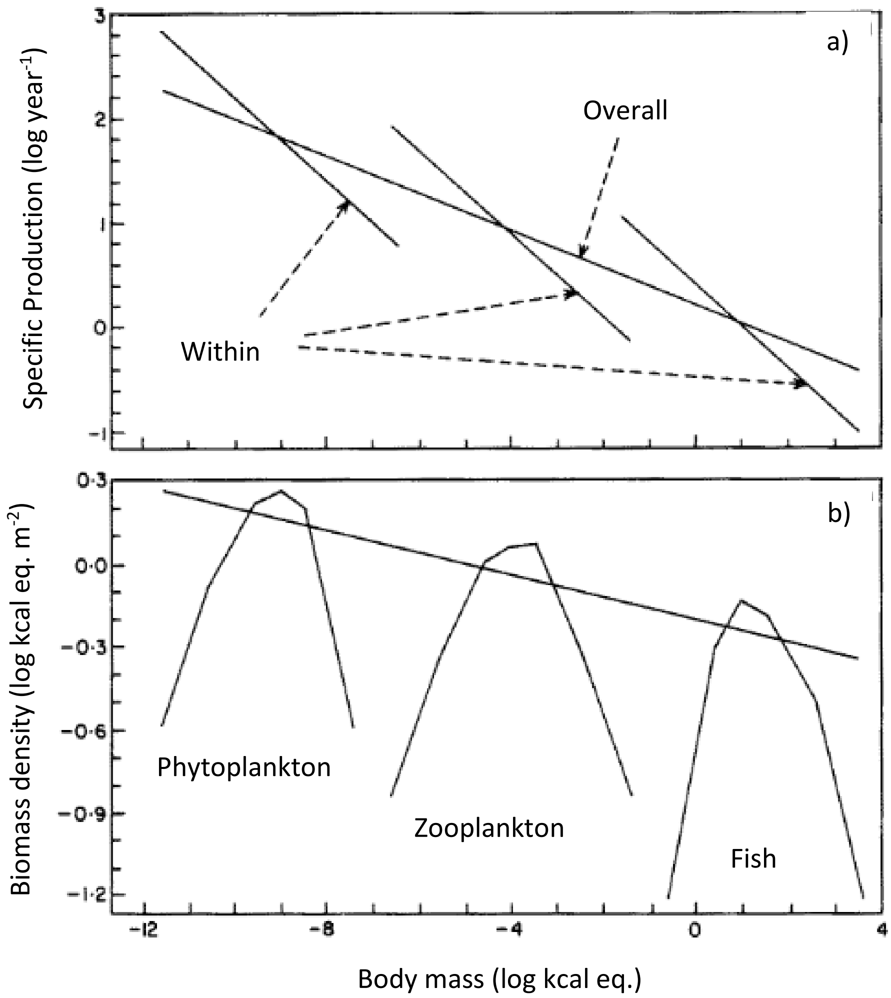


Figure 1. 11: Schematic representation of the equivalent body-size spectra of: (a) specific production, expressed as log P/B by trophic positional groupings. Here specific production is the measure of energy being transferred within groups of similar organisms and between trophic levels. (b) Biomass density of a given environment, showing how energy flows through the ecosystem through organisms of increasing size. (Figure from Boudreau et al., 1991)

Further to this, a number of theoretical studies have looked into the flow of biomass from small to large particles (Platt & Denman, 1977), with Platt and Denman (1977) proposing the theory that biomass flux is a continuous flow of energy through larger sizes (Figure 1.11b). The biomass flux leaving a size class is dependent upon the growth rate of the population and metabolic rates. The Platt and Denman model proposed that the biomass slope of pelagic communities would be -0.22. However, this was a simple model containing parameters for population growth and metabolism only. Later modelling carried out by Banse & Mosher, (1980) incorporated a greater number of physiological and ecological processes and found that the slopes changed with trophic groups, in which combined data for all species had a shallower slope of -0.18, and individual trophic groups had a steeper slope of -0.32. This indicated that predator biomass declined faster within trophic groups than between trophic groups (Sprules and Barth, 2016). Law et al., (2009) took this further and constructed a parameterised model of specifically sized predators feeding on smaller prey. Parameters included growth as a result of feeding, death (either as a result of being eaten or natural mortality), and renewal (by replacing individuals in size classes), prey size selection and prey encounter rates. In line with the work of Sheldon et al., (1972), this model found the total biomass of each log size class to be roughly equal. However, the regression slope produced by this model was found to change with prey size range. If predators were modelled to feed on a wide range of prey sizes, then the slope was found to be -1.1. However, if the predators were constrained to a narrow size range of prey, the model oscillated and did not settle on a single slope. Fuchs and Franks (2010) also found predator-prey relationships to be influential when considering plankton size spectra. These authors report that slopes were flatter for zooplankton with high predator-prey mass ratios (i.e. predators are much larger than their prey) but that spectral slopes steepened as predator-prey ratios decreased.

Due to a large size span across the copepod taxonomic group and many species having many different body sizes throughout their life span, sized-based approaches and the application of size-spectrum theory can provide unique insights into how energy flows through this major part of marine pelagic community.

1.12 Thesis Overview

Given the importance of copepods to the BCP within high latitude regions, this thesis explores vertical distribution and VM within copepods, with a particular focus on how the new paradigm of foray behaviour revises our view of how this community contributes to the BCP. I analyse copepod samples collected over the course of two Southern Ocean cruises and one Arctic Ocean cruise with my investigations covering aspects of community composition and biomass distribution through the water column, individual foray behaviour, and metabolic (respiration) responses to vertical distribution.

In Chapter 2, MOCNESS net samples from eight depths, from day and night, at two environmentally contrasting stations within the Scotia Sea were analysed for copepod size distribution patterns using a semi-automated zooplankton imaging device (ZooScan). I apply a size spectral approach to the image analysis data to assess the distribution of biomass according to size within the copepod community. Depth stratified samples are analysed to investigate whether the copepod size spectra changes throughout the water column. My use of paired day-night samples further gives an indication of the presence and extent of VM behaviour and how this affects size spectra distributions through the water column over diel cycles. I also compare size spectral patterns between differing primary productivity regimes to explore whether primary productivity influences copepod community size structure and the subsequent flow of energy through it. Specifically, I address the hypothesis that regions of higher primary productivity have greater levels of energy retention with copepod communities due to the presence of a greater proportion of larger species and stages. This work provides a new perspective on how energy is transported from the surface waters to deeper layers through the copepod community as well adding to our knowledge on copepod VM in the Scotia Sea.

In Chapter 3, I examine samples from a custom-made open-ocean zooplankton trap (MUDL net), capable of capturing zooplankton travelling both upwards and downwards during the same time interval. This is the first time such a net has been successfully deployed in the open ocean. The aim is to resolve the nature and extent of foray behaviour within the varied copepod communities of the Southern Ocean. Samples were taxonomically identified and counted to provide an insight into which species carry out forays and when. By deploying the MUDL net across a number of locations and times, I determine how widespread this behaviour is. I hypothesise there is a variety of foray patterns across different copepod communities, depending on taxonomic composition and environmental conditions. I consider the results in light of how this revises our assumptions when parameterising the active flux of carbon via zooplankton VM.

In Chapter 4, respiration incubations were carried out on an abundant Arctic copepod species, *Metridia longa*, which exhibits a prolific VM behaviour between the epipelagic and mesopelagic layers. Respiration in the mesopelagic of species that feed in the epipelagic is an important contributor to active carbon flux. Respiration incubations of *M. longa* were carried out during an Arctic field cruise. The aim was to establish whether capture depth, body condition or sex influences respiration rates and to what extent this might affect the parameterisation of active flux by this species. In particular, I considered whether a parameterisation solely based on the temperature experienced at different depths was sufficient or whether aspects of the life-cycle must also be considered when calculating active flux by this species.

Together, these chapters aim to enhance our understanding of the complexity of VM behaviour in zooplankton and to improve the parameterisation of this behaviour within estimates of the BCP.

Chapter 2: Copepod Size Spectra in the Scotia Sea

2.1 Introduction

2.1.1 Vertical structure in the Zooplankton Community

A variety of factors including nutrients, temperature, oxygen content, currents, food availability and physiological state may influence zooplankton community structure. Studies have reported higher zooplankton abundance in shallow waters with reductions in both biomass and abundance occurring with depth (e.g. Banse, 1964; Roe, 1972; Yamaguchi et al., 2002). However, Roe (1972) found the number of copepod species increased with depth in the North Atlantic, with a peak in species numbers occurring in the mesopelagic. De Puelles et al., (1996) found that the vertical distribution of copepods appeared to be determined by food concentration irrespective of other environmental variables. One approach to considering the drivers of vertical structure in the zooplankton community is to consider feeding strategies. Herbivorous zooplankton are most likely to be found within the surface waters where phytoplankton is abundant, while detritivores are found deeper in order to intercept sinking matter and carnivorous species are apparent throughout the water column depending on the distribution of their prey (Yamaguchi et al., 2002). This approach nevertheless presents complexities in determining life-styles and diets and has mainly been applied only to biomass dominant species (Mackas et al., 1993).

2.1.2 Size Spectra

Another way to considering the vertical structure copepod communities through the water column is to take a sized based approach. As described in Chapter 1, a sized based approach can indicate energy flux within a community and provide a measurable index of inefficiencies and combined effects across assemblages (Jennings et al., 2002). The normalised biomass spectral theory, as described by Platt and Denman (1978), is a linear model on a double logarithmic plot of normalised biomass versus particle size. The slope of this linear model indicates the energy retention within the system, with steeper slopes representing greater energy loss from the system and shallow slopes representing more efficient communities with greater energy retention rates. When looking at vertical distributions of zooplankton, this approach can be applied to each depth layer sampled in order to ascertain differences in energy retention rates throughout the water column. An understanding of this is crucial to understanding the role copepods play in the transport of energy and carbon through the different layers of the ocean. However, this is yet to be done, with many zooplankton size spectral studies applying this theory to the water column as a whole (e.g. Tarling et al., 2012) or only sampling the upper most layers of the water column (e.g. San Martin et al., 2006; Thompson et al., 2013). If the vertical distribution of copepods within the water column is as according to feeding strategy theory, with herbivores residing in the uppermost water layers, then it would be expected that normalised biomass slopes would become shallower with depth as energy is retained within the community in deeper dwelling detritivores and carnivores.

2.1.4 Optical Instruments

The development of optical instruments has greatly facilitated the extraction of size-based data from zooplankton samples. Optical instruments can be divided into two types, particle counters that rely on the interruption of light beams (e.g. optical particle counters) and image producing instruments (e.g. under water vision profilers) (Benfield et al., 2007; Wiebe & Benfield, 2003). Both types are capable of producing high-quantities of data in a non-destructive manner. Particle counters pass a sample through a chamber containing light beams, recording the number of times the light beam is broken. These instruments are often deployed from ships, giving information soon after retrieval. This is then used to count the number of particles in the sample as well as their size, although no further classifications of the particles are made (Wiebe & Benfield, 2003). While these systems provide valuable information, they do have limitations. The most notable is that they are unable to distinguish between particles in high densities, missing some particles and mistaking clumps for larger particles (Foote, 2000).

Silhouette photography has also been effective when examining plankton, due to the ability to produce sharp, high-resolution images (Benfield et al., 2007). An example of a recently developed optical instrument able to collect data and take images of particles is the Hydrobios ZooScan. This device is a benchtop scanner, with specially built lighting and a watertight chamber, designed for imaging plankton (Benfield et al., 2007; Gorsky et al., 2010; Grosjean et al., 2004). The ZooScan produces high-resolution silhouette images of numerous plankton simultaneously with associated data. Due to the automation of particle counts and machine assisted learning of plankton identification, the ZooScan is a powerful device enabling a subset, here copepods, to be extracted and enumerated efficiently. Through applying calibrations, the Zooscan data can be converted to individual biomass allowing total biomass and the size spectra to be determined. However, the ZooScan is not without limitations. Plankton are 3D objects and may be positioned in different orientations or planes within the scanning chamber, leading to a sub-optimal image (Culverhouse et al., 2006). Furthermore, silhouette images are not able to convey the same level of detail as a live or preserved specimen, limiting the level to which images can be taxonomically resolved (Benfield et al., 2007).

2.1.5 Scotia Sea

The present study was carried out using two locations in the Scotia Sea, P2 and P3. These sites are an example of different productivity regimes within the same water mass (Korb et al., 2012). The sites have a close proximity to each other and lie to the south of the Polar Front but vary greatly in productivity (Figure 2.1). The first, P2, lies to the south west and upstream of South Georgia and has a limited iron input, and therefore a relatively low primary productivity (0.3 mg chl m^{-3} (Korb et al., 2012)). The second site, P3, sits to the northwest and downstream of South Georgia. This area is naturally iron-fertilised by South Georgia (Korb et al., 2012) and has one of the highest chlorophyll concentrations (up to 1.5 mg chl m^{-3} (Korb et al., 2012) found within the Scotia Sea (Venables et al., 2012). These waters have a large and recurrent diatom dominated phytoplankton bloom (Borrione & Schlitzer, 2013; Korb et al., 2004; Ward et al., 2002) with either unimodal (Park et al., 2010) or bimodal (Borrione & Schlitzer, 2013) peaks each year. Primary production and phytoplankton abundance have been found to be 50 % higher to the north of South Georgia than in other areas of the Scotia Sea (Ward et al., 2012a). This high primary production supports a high abundance of zooplankton (Atkinson et al., 2008,2009; Ward et al., 2012a), mesopelagic fish (Collins et al., 2012) and higher predators (Atkinson et al., 2001). Despite this difference in primary production, the two sites appear to have similar mesozooplankton species compositions (Ward et al., 2012a).

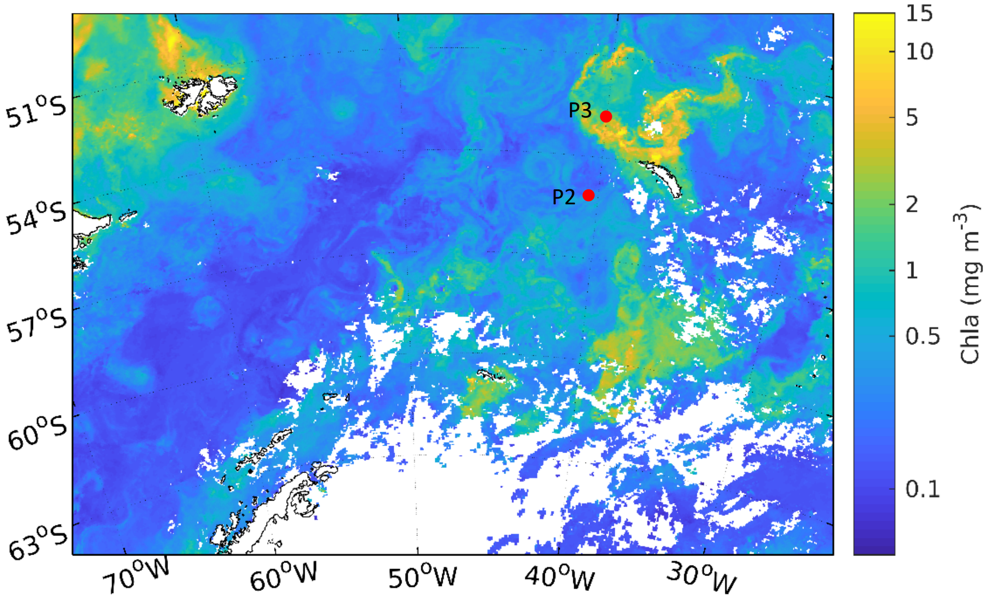


Figure 2. 1. Satellite image of chlorophyll in the Southern Ocean, January 2018 (adapted from *NASA Ocean Color* MODIS Aqua)

To some extent, the zooplankton community of the Southern Ocean differs from other oceans due to euphausiids (principally Antarctic krill, *Euphausia superba*) making up a large part of the pelagic biomass (Ward et al. 2012b). Nevertheless, in certain Southern Ocean areas, such as the Scotia Sea, copepods still make up >75 % of pelagic zooplankton biomass (Atkinson et al., 2012). In the present study, copepods were found to be the dominant taxa across all samples and therefore were the focus of the present analysis. The copepods of the Scotia Sea play a vital role in the zooplankton community and have been well described (e.g. Ward et al., 2004, 2006a, 2012a, 2012b), with the horizontal and temporal distribution patterns now relatively well understood (e.g. Atkinson & Sinclair, 2000; Conover & Huntley, 1991). However, very little attention has been paid to the vertical biomass structure throughout the water column within this area. This is of importance due to the vertical flux of matter, such as carbon, to the ocean interior. The vertical structure of detritivorous copepods is particularly poorly known despite their vital role in carbon cycling (Anderson & Tang, 2010). Further, the copepod life cycle has a number of developmental stages, each of which may require different environmental conditions, different depth strata and diel vertical migration (DVM) behaviours. Hence, developmental stage and hence size structure may vary have a distinct depth component, for instance, with larger copepods, principally later developmental stages, residing reside deeper to minimise their visibility to visual predators (Atkinson et al., 1992; De Robertis et al., 2000; Hays et al., 2001; Hays, 1995). If this is the case, it would be expected that copepod biomass spectra will change with depth. DVM is a common but not universal behaviour in copepods and, where it predominates, the vertical biomass structure over the day-night cycle will change, further altering the size structure of deep and shallow communities.

2.1.6 Purpose of Study

The majority of studies assessing zooplankton distribution in the Scotia Sea have been limited to near surface waters (Ward et al., 2012a). A limited number have investigated the vertical structure of zooplankton in other areas of the Southern Ocean such as the Weddell Sea and southern Scotia Sea (Hopkins & Torres, 1989; Lancraft et al., 1989) and the Western Antarctic Peninsula (Wiebe et al., 2011). However, zooplankton play a major role in the active transport of carbon and other materials and therefore their vertical structure is important when considering the flux of these materials. This is of particular importance in areas such as the Scotia Sea where carbon sequestration is relatively high (Toggweiler et al., 2003).

The current study aims to gain an insight into the vertical structure of the copepod community within the Scotia Sea. This was carried out through using ZooScan to analyse MOCNESS (Multiple Opening and Closing Net with Environmental Sensing System) samples taken at consecutive 125m intervals from the surface to 1000m. Samples were taken during the day and night in three consecutive years. It was not always possible to take samples from both P2 and P3 in all years, so detailed analytical comparisons were mainly performed on 2017/2018 samples, with comparisons to other years where possible. Using size data obtained from the ZooScan, copepod size structure, and inferred biomass, through the water column was evaluated, across sites and over the day-night cycle. The work addresses the following hypotheses:

i. Primary productivity levels influence the size structure of the copepod community.
ii. Copepod community size structure alters with depth reflecting a greater proportion of larger individuals and detritivorous species at depth.
iii. The pattern of size structure with depth varies over the day-night cycle.

Firstly, the differing levels of phytoplankton biomass at the two sample sites offer the ability to compare how this influences the copepod community. It may be expected that, where food availability is high (P3), the community is dominated by primary consumers, particularly larger copepods who have the capability to store this primary production within lipid sacs. However, this high food availability may also favour smaller copepods with shorter generation times which may more rapidly exploit primary productivity through increased reproduction and more rapid population growth. Where phytoplankton biomass is low, the recycling community (those that feed on particulate organic carbon) may play a comparatively greater role in energy transfer than primary consumers. This recycling community is typically made up of smaller individuals, such as *Oithona spp*., possibly leading to smaller copepods dominating the copepod biomass in these areas. In opposition to this, the lower productivity at P2 may lead to resident communities being required to store comparatively large amounts of energy in order to outlast periods of very low food availability, favouring larger copepods. Size spectral slopes are often used to indicate the energy transfer through a community and while this is an oversimplification and can be influenced by a range of factors, including predator-prey ratios (Atkinson et al., 2020) and food availability, the comparisons between the two sites in this study allows us to gain an understanding behind the differing communities. In this example, if the copepod biomass is dominated by large copepods positioned at higher trophic levels, shallow size spectra slopes will be present indicative of comparatively higher levels of primary production being retained within the system (i.e. a high level of energy retention). Conversely, if small copepods are responsible for the majority of the biomass, size spectra slopes will be steep, indicating that storage levels are lower and greater levels of energy are lost from the community.

Secondly, the acquisition of depth discrete samples to a depth of 1000 m allows for the vertical structure within the copepod community to be examined. It would be expected that larger copepods reside deeper in the water column in order to avoid detection by visual predators, leading to the dominant copepod size increasing with increasing depth. This would lead to greater energy retention in deeper layers due to larger copepods having the capacity to store more resources. On the other hand, many herbivorous copepods in the Southern Ocean have large body sizes, and these copepods need to spend some time in the surface layers to feed on phytoplankton. The presence of large herbivores may lead to surface communities being dominated by larger copepods.

Day and night samples allow comparisons to be made across these time points with a view to investigating whether DVM can be detected, and its impacts on the size spectra and energy flux within different depths of the water column ascertained. If a DVM pattern is present, it would be possible to see a change in copepod biomass structure over depth and time. If normal DVM (i.e. near surface at night, deep in the day) is the prevailing migration pattern, it would be expected that biomass would peak in the near surface layers during the night but spread across many depth strata during the day, reflecting different residence depths. Further to this, large copepods may make the largest migrations, enhancing day time biomass in the deeper layers but having a large impact upon night time biomass and size structure in the surface layers.

2.2 Methods

2.2.1 Field Sampling

The data were collected during three cruises, carried out on the *RRS James Clark Ross*, to the Scotia Sea during austral summer in 2015-16 (JR15002: November-December), 2016-17 (JR16003: December-January) and 2017-18 (JR17002: December-January). Zooplankton samples were collected from two stations to the west of South Georgia, P2 (55˚11 S, 41˚07 W) and P3 (52˚43 S, 40˚08 W) (Figure 2.2). Where, possible each station was sampled twice within a 24-hour time period, once during the day and once during the night (Table 2.1) in order to get samples collected during both light and dark conditions. External factors, such as adverse weather conditions, meant that it was not always possible to sample each location during both day and night, resulting in incomplete sample sets for some cruises. Due to this, the majority of analysis presented here has been carried out using data collected on the research cruise of 2017/18 (JR17002), where the most complete sample sets were obtained.

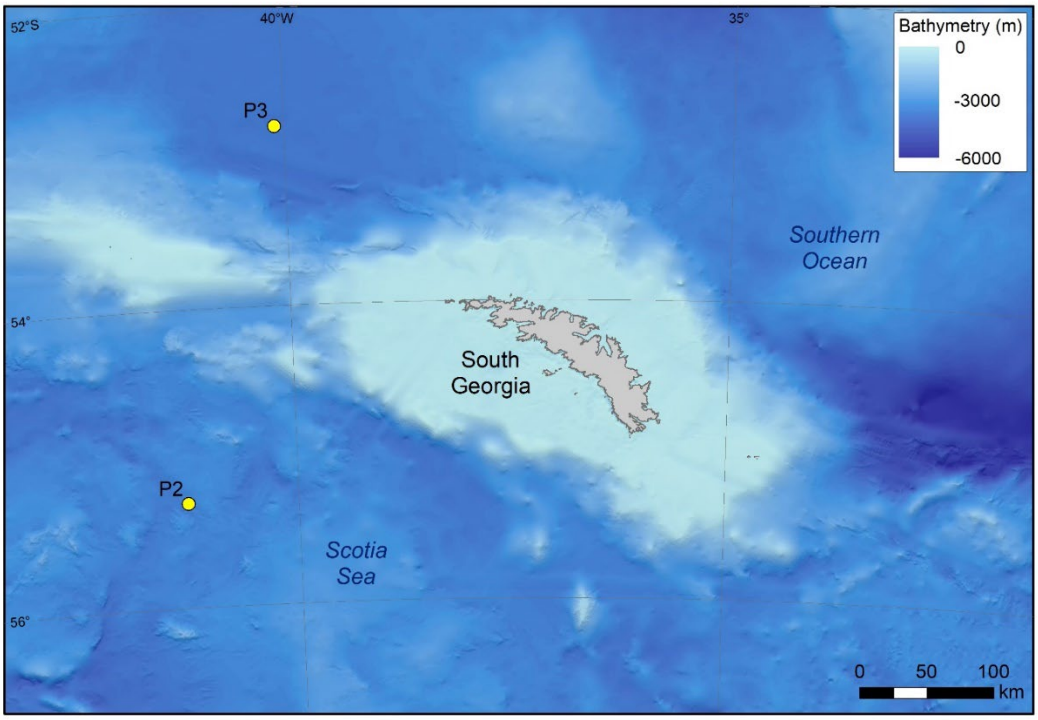


Figure 2. 2: Map of South Georgia showing locations of sampling stations P2 and P3.

Location	Date	Start Time (GMT)	End Time (GMT)	Event No	Latitude	Longitude
P3	04/01/2018	18:42:00	21:10:00	26	-52.8223	-40.1095
P3	05/01/2018	01:31:00	04:12:00	30	-52.7952	-40.1225
P2	16/01/2018	12:51:00	15:15:00	110	-55.2501	-41.2734
P2	17/01/2018	01:17:00	03:54:00	117	-55.2452	-41.2292

Table 2. 1: MOCNESS deployments during *RRS James Clark Ross* cruise JR17002. See Appendix 1 for further details.

Samples were collected using a MOCNESS towed behind the research vessel at a nominal speed of ~2 knots. The net consisted of a rectangular frame holding environmental sensors and nine 1 m^2 nets. These sensors recorded conductivity, temperature and depth. The net was operated through a cable linked to the ship, through which signals were sent to open and close nets during the deployment. As the net was hauled upwards, electronic signals were sent to the frame, triggering a release mechanism, releasing the next net in the sequence. As this net opened, the previous one was closed giving a depth discrete series of samples. All deployments went to a maximum depth of 1000m, with the first net being opened during the descent to 1000m and subsequent nets opened and closed as the net was hauled in. Each net was open for a vertical depth of 125m on the recovery to give eight depth intervals from 1000m to the surface.

The nets had a mesh size of 330 µm to allow small particles (such as phytoplankton) to pass through but retaining meso- and macrozooplankton. The nets were dark in colour to avoid detection by zooplankton and tapered to a large cylindrical cod end. Upon recovery of the net, the cod ends were removed, and the catch split in two by adding water to the catch, ensuring it was well mixed and removing half. This half was filtered onto 200 µm mesh and frozen at -80 ˚C immediately. The remainder of the sample was transferred to a Nalgene bottle and preserved in 95 % ethanol or 4 % buffered formaldehyde. The present study is based on the analysis of these preserved samples.

2.2.2 Sample analysis

Preserved samples were analysed within 18 months of collection, this was done by rinsing in tap water and splitting into further sub samples using a Folsom splitter. Samples were split until the aliquots contained a number of individuals that could be separated efficiently to enable them to be scanned by the ZooScan (sub sample fractions can be found in Appendix 1, Table 6.1). Sub- samples were made up to 500 ml and well mixed. A smaller aliquot of 25 ml was taken from the sub-sample and placed in a Hydroptic ZooScan (Biotom, Hydroptic, France). Samples were processed through the Hydroptic ZooScan using the methods described by Gorsky et al., (2010). In brief, the ZooScan body was filled with water and a clear frame inserted, taking care to avoid any bubbles. The 25 ml aliquot was gently poured into this water within the frame and plankton were gently separated using cactus sticks. The lid was closed, and a scan was taken. The sample was scanned at 2400 dpi using VueScan (Professional Edition, 9.0.51). A blank image was scanned each morning before use for background subtraction in the subsequent processing. The digitised scan was processed though imageJ to produce individual vignettes and data for all plankton scanned. These vignettes and data were uploaded onto Ecotaxa 2.0 (Picheral et al., 2017), an online machine assisted learning tool. Using this platform, plankton were identified and sorted into categories. Categories at this stage included Annelida, Amphipoda, Cheatognatha, Copepoda, Cnidarian, Euphausiacea, Gastropoda, Ostracoda and Salpa as well as categories for detritus and other non-biological material. At this stage, the plankton in each category were enumerated to ascertain relative abundances. Copepods and gastropods were found to have the greatest abundance across all samples (Figure 2.3). However, gastropods were patchily distributed between samples whereas copepods were universally abundant. A data filter was applied within the Ecotaxa 2.0 online software to select only copepods for further analysis, ensuring detailed body size measurements for each specimen were collected (Picheral et al., 2017). This procedure was performed on all 8 depth-strata sampled by each MOCNESS deployment.

2.2.3 Data Analysis

2.2.3.1 Scaling for water flow

All measurements, abundance counts and biomass estimates were scaled to the volume of water (m^3) that passed through the open net. The volume of water flow (m^3) of the net was calculated using (i) the time the net spent open (minutes), (ii) speed through the water (this speed varied around 2 knots therefore a nominal speed of 2 knots, converted to m/min, was used) and (iii) the average opening area (m^2) of the net, calculated using the sine of the angle (radians) of the net, reported from the down wire net monitor, as expressed in the following equation:

$$\text{Water flow } (m^3) = \text{net speed } (m\ min^{-1}) * \text{time opened } (min) * \text{opening area } (m^2)$$

(Equation 2.1)

Water flows and further net deployment details can be found in Appendix 1, Table 6.2.

2.2.3.2 Copepod Size Calibrations

Validation of copepod sizes was carried out by identifying and scanning a number of copepods from the samples. A total of 23 different copepod categories (defined by a stage class within each species where possible) were scanned, spanning varying stages of 11 species (Table 2.2). For each category identified, a minimum of 30 individuals were scanned using the ZooScan. These scans were processed in the same way as scanned sample aliquots (see below), via Ecotaxa. Pixel measurements were converted to mm using the same conversion before being averaged to give an average copepod length for each category. Average sizes were compared to size ranges found in the literature to ensure ZooScan sizes were comparable and could be used for further analysis. These average sizes were further converted to biomass (Table 2.2) as described below to enable species to be associated with biomass class intervals within the samples. When comparing total lengths obtained from the ZooScan, just under 50 % of the ZooScan measurements were smaller than those reported in the literature and approximately a quarter were larger (Table 2.2). The average difference between ZooScan measurements and reported literature values was 15 % (± 18 % SD). Natural variation is likely to account for a proportion of this difference, however, as ZooScan measurements were mainly smaller than literature values, it was assumed that Zooscan measurements often represented the dimensions of the prosome rather than the whole copepod.

2.2.3.3 Copepod size calculation

Copepod length was calculated using the 'object_major' measurement from the Ecotaxa output. This measurement relates to the maximum length of an ellipsoid drawn around the plankton and was chosen due to it being the best match available for the total length of each copepod (Gorsky et al., 2010). The object_major value was converted from pixels to mm using a conversion of 0.0106 mm/pixel according to the scan resolution detailed in Grosjean et al., (2004).

Total copepod lengths, as calculated from the object major measurement, were converted to ash free dry weight (AFDW) using conversions in Hopcroft et al., (2005). While these Hopcroft equations use prosome length and the present study nominally measures total length, the differences when converted into dry weight are likely to be very small. Furthermore, as highlighted above, it is most likely that many Zooscan measurements represented prosome rather than whole body dimensions. The following equations from Hopcroft et al., (2005) were applied in a length-specific manner:

1. Copepods with a length of less than 1mm

$$\log(\text{Ash Free Dry Weight [AFDW]}) = 3.16 * \log(\text{Prosome length [PL]}) - 8.18 \ (\mu m, \mu g) \qquad \textit{(Equation 2.2)}$$

2. Copepods with a length between 1 and 1.5 mm

$$\ln AFDW = 2.73 * \ln PL - 16.41 \ (\mu m, \mu g) \qquad \textit{(Equation 2.3)}$$

3. Copepods with a length between 1.5 and 3 mm

$$AFDW = 0.0101 * PL^{3.0996} \ (mm, mg) \qquad \textit{(Equation 2.4)}$$

4. Copepods with a length greater than 3 mm

$$AFDW = 0.0089 * PL^{3.4119} \ (mm, mg) \qquad \textit{(Equation 2.5)}$$

2.2.4 Size Spectra

Dry weight biomass, calculated using the equations above, was converted into carbon mass for size spectra analysis. A factor of 0.533 was used for the conversion of dry biomass to carbon biomass (µg C) (as used in Tarling et al., 2012), a % value that is midway within the range of conversion values reported by Omori (1969). Following this, 17 logarithmic (to the base 10) carbon weight size class intervals were generated with a width of 0.25, from -3 to 1.25 (in linear units, this is equivalent to 0.07 – 20924.77 µg C). Each copepod was assigned to a log category according to its carbon biomass. The sum of copepod biomass in each log category in each net was calculated to give a total carbon biomass per depth interval per deployment.

A normalised biomass spectrum was derived using the above carbon biomass data. Normalisation (log b) was achieved through dividing the log of the sum of the carbon biomass in each size interval by the width of the size interval (0.25). Due to the similarities between depths and the clustering seen within the samples, depths were combined to give three depth integrals: epipelagic (0-250m), upper mesopelagic (250- 625m) and lower mesopelagic (625- 1000m). The normalised slopes for these depth categories were plotted for all sampling times and locations in 2017/18 (JR17002).

After scanning, a sub-sample of each sample was sent to the Morski Instytut Rybacki, Poland to determine species and developmental stage to compare against the results generated by Zooscan and Ecotaxa. In brief, displacement aliquots of the sample were taken dependent upon the total volume of the sample. This aliquot ranged from ½ to 1/128th of the sample. Any organisms larger than 10 mm were removed from the aliquot and recorded before the sample was sorted. The aliquot was then sorted and all plankton identified to the lowest possible taxonomic level. The raw counts of each species were multiplied by the split of the sample to give whole sample counts for each species and development stage where possible.

2.2.5 Statistical Analysis

In order to investigate whether the copepod community structure differed across locations and time, multi-variate analyses were carried out on the biomass data from MOCNESS deployments in 2017/18 using PRIMER v7 (v7.0.13 PRIMER-e). Biomass in log carbon weight categories were imported into PRIMER as a sample-variable matrix, where each net from each MOCNESS deployment was a sample and variables consisted of the log weight categories, giving 32 samples across 19 variables. Samples were square root transformed to normalise the data. In order to carry out comparisons between the samples, Euclidean distances were calculated, and a resemblance matrix produced containing these distances. A group average cluster analysis was performed with a Type 1 similarity profile (SIMPROF) test to determine the underlying structure within the data. Following this, a non-metric multidimensional scaling (nMDS) analysis (Kruksal stress formula 1) was carried out, resulting in a multidimensional ordination representing the relative distances between samples in the underpinning resemblance matrix. The factors of location, time and depth were overlaid onto the nMDS in order to represent spatial ordinations of groups of samples.

To further understand the structuring reported by the SIMPROF test and ordination analyses, non-parametric analysis of similarities (ANOSIM) and similarity percentage (SIMPER) tests were performed. One-way ANOSIM tests were carried out separately for the factors of location, time and depth. The test generates a sample statistic (R) to assess the significance of each of the ANOSIMs. Where there was no statistical differences in factors, no further analysis on these factors was performed. Where differences in factors was significant, pairwise tests were carried out to assess further the nature of these differences. A SIMPER analysis was carried out at a resemblance level of 3.3 due to this being a level at which two clusters were seen. These tests were carried out using the size structure data to look for similarities in the log C weight categories between the samples.

Species	Stage	Prosome length reported in literature (mm)	Average size as calculated using Zooscan 'object_major' measurement (± SD) (mm)	Biomass as calculated from Hopcroft equations (AFDW, mg)	C mass (mg)	Log C mass (mg)
Calanoides acutus	CIV	2.68	2.50 ± 0.07	0.14	0.08	-1.12
Calanoides acutus	CV	3.84[d]	3.00 ± 0.07	0.23	0.12	-0.91
Calanus propinquus	CIII	1.75[d]	2.09 ± 0.07	0.10	0.05	-1.28
Calanus propinquus	CV	3.84[d]	4.08 ± 0.14	1.08	0.57	-0.24
Calanus simillimus	CIII	0.925[d]	1.45 ± 0.03	0.03	0.02	-1.77
Calanus simillimus	CIV	1.80[d]	1.83 ± 0.06	0.07	0.04	-1.46
Calanus simillimus	CV	2.30[d]	2.58 ± 0.06	0.19	0.10	-1.00
Ctenocalanus	CV	0.78[d]	1.07 ± 0.02	0.01	0.01	-2.13
Ctenocalanus	Male	0.99-1.45 (1.22)[a]	1.13 ± 0.02	0.02	0.01	-2.06
Heterorhabdus	CIV	1.80[d]	1.59± 0.03	0.04	0.02	-1.65
Lucicutia ovalis	CV	1.20-1.80 (adult)[a]	1.20± 0.04	0.02	0.01	-2.02
Metridia spp.	CIII	1.15[c]	1.11± 0.03	0.01	0.01	-2.11
Metridia	Male	1.50-3.70 (2.6)[a]	1.79 ± 0.03	0.06	0.03	-1.49
Metridia	CIV	1.55[c]	1.31± 0.03	0.02	0.01	-1.89
Metridia lucens	CIV	3.38-4.25 (3.8)[a]	1.28 ± 0.02	0.02	0.01	-1.90
Metridia lucens	CV	2.39-2.93 (2.66)[a]	1.70 ± 0.05	0.05	0.03	-1.56
Oithona frigidia	Female	1.13[b]	1.03 ± 0.03	0.01	0.01	-2.17

Species	Stage	Prosome length reported in literature (mm)	Average size as calculated using Zooscan ‘object_major’ measurement (± SD) (mm)	Biomass as calculated from Hopcroft equations (AFDW, mg)	C mass (mg)	Log C mass (mg)
Triconia spp.	All stages	0.59-1.26 (0.93)[a]	1.10 ± 0.02	0.02	0.01	-2.10
Rhincalanus gigas	CIII	2.88[d]	2.95 ± 0.11	0.29	0.15	-0.81
Rhincalanus gigas	CIV	4.20[d]	4.01 ± 0.13	1.02	0.54	-0.27
Rhincalanus gigas	CV	6.00[d]	4.40 ± 0.21	1.40	0.74	-0.13
Rhincalanus gigas	Female	6.46-9.30 (7.88)[a]	4.80 ± 0.26	1.88	1.00	0.00
Scolethricella	Female	1.08-2.39 (1.74)[d]	1.27± 0.03	0.02	0.01	-1.92
Euchaeta antarctica	adult	6.60-9.90 (8.25)[a]	NA	11.92	6.35	0.80

Table 2. 2: Southern Ocean copepod sizes obtained from ZooScan and literature with corresponding mass values using the ZooScan sizes. Biomass AFDW calculated by processing the average ZooScan values through equations found in Hopcroft et al., 2005: [1] $\log \mathrm{AFDW}=3.16*\log \mathrm{PL}-8.18$, [2] $\ln\mathrm{AFDW}=2.73*\ln\mathrm{PL}-16.41$, [3]$\mathrm{AFDW}=0.0101*\mathrm{PL}^{3.0996}$, [4]$\mathrm{AFDW}=0.0089*\mathrm{PL}^{3.4119}$. Carbon mass was then assumed to be 53.3 % of the AFDW as reported in Tarling et al., (2012). Letters denote literature used to obtain size range. a: Boltovskoy, (1999) b:Vervoort, (1957), c: Mizdalski, (1988), d: Ward (Unpublished data), e:Hsiao et al., (2004).

2.3 Results

ZooScan analysis showed a range of zooplankton taxa to be present within the samples from 2017/18 (Figure 2.3). When grouped into taxa, copepods were approximately 10 times more abundant than any other taxa, lending support to them being the most important component of the Scotia Sea plankton community. Gastropods were also found to have high abundances in some samples, however, this was not consistent across all nets.

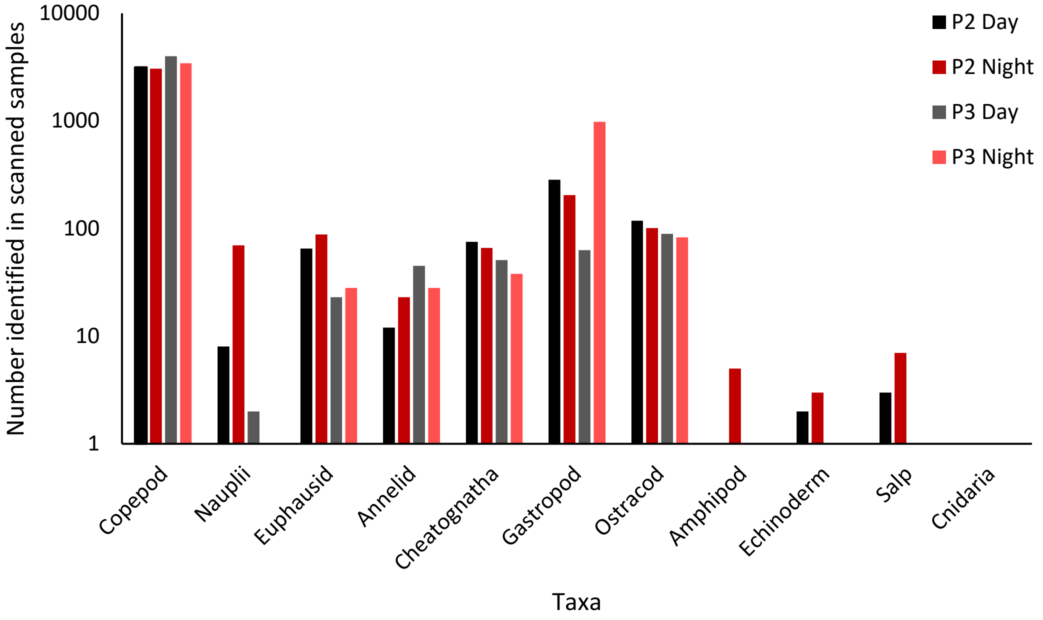


Figure 2. 3: Total relative numbers of zooplankton identified in each taxa across scanned sub-samples during 2017/18 (JR17002). Note log scale.

2.3.1 Inter-annual Changes

Inter-annual variation was observed in copepod abundance at P2 across the three years sampled (Figure 2.4), with the highest abundance being in 2017/18. The average copepod abundances across all net deployments in 2015/16 and 2016/17 were similar to each other (6.03 ± 0.01 SE and 8.9 ± 0.01 SE copepods m^{-3}, respectively), with each being approximately 30 % of the 2017/18 abundance (27.7 ± 0.04 SE copepods m^{-3}).

The size distribution of copepods at P2 was also comparable between years, with all samples having a main peak in copepods of 1.5 to 1.7 mm in length (Figure 2.5). However, samples taken in 2016/17 contained a greater proportion of copepods larger than 2 mm than was present in the other years.

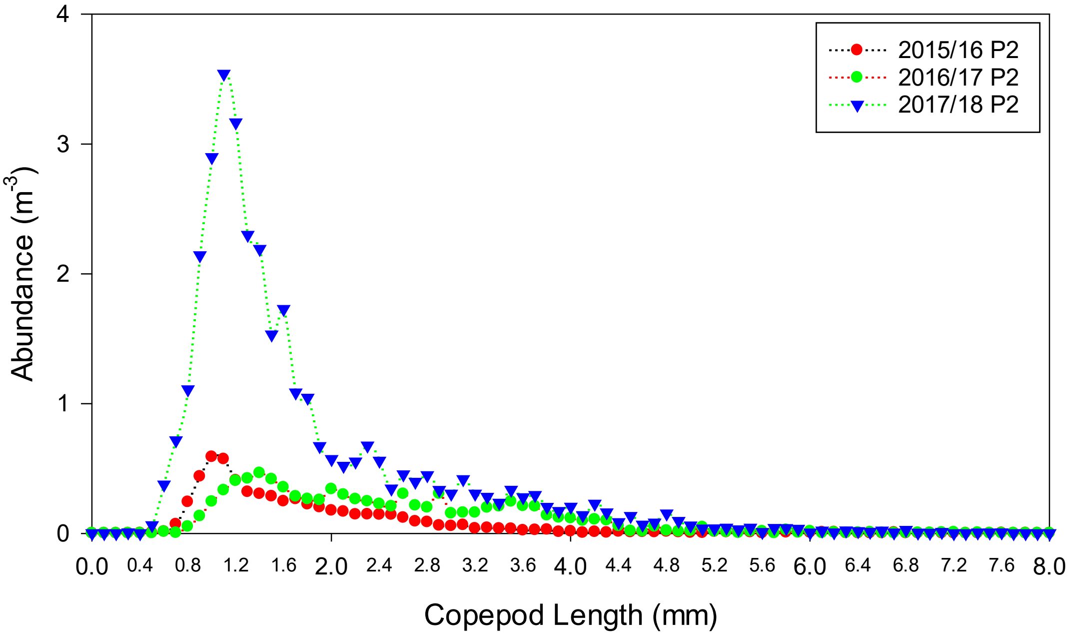


Figure 2. 4: Copepod abundance at P2 through their size range for all three years sampled. Copepod length as calculated from ZooScan measurements. Abundances represent averages across all MOCNESS deployments and nets within each deployment at P2 during each sampling campaign. Each point represents the abundance of copepods within a 0.1 mm copepod length range.

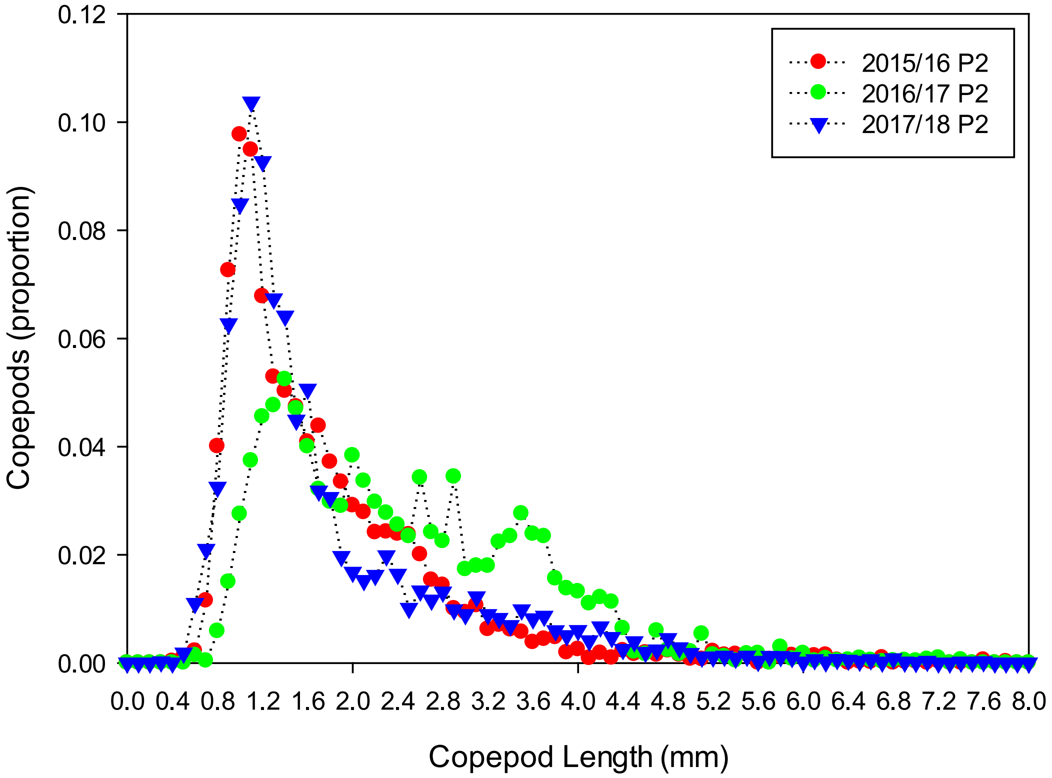
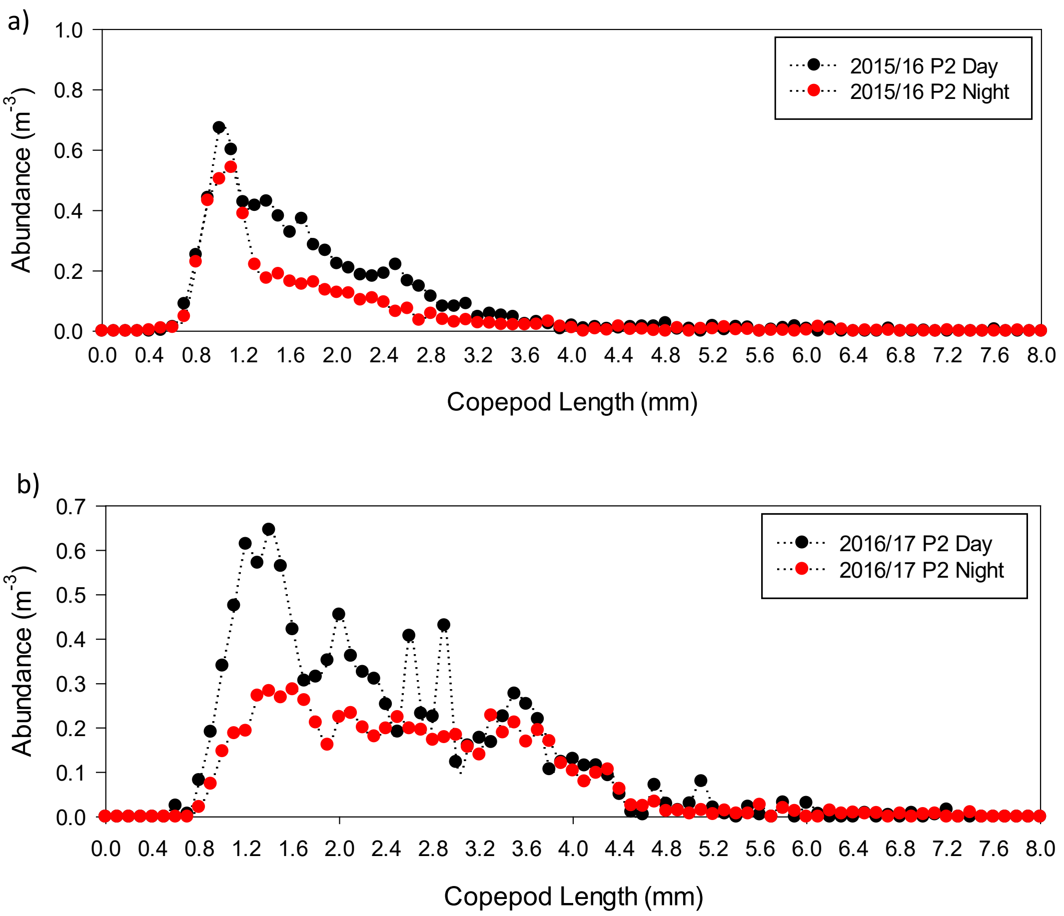


Figure 2. 5: Proportional abundance of copepods through their size range at P2 for three consecutive years. Proportions calculated from average number of copepods found across all MOCNESS deployments and nets at P2 during each sampling campaign. Each point represents the proportion of copepods within a 0.1 mm copepod length range.

2.3.2 Day/Night Changes

When comparing abundances between day and night for each year at P2, slight differences were found. Night samples had lower abundances than day samples (Figure 2.6), with the night time abundance found in 2016/17 being less than 65 % of that found during the day in this year. However, while abundances across the size ranges varied the size distribution range remained similar between day and night in each respective year. The greatest size range was found in 2016/17, where larger copepods had a greater abundance than either 2015/16 or 2017/18.



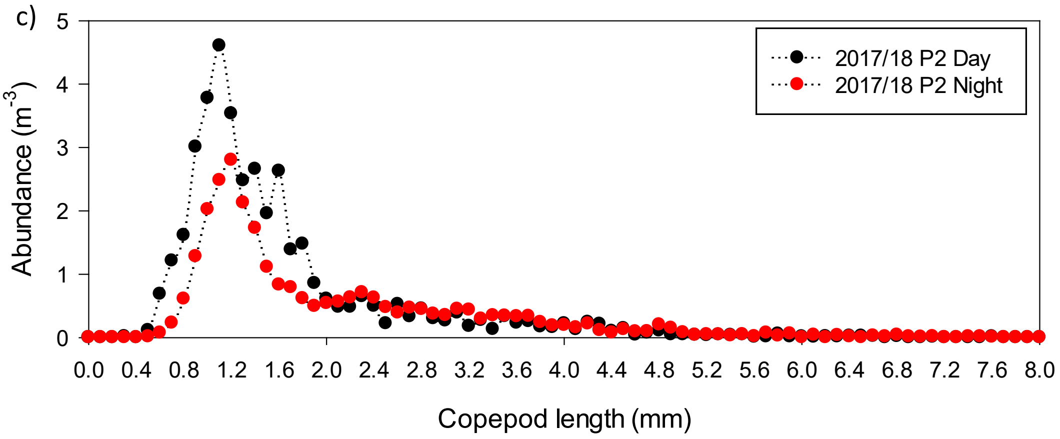


Figure 2. 6: Copepod abundance through the copepod size ranges found during day and night sampling (abundances averaged across all nets from 0-1000 m) at P2 for all three cruises with a) showing 2015 (JR15002), b) 2016/17 (JR16003) and c) 2017/18 (JR17002). Black denotes day time samples, red, night time samples. Each point represents the abundance of copepods within a 0.1 mm copepod length range.

2.3.3 Sample Location

A higher average copepod abundance was found at P3 (52 copepods m^{-3}) than P2 (34 copepods m^{-3}) during January 2018 (Figure 2.7). The size distribution of copepods also differed between the two sites. At P2, the copepod abundance was dominated by those of 1 mm length while, at P3, it was dominated by copepods of 1.2 mm in length and with larger copepods being present in greater numbers than seen at P2. In particular, copepods with an approximate length of 4 mm contributed to the copepod abundance at P3 to a much greater extent than observed at P2.

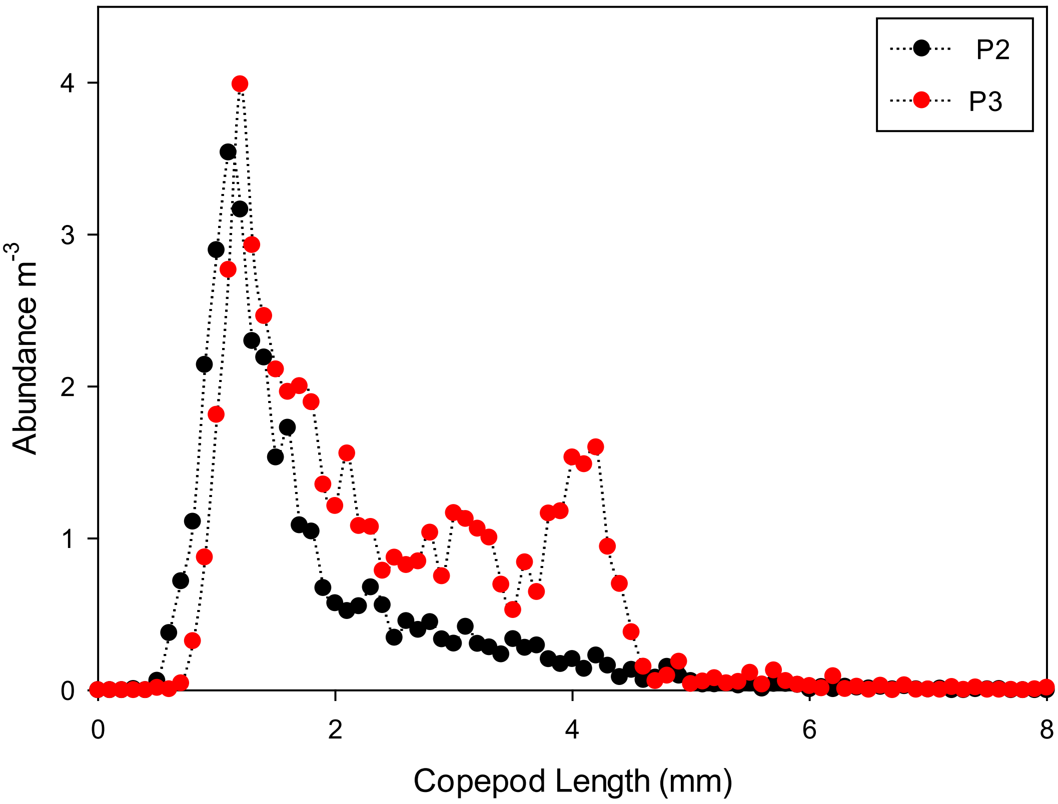


Figure 2. 7: Copepod abundance at P2 and P3 during austral summer 2017/18. Abundance data obtained from ZooScan measurements, averaged across all depths and deployments (day and night) for each station during 2017/18.

2.3.4 Taxonomic analysis

The taxonomic analysis showed a difference in the species composition from P2 and P3 and variations with depth at both sites (Table 2.3). At both sites, *Metridia* spp. of various stages (C3 through to adults) appears to have a high relative abundance at most depths. Copepod density was highest in shallow waters at both locations; however, the composition differed with location. At P2, these upper layers had a greater presence of smaller copepods such as *Oithona spp.*, *Ctenocalanus spp*. and *Scolethricella spp*. By comparison, the community at P3 appeared to be composed of relatively high abundances of larger calanoids such as *C. acutus* and *R. gigas*. At mesopelagic depths at both locations, there was a shift in species composition to include other species such as *Heterorhabdus spp, Triconia spp.* and *Lucicutia spp*; however, these copepods did not reach the same densities as those found in shallow waters.

	P2 Day				P3 Day			
Depth	Species	Stage	Whole sample count	Count per m^3	Species	Stage	Whole sample count	Count per m^3
5-125 m	*Metridia spp.*	C4	6272	27.65	*Calanoides acutus*	C4	9152	27.07
	Oithona atlantica	AD F	5504	24.26	*Calanoides acutus*	C3	4864	14.39
	Ctenocalanus spp.	C5	4352	19.18	*Calanoides acutus*	C5	3712	10.98
	Oithona spp.	C5	4096	18.05	*Calanus simillimus*	C5	1472	4.35
	Calanus simillimus	C3	3968	17.49	*Rhincalanus gigas*	C4	960	2.84
125-250 m	*Metridia lucens*	C5	4512	12.63	*Calanoides acutus*	C5	12096	32.67
	Metridia spp.	C4	2848	7.97	*Metridia lucens*	C5	6592	17.8
	Calanoides acutus	C4	1024	2.87	*Calanoides acutus*	C4	6208	16.77
	Ctenocalanus spp.	C5	960	2.69	*Metridia spp.*	C4	5312	14.35
	Scolecithricella minor	AD F	800	2.24	*Rhincalanus gigas*	C3	1984	5.36
250-375 m	*Ctenocalanus spp.*	C5	2592	7.61	*Metridia spp.*	C4	7424	18.29
	Metridia lucens	C5	1920	5.64	*Metridia lucens*	C5	7296	17.98
	Metridia spp.	C3	1440	4.23	*Calanoides acutus*	C5	4992	12.3
	Calanoides acutus	C4	1408	4.14	*Metridia lucens*	AD M	3136	7.73
	Metridia spp.	C4	960	2.82	*Metridia lucens*	AD F	1984	4.89
375-500 m	*Metridia lucens*	C5	2784	9.11	*Calanoides acutus*	C5	4384	11.47
	Ctenocalanus spp.	C5	2432	7.96	*Metridia lucens*	AD M	3232	8.45
	Metridia lucens	AD M	1568	5.13	*Metridia lucens*	C5	1600	4.19
	Ctenocalanus spp.	AD M	1248	4.08	*Metridia spp.*	C4	1536	4.02
	Metridia lucens	C4	1056	3.46	*Metridia lucens*	AD F	736	1.93

	P2 Day				P3 Day			
Depth	Species	Stage	Whole sample count	Count per m^3	Species	Stage	Whole sample count	Count per m^3
500-625 m	*Ctenocalanus spp.*	C5	1856	5.51	*Triconia spp.*	AD F	1200	3.9
	Metridia lucens	C5	1824	5.42	*Calanoides acutus*	C5	1008	3.27
	Ctenocalanus spp.	AD M	1792	5.32	*Heterorhabdidae*	C4	480	1.56
	Calanoides acutus	C5	960	2.85	*Scolecithricidae*	C5	384	1.25
	Metridia lucens	AD M	896	2.66	*Scolecithricidae*	C4	320	1.04
625-750 m	*Ctenocalanus spp.*	C5	680	2.21	*Triconia spp.*	AD F	2144	6.18
	Triconia spp.	AD F	512	1.67	*Calanoides acutus*	C5	1152	3.32
	Calanoides acutus	C5	360	1.17	*Metridia lucens*	AD F	416	1.2
	Metridiidae	C3	176	0.57	*Heterorhabdidae*	UN	352	1.01
	Metridia spp.	C4	160	0.52	*Calanoides acutus*	C4	256	0.74
750-875 m	*Ctenocalanus spp.*	C5	608	2.11	*Triconia spp.*	AD F	452	1.34
	Triconia spp.	AD F	400	1.39	*Calanoides acutus*	C5	396	1.17
	Calanoides acutus	C5	172	0.6	*Calanoides acutus*	C4	156	0.46
	Metridia spp.	C4	116	0.4	*Lucicutia ovalis*	C5	156	0.46
	Lucicutia spp.	C4	44	0.15	*Metridia spp.*	C4	100	0.3
875-1000 m	*Triconia spp.*	AD F	784	1.91	*Triconia spp.*	AD F	1808	5.49
	Lucicutia spp.	C5	288	0.7	*Calanoides acutus*	C5	504	1.53
	Calanoides acutus	C5	264	0.64	*Calanoides acutus*	C4	248	0.75
	Heterorhabdus spp.	C4	152	0.37	*Metridia spp.*	C3	192	0.58
	Ctenocalanus spp.	C5	128	0.31	*Metridia curticauda*	C5	144	0.44

Table 2. 3: Copepod species and stages found to be most abundant in MOCNESS nets at different depth strata for P2 and P3 daytime samples during 2017/18. Taxonomy and counts carried out by Morski Instytut Rybacki, Poland. C represents copepodite and the subsequent number the specific developmental stage; AD F – adult female; AD M – adult male; UN – developmental stage unclassified

2.3.5 Depth Stratification

Copepod abundance distribution through the water column was largely unchanged from day to night at both P2 and P3 (Figure 2.8). Proportionally, abundance was dominated by copepods collected from shallow water with over 75 % of the copepods collected in all samples being found in the top 500 m and 50 % collected from the top 250 m in the day and night at P3 and day at P2. However, at both P3 and P2, the proportion of copepods found in the top 125 m reduced in relative terms at night compared to the day.

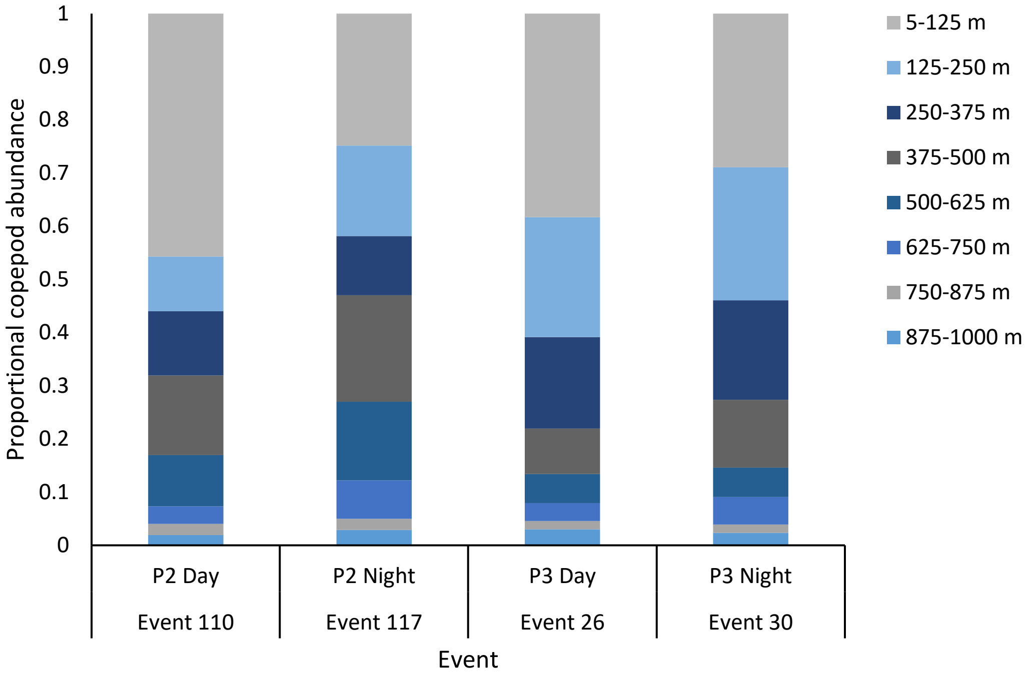


Figure 2. 8: Proportional copepod abundance for each depth interval in relation to the total catch in each MOCNESS deployment for day and night catches at P2 and P3 during 2017/18.

In line with abundance, copepod biomass was also greatest in the upper water column at both locations, with 50 % of the biomass being present in the surface 500 m at P2 and 250 m at P3 (figure 2.9). However, once converted from length to AFDW, the stratification patterns seen within the water column changed, with the proportion of biomass in the top strata being comparatively lower. At P2, the greatest proportion in copepod abundance was found to be in the top 125 m whilst the greatest proportion of biomass was found to be at a greater depth of 375-500 m. P3 also showed a slight deepening in the greatest proportion of biomass when compared to abundance, with the former being found in the top 125 m and the latter, slightly deeper, at 125- 250 m.

In addition to this, the proportion of biomass within the different depth strata changed between day and night at both sampling locations. Biomass found within the top 500 m was greatest during the day at both sites, with an increase in biomass below 500 m during the night. At P2 at night, a reduction in the proportion of biomass was seen at 5-125m, 250-500 m and 875-1000m while it increased at 125-250 m and 500-750 m. By comparison, at P3 at night, an increase in the relative biomass was seen at 125- 250 m and 375- 500 m, while there was a reduction at 5-125m and 250-375 m. Nevertheless, these proportional changes between day and night were notably smaller in P3 compared to P2. Overall, the distribution of biomass within mesopelagic depths showed some marked changes between day and night at P2 that were not observed at P3, while day-night changes in the epipelagic layers appear minimal at both sites.

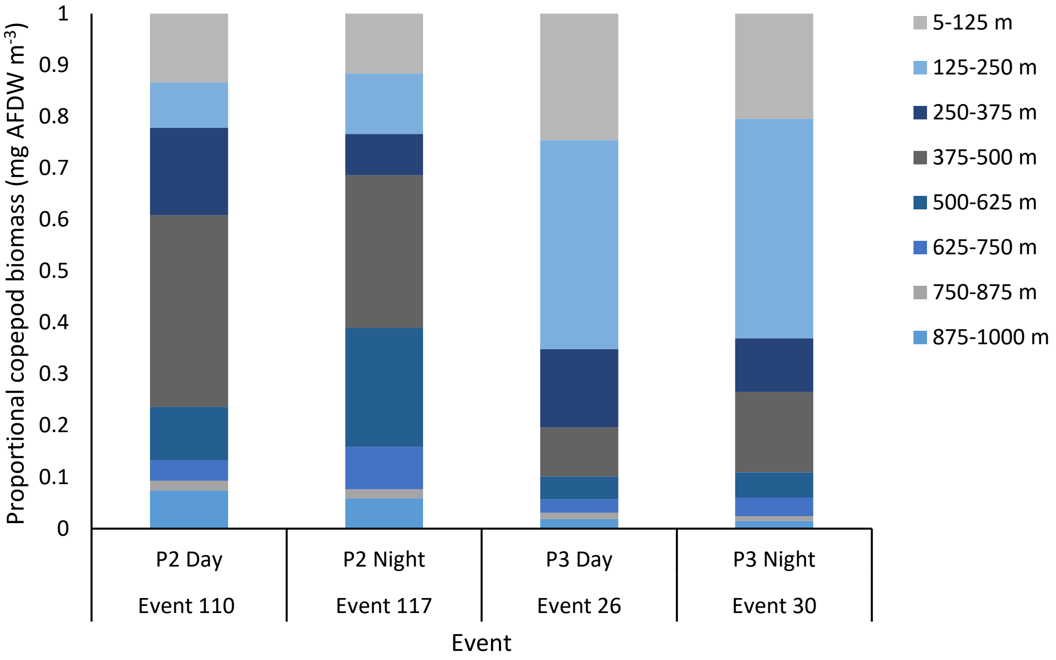


Figure 2. 9: Proportional copepod biomass (ash free dry weight, AFDW) for each depth integral in relation to the total catch in each MOCNESS deployment for day and night catches at P2 and P3 during 2017/18.

2.3.6 Size contribution to biomass

Copepod community biomass was dominated by larger copepods at both P2 and P3 (Figure 2.10). Copepods with a length smaller than 3 mm had a negligible contribution to the total, despite being numerically abundant (Figure 2.7). Biomass was higher at P3 across all sizes, in line with a higher abundance overall (Figure 2.7). In addition to this, at P3, biomass was heavily dominated by copepods of approximately 4 mm in length, whilst the biomass was spread more evenly across copepods ranging from 3.5 to 8 mm at P2 (Figure 2.10).

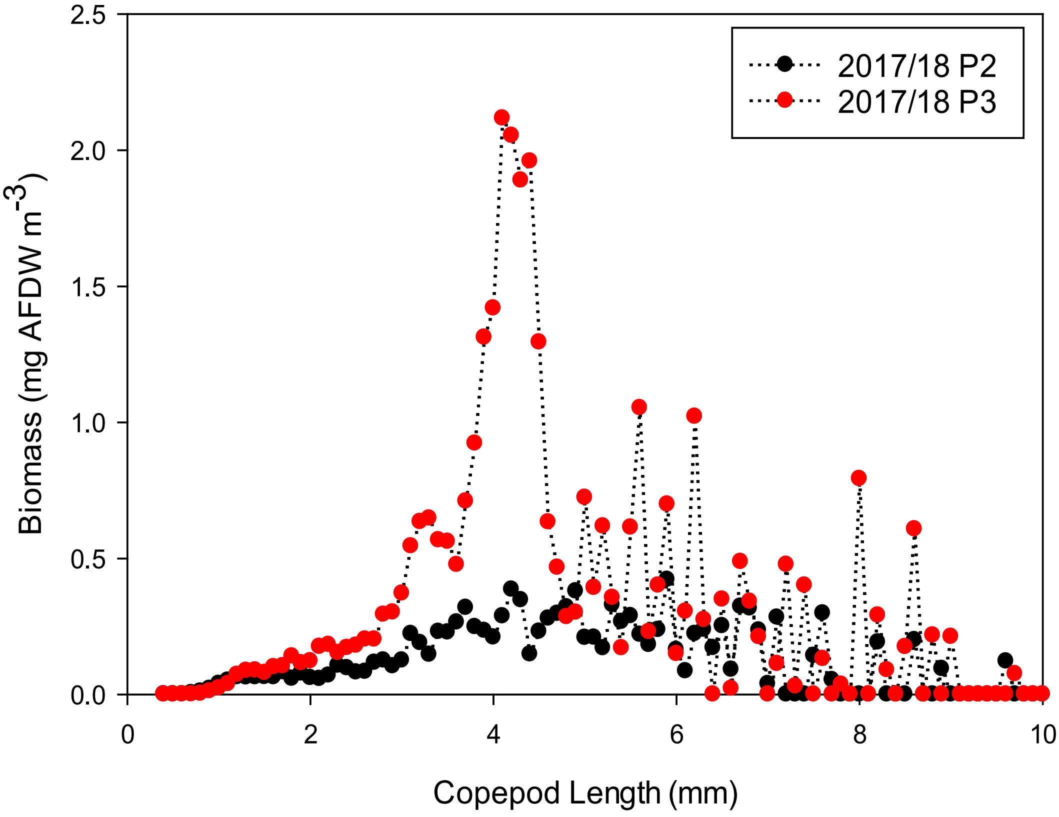


Figure 2. 10: Copepod biomass (ash free dry weight, AFDW) across the copepod length range, as converted from the Object_major measurement, averages for all depths and net deployments for P2 and P3 during austral summer 2017/18.

2.3.7 Log Spectra

After converting AFDW to carbon (C) content (using a C content of 0.533 AFDW) copepods were assigned to a corresponding logarithmic weight class. Both locations had similar copepod size spans, with copepods ranging from -2.5 log C weight to 1 log C weight at both P2 and P3 (Figure 2.11 and Figure 2.12). However, the composition of the copepod community across the logged size spectra differed. At P2, copepod C biomass was more spread across the C weight size classes. However, certain classes made a large contribution to the C biomass, particularly between -0.5 to 0 log C weight. At P3, biomass was more heavily dominated by a small number of size classes, in particular copepods within the -0.25 log C weight class.

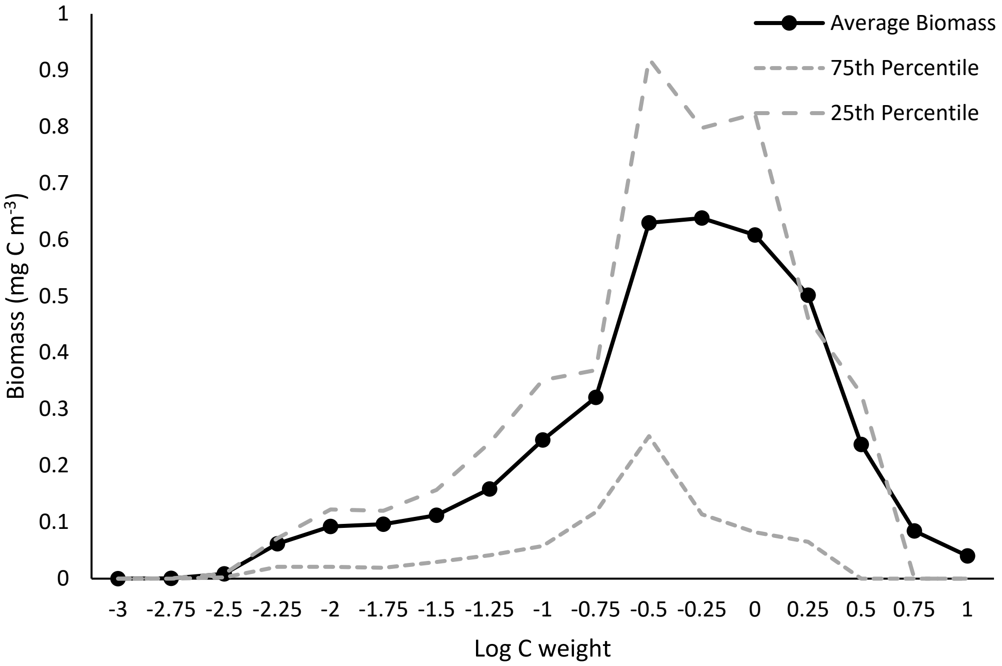


Figure 2. 11: Copepod carbon (C) biomass found at P2 in 2017/18 across logged C weight size intervals. C biomass averaged across all nets within both day and night MOCNESS deployments. Dashed lines show 25th and 75th percentiles.

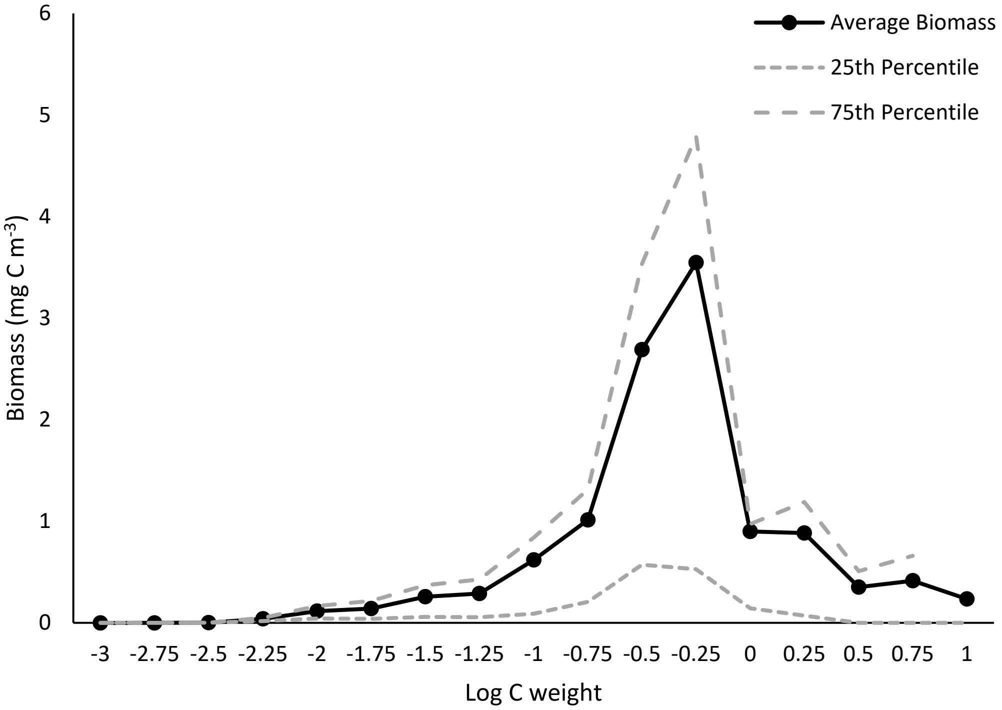


Figure 2. 12: Copepod carbon (C) biomass found at P3 in 2017/18 across logged C weight size intervals. C biomass averaged across all nets within both day and night MOCNESS deployments. Dashed lines show 25th and 75th percentiles.

2.3.8 Depth discrete size structure

Stratifying the sample set according to discrete net depth revealed further variability in size structure of the copepod community through the water column. The depth specific size spectra were also influenced by time and location (Figure 2.13 and Figure 2.14). At both locations, a more complex size structure was found within the epipelagic and upper mesopelagic layers. However, this structure differed between the two sites, with P2 having a greater variability across the different depths than P3. At P2, the uppermost 200 m contained copepods encompassing a wide size span, starting at -2.5 log C weight through to 0.2 log C weight (Figure 2.13). As depth increased, the highest copepod C biomass was found in larger size classes, suggesting that the more abundant smaller copepods such as *Ctenocalanus spp*., *Metridia spp*. and *Oithona spp*. make a greater contribution to the copepod C biomass in shallow waters than deeper waters. Differences were also observed between day and night at P2. During the day, the maximum C biomass was often found to be in the -0.75 log C weight category, with large secondary C biomass peaks being present in larger size categories, suggesting that the C biomass was dominated by large calanoids such as *R. gigas* and *C. propinquus* throughout the water column. During the night, at P2, the majority of the biomass was above 750 m (Figure 2.13). Unlike the day sample, no single size class-dominated the C biomass throughout the water column.

At P3, the copepod size structure remained relatively constant throughout the water column across day and night, despite C biomass decreasing with depth (Figure 2.14). Here, the copepod size constituting the majority of the C biomass was the -0.25 log C weight class. This size class was likely comprised of larger calanoid species, suggesting that they play a greater role in the copepod community at P3 than at P2.

Copepods within larger size classes (above 1.0 log C weight) contributed substantially to the C biomass at both locations. This size class was larger than that attributed to the largest copepod scanned within the ZooScan calibrations, i.e. *Rhincalanus gigas*. This suggests that larger copepods, such as *Euchaeta* spp. were present within the samples, despite their absence when looking at the highest numerically abundant species (Table 2.3). Due to this absence, *Euchaeta* spp. were not selected for ZooScan calibration, however they have a length between 6.6 and 9.9 mm for adults (Boltovskoy, 1999), placing them in a log C weight category of 1.0 or above. It is therefore likely that, while *Euchaeta* spp. may not be numerically abundant, they make an important contribution to copepod community C biomass in the region.

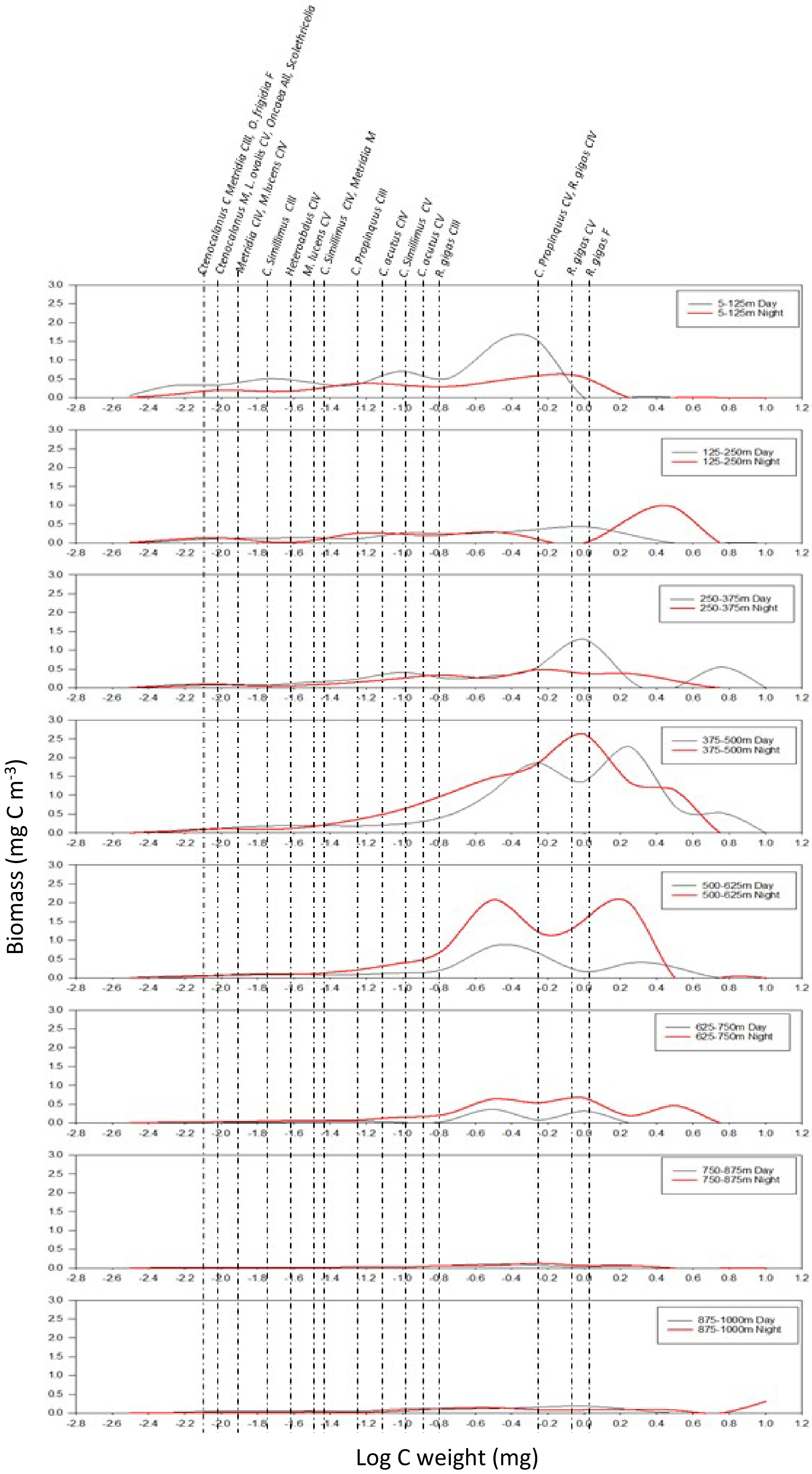

Ctenocalanus C Metridia CIII, O. frigida F
Ctenocalanus M, L. ovalis CV, Oncaea All, Scolethricella
Metridia CIV, M.lucens CV
C. Simillimus CIII
Heteroabdus CIV
M. lucens CV
C. Simillimus CIV, Metridia M
C. Propinquus CIII
C. acutus CIV
C. Simillimus CV
C. acutus CV
R. gigas CIII
C. Propinquus CV, R. gigas CIV
R. gigas CV
R. gigas F
5-125m Day
5-125m Night
125-250m Day
125-250m Night
250-375m Day
250-375m Night
375-500m Day
375-500m Night
500-625m Day
500-625m Night
625-750m Day
625-750m Night
750-875m Day
750-875m Night
875-1000m Day
875-1000m Night
0.0
0.5
1.0
1.5
2.0
2.5
3.0
-2.8
-2.6
-2.4
-2.2
-2.0
-1.8
-1.6
-1.4
-1.2
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Biomass (mg C m-3)
Log C weight (mg)

Figure 2. 13: Copepod carbon (C) biomass in Log C categories within 125m net intervals at P2 during 2017/18. Depth increases from the top of the panel to the bottom with the shallowest depth of 5-125m at the top and the deepest samples (875-1000m) at the bottom. Black lines represent day samples; red lines show night samples. Dashed lines represent placings of key species scanned for ZooScan calibrations.

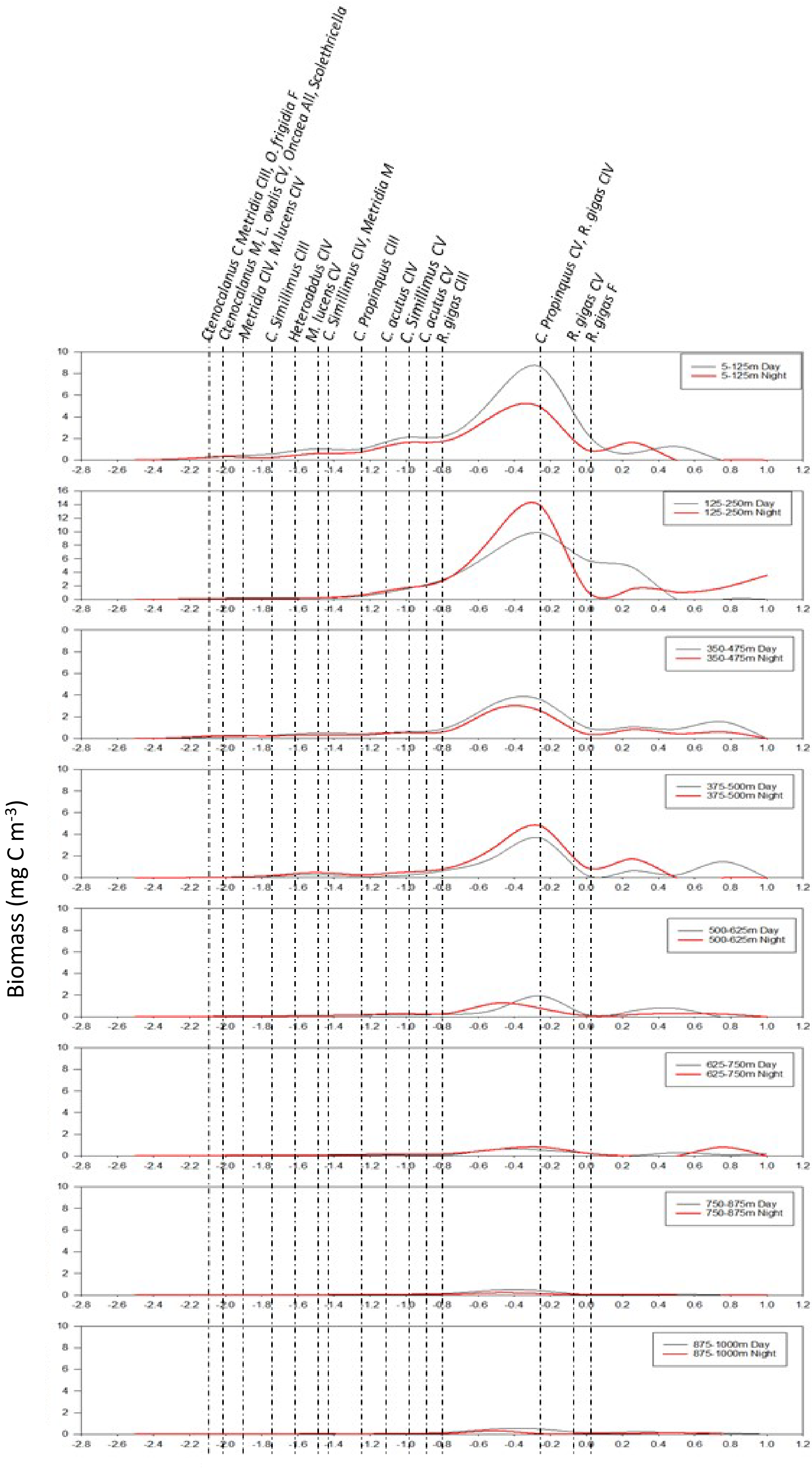

Ctenocalanus C Metridia CIII, O. frigidia F
Ctenocalanus M, L. ovalis CV, Oncaea All, Scolethricella
Metridia CIV, M.lucens CIV
C. Simillimus CIII
Heteroabdus CIV
M. lucens CV
C. Simillimus CIV, Metridia M
C. Propinquus CIII
C. acutus CIV
C. Simillimus CV
C. acutus CV
R. gigas CIII
C. Propinquus CV, R. gigas CIV
R. gigas CV
R. gigas F
5-125m Day
5-125m Night
125-250m Day
125-250m Night
350-475m Day
350-475m Night
375-500m Day
375-500m Night
500-625m Day
500-625m Night
625-750m Day
625-750m Night
750-875m Day
750-875m Night
875-1000m Day
875-1000m Night
Biomass (mg C m^{-3})
Log C weight (mg)
-2.8
-2.6
-2.4
-2.2
-2.0
-1.8
-1.6
-1.4
-1.2
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0
2
4
6
8
10
12
14
16

Figure 2. 14: Copepod carbon (C) biomass in Log C categories within 125m net intervals in P3 during 2017/18. Depth increases from the top of the panel to the bottom with the shallowest depth of 5-125m at the top and the deepest samples (875-1000m) at the bottom. Black lines represent day samples; red lines show night samples. Dashed lines represent placings of key species scanned for ZooScan calibrations.

2.3.9 Sample Structure

Multi-variate analysis on the size structure of P2 and P3 day and night samples from 2017/8 revealed further patterns within the data. Cluster analysis formed a number of groups within the biomass data (Figure 2.15). An initial branching resulted in two groups, a smaller group containing shallow nets from P3 and a second group containing the remainder of the samples. Secondary branching within the larger group resulted in a cluster containing samples exclusively from depths above 500m from both P2 and P3 day and night. The other secondary branch contained a wide range of samples across all the data, including a cluster made up of samples exclusively from deep water (625-1000m).

The nMDS plot showed deep samples positioned close together whilst samples from shallow depths appear to be more separated (Figure 2.16). This indicates that samples from similar depths were more similar in both size structure and abundance than samples from different depths, irrespective of location or time. Within deep water, C biomass across the size spectrum is relatively equal when compared to shallow water samples (Figures 2.13 and 2.14), resulting in deep samples being close to each other in the underpinning resemblance matrix. However, in the shallow water samples, the C biomass peaks for the larger copepods vary greatly in magnitude and position within the size spectrum, resulting in samples differing more from each other. Supporting this, ANOSIM analysis found no significant differences between location or time of day but depth was found to be a significant factor for the differences seen in the samples (R=0.287, significance level= 0.1 %).

A subsequent SIMPER analysis identified the -0.75 and 0.25 Log C weight categories to be driving the differences seen within the samples. Of these categories, -0.25 was found to account for a third of the variation within the samples, followed by -0.5, accounting for 21 %.

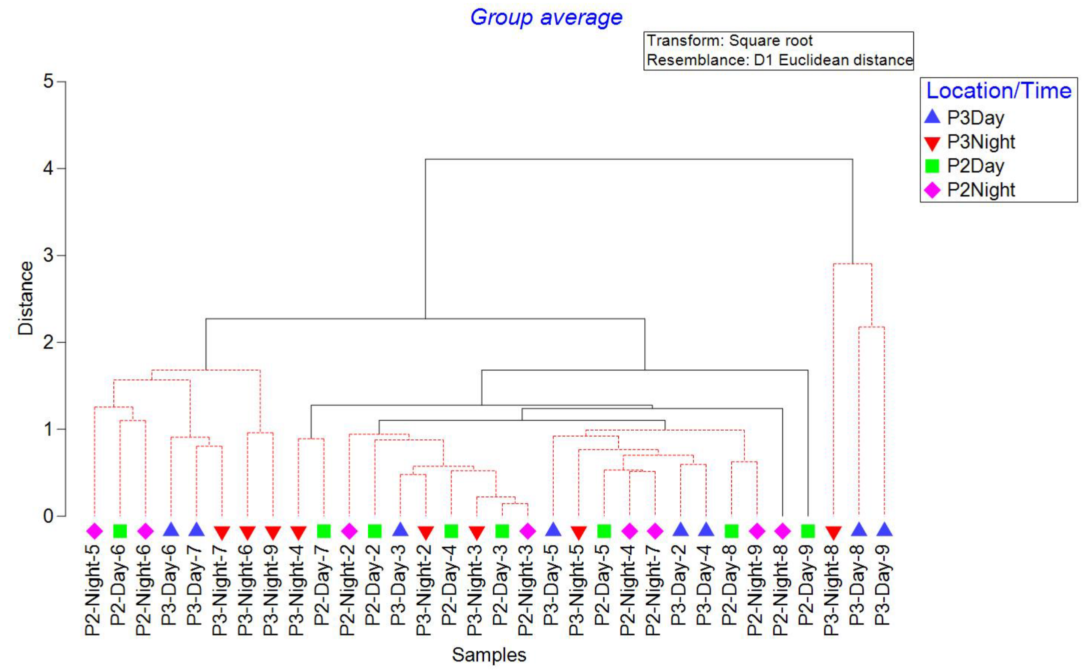


Figure 2. 15: Dendogram showing cluster analysis on biomass found in Log C categories of the MOCNESS nets. Numbers relate to net depths with 9 being the shallowest (surface to 125m) and 2 being the deepest (875-1000m). Red, dashed lines show groups found to be significantly clustered following SIMPROF analysis.

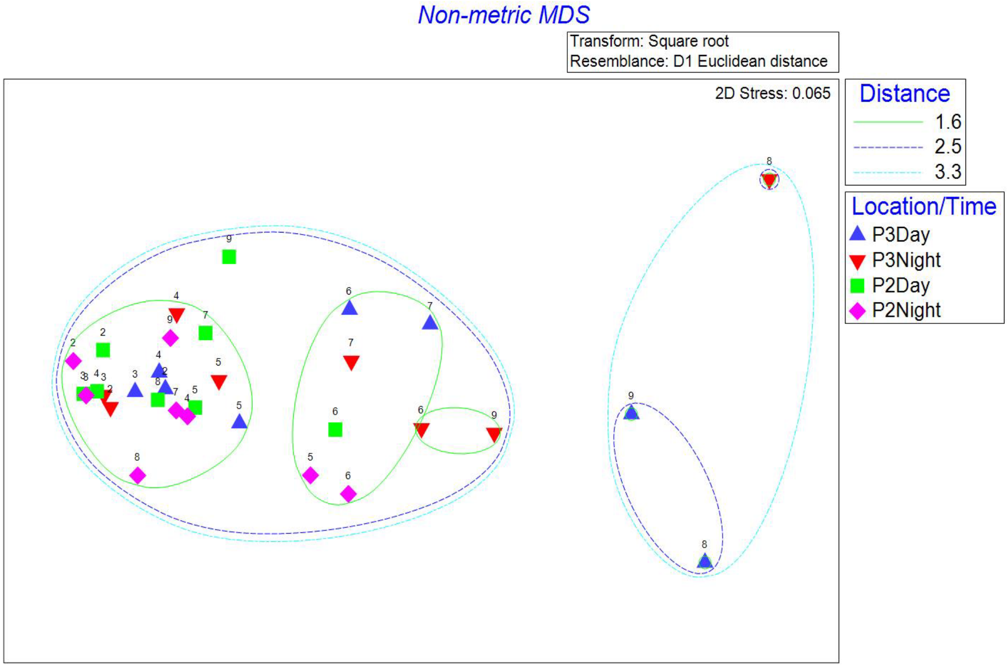


Figure 2. 16: nMDS plot of the copepod biomass found in the MOCNESSS deployments at P2 and P3. Numbers refer to 125m net intervals, with 9 being the shallowest (surface to 125m) and 2 being the deepest (875-1000m). Clusters overlain at 1.6, 2.5 and 3.3 % dissimilarities.

2.3.10 Normalised Biomass Spectra

Regressions fitted to the log size structured data were significant (Figure 2.17). However, in some cases the R^2 values were quite low (for example P3 day epipelagic: 0.13 and P2 night upper mesopelagic: 0.31), showing that there was a lot of unexplained variance around the slopes. This illustrates that, in certain depth strata, the copepod community does not conform to negative linear regression for normalised biomass spectra. In the following, I identify those instances where large variances around the slope were particularly evident, as well as the slope gradients in those where a linear regression was at least a reasonable fit.

The average regression gradient for all depths, locations and times was -0.56. However, these slopes varied slightly with depth, location and time (Figure 2.17). In general, the slopes found at P3 during the day were shallower than those during the night or at P2. However, slope gradients were not found to be significantly different between locations or times (Paired t-tests, assessing slope gradients from each depth integral at each location and time: P2 Day vs P2 Night, P=0.90, P3 Day vs P3 Night, P= 0.07, P2 day vs P3 day, P=0.91, P2 Night vs P3 Night, P=0.78). The lower mesopelagic biomass had, on average, the steepest regressions, whilst the upper mesopelagic biomass had the shallowest gradients across both locations and times.

At P2, the steepest regression slope was in the day time epipelagic sample, which also had a reasonable R^2 indicating a reliable representation of energy flow through the size classes. The night time upper mesopelagic sample had the gentlest slope but also a low R^2 value (Table 2.4), indicating that, at this depth strata and time, the energy retention within the copepod community was not accurately depicted using a linear regression. Slopes also varied slightly across the time points at P2, with the epipelagic and upper mesopelagic slopes being shallower at night than the day sample. In contrast to these depths, the lower mesopelagic slope remained similar across both times and had a good fit, suggesting that energy retention remained similar within this depth strata across day and night.

At P3, the day time epipelagic sample had the shallowest regression, with the day time lower mesopelagic sample having the steepest regression. There was a variation in slopes across day and night caused by a steeper epipelagic slope during the night than the day. The upper and lower mesopelagic slopes remained similar at both time points. However, in contrast to P2, the R^2 values associated with the regression slopes were low (Table 2.4), indicating that the copepod community at this location does not conform to linear regressions for normalised biomass spectra. Nevertheless, R^2 values were consistent across day and night in the mesopelagic depth strata and, when combined with similar slope gradients, indicate that the copepod community remained similar at both time points.

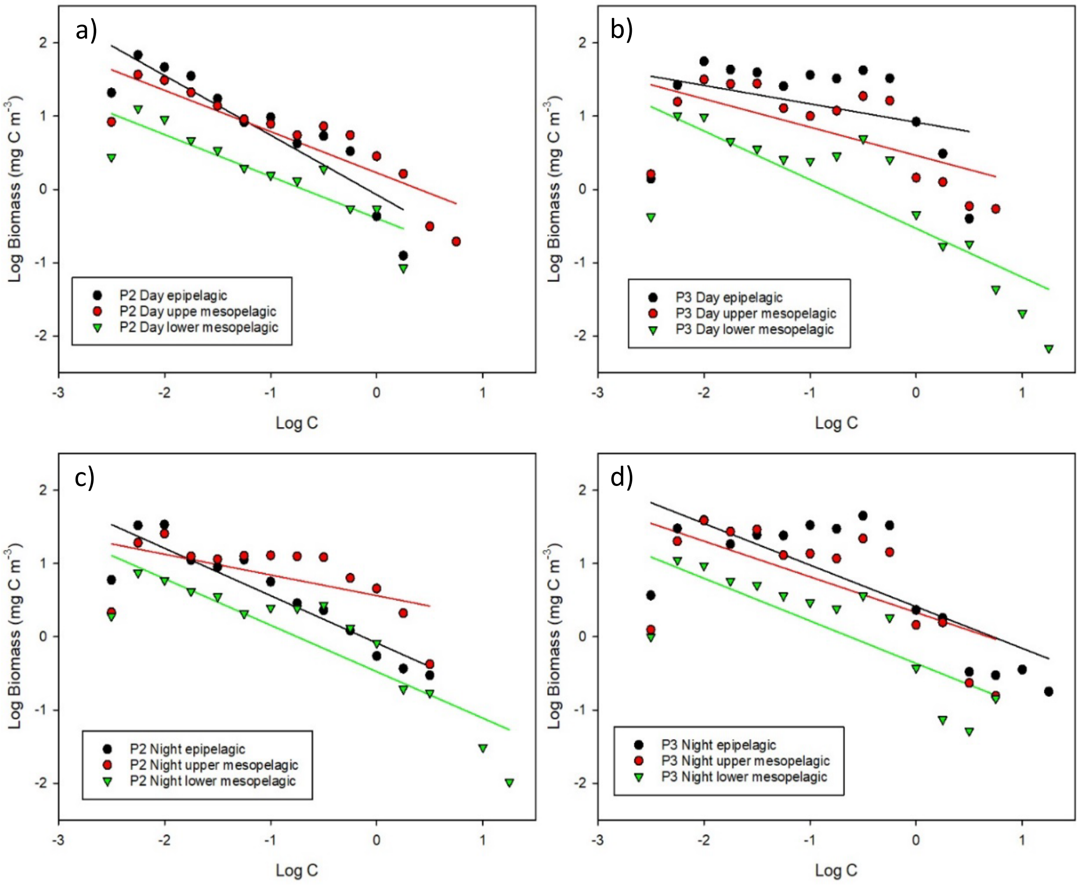


Figure 2. 17: Normalised carbon (C) biomass spectra for a) P2 day, b) P3 day, c) P2 night and d) P3 night. Depth integrals combined to create three depth categories: Epipelagic 0-250m, denoted by black circles and black regression line, upper mesopelagic, 250-625m, denoted by red circles and red regression line, and lower mesopelagic, 625-1000m, denoted by green triangles and green regression line.

	P2 Day		P2 Night		P3 Day		P3 Night	
	regression gradient	R^2	regression coefficient	R^2	regression coefficient	R^2	regression coefficient	R^2
Epipelagic	-0.81	0.82	-0.65	0.83	-2.5	0.13	-0.57	0.57
Upper mesopelagic	-0.56	0.77	-0.28	0.31	-0.39	0.39	-0.49	0.41
Lower mesopelagic	-0.57	0.77	-0.64	0.77	-0.67	0.65	-0.58	0.62

Table 2. 4: Regression gradients and R^2 values for the regression slopes shown in Figure 2.17. Epipelagic values refer to the black lines in Figure 2.17, upper mesopelagic are associated with the red lines and lower mesopelagic with the green lines.

2.4 Discussion

The present study aimed to gain a greater understanding of the size structure within the copepod community at two locations in the Scotia Sea. It was expected that size structure would be influenced by primary productivity regimes, depth and time of day. In line with this, the study found that the copepod community structure differed at the two sample sites. A high abundance of copepods was found at both locations, however, a greater number of larger copepods were present at P3, in line with the higher levels of primary productivity there (Korb et al., 2012). At both locations, the copepod community encompassed a range of differently sized copepods, with P2 displaying a greater size range. The species composition also differed, with larger copepods, such as *Calanoides acutus* and *Rhincalanus gigas*, being more dominant at P3, while P2 was dominated by smaller copepods such as *Oithona spp*. and *Metridia spp.* The majority of the copepod biomass was located in the upper 500 m where a small number of species were particularly dominant. At P2, the surface 500m contained approximately 60 % of the copepod biomass, whilst the upper 500m at P3 contained around 90 %. There was a greater similarity between sites in the species compositions below 500m compared to above 500m, with *Metridia spp., Triconia spp.* and *Ctenocalanus spp.* being relatively dominant at depth in both sites. Normalised biomass regression slopes were similar at both locations, with slightly steeper slopes being found in the deeper depths. However, the variability around these slopes was sometimes large, indicating that the community in certain depth strata did not conform to such linear size-spectral relationships. In terms of multivariate structure, depth had a greater influence on clustering patterns than location or time of day. Day and night samples were found to differ slightly in abundance, which was higher during the daytime.

2.4.1 ZooScan Evaluation

In the present study, a non-destructive imaged-based technique to measure biomass from preserved samples was used. While biomass measurements would ideally be taken from fresh samples, this is often impractical during ship based sampling (Kapiris et al., 1997). Here, I used the ZooScan and its associated software to extract copepod size data from preserved zooplankton at the home laboratory. The size data produced by the ZooScan in the present study differed slightly from copepod lengths published within the literature. However, these differences were not consistent across all copepod species, likely resulting in the ZooScan providing a reasonably accurate measurement for the present purposes.

The differences between ZooScan measurements and those in the literature may be as a result of many published lengths referring to prosome length rather than total length. The ZooScan works by measuring an image produced when the zooplankton are scanned (Gorsky et al., 2010) and is not able to determine the different sections of an individual zooplankton. This leads to the measurements incorporating all sections, potentially leading to a measure greater than the prosome lengths reported in other studies. This may have implications when using ZooScan measures to obtain biomass, as many conversions, including those found in Hopcroft et al., (2005), calculate biomass using prosome length. This issue has been considered previously, with Schultes & Lopes (2009) finding that copepod biovolumes were 67 % larger when using measurements taken from the ZooScan than when using prosome lengths obtained by microscopy methods.

This inclusion of the whole copepod may explain some of the large sizes reported by the ZooScan, however the vast majority of the average species measurements were found to be smaller than those reported within the literature. This may be explained by the method by which the ZooScan images plankton. The ZooScan is a flatbed scanner, using a light beam passing underneath the bed to image the plankton that are suspended in water (Gorsky et al., 2010; Grosjean et al., 2004). This suspension allows plankton to be orientated in a number of ways, including orientations where length is not discernible. If a copepod was to be orientated vertically rather than horizontally, the maximum length measured by the ZooScan would be the width rather than the total length, leading to shorter lengths. However, during the validation process within the present study, copepods deemed to be too far from a horizontal orientation were discounted in order to reduce this source of bias. In addition, zooplankton within a liquid may be positioned in a number of planes, and while care was taken to ensure copepods were on the base of the scanner, this was not always possible. Any copepods that were not lying on the base of the scanner but were suspended or floating at the surface would appear to be smaller due to the distance between them and the light source. This would not be picked up during the validation stage and may reduce the average size of the copepods scanned. However, as care was taken to ensure as many copepods as possible lay on the base of the scanner, any decrease in average size as a result was not likely to be substantial.

2.4.2 Primary Production and Energy Retention

The present study examined two differing primary productivity regimes within the Scotia Sea. The first, P2, is upstream of South Georgia and an oceanic nutrient poor area, while the second, P3, is an oceanic area downstream of South Georgia, enriched with nutrients and highly productive (Korb et al., 2012). Atkinson et al., (2020) found that, when looking at a number of factors influencing normalised biomass slopes, chlorophyll concentration had the closest relationship. In the present study, the differences in primary productivity between sites appeared to be reflected within the copepod community structure, with higher abundances and biomass found at P3. These findings align to those of Ward et al., (2012a) in which copepod biomass was found to be higher in the productive region downstream of South Georgia. P2 and P3 have also been found to differ in the flux of material sinking to deeper layers (Manno et al., 2015). The higher volume of particulate organic matter and faecal pellets caught within sediment traps at P3 was attributed to the higher primary productivity and differences within plankton community structure (Manno et al., 2015).

However, in contrast to the higher abundance and biomass, P3 had a narrower size distribution than P2, suggesting that P2 had a greater diversity of copepod species and/ or stages. Taxonomic identification of copepods supported this, with fewer species and stages dominating at P3. The species of numerically dominant copepods also differed between the locations. At P2, the *Metridia* spp*., Ctenocalanus* spp. and *Oithona* spp. dominated while, at P3, *Calanoides acutus*, *Metridia spp.* and *Triconia* spp. were dominant. Further to this, *Ctenocalanus* spp*.* and *Oithoina* spp*.* were not amongst the most dominant species at any depth at P3 despite being highly dominant at P2. A further difference was the relatively high numerical abundance of *Rhincalanus gigas* at P3, yet this species was not in the top five most dominant species at P2, where smaller species were more dominant. This relatively high proportion of smaller copepods at P2 when compared to P3 was also found by Belcher et al., (2017), when analysing sediment traps positioned at or below 2000m. The sediment traps at the two locations had similar abundances of small copepods, but almost double the number of large copepods at P3 than at P2. Differences in copepod communities in the Southern Ocean as a result of chlorophyll concentrations has been previously considered by Chiba et al., (2001). When looking into the zooplankton community off East Antarctica, Chiba et al., (2001) found that areas of high chlorophyll had greater copepod abundance, but in contrast to the present study, high chlorophyll also corresponded with high relative proportions of small copepods.

Differences in copepod biomass size structure were also evident between the two sites. At both locations, the largest biomass peaks occurred within the larger size classes, however, the positioning of peak biomass domes differed with location and depth. At P2, there was one dominant peak at each depth that varied in position from -0.5 Log C weight to 0.5 Log

C weight. Secondary domes positioned at larger size categories were present at some depths. P3 exhibited a similar pattern of a single dominant dome being present at most depths. However, the position of this dome was not as variable, with the peak being located between -0.4 and -0.2 log C weight through most depths. Similarly, secondary domes were also seen in larger size categories at P3 throughout the water column. At both locations, the domes in the larger size categories indicate that a large contribution to community biomass came from larger copepods, with the dominant domes likely comprising of *R. gigas* and *Calanus propinquus,* and the secondary domes *Euchaeta spp.* Although not the most numerically abundant copepods, due to their large size, a small number of these copepods may account for a large proportion of the biomass. In general, the largest peaks were located between -0.75 and 0.5 Log C weight categories at both locations. This is slightly different to the finding of Tarling et al., (2012) who reported a dominant zooplankton biomass peak between -1 and -0.5 log C weight. While that category overlaps with the one reported here, it suggests that the biomass was dominated by slightly smaller plankton than in the present study. However, the present study only considered copepods rather than the whole zooplankton community, as considered in Tarling et al., (2012). Slight offsets between the current study and Tarling et al., (2012) are also explicable in terms of data processing differences since sizes were mainly estimated from published records than directly measured using ZooScan, as was the case in the present study. Despite this, both studies found large grazing copepods to dominate biomass, suggesting they play a pivotal role within both the copepod community and the wider zooplankton community.

The present study shows that large calanoids, such as *C. acutus* and *R. gigas,* play an important role within the Scotia Sea and make large contributions to the copepod biomass, irrespective of productivity levels. This is consistent with previous work that found that these large copepods are often dominant within the Southern Ocean and, due to their large size, account for the majority of copepod biomass (Atkinson et al., 2012). However, their relative dominance at P3 suggests that the higher productivity of the area favours them. The life-strategies and latitudinal distribution of these large copepods are relatively well known (e.g. Atkinson, 1998; Conover & Huntley, 1991) but environmental drivers of these patterns are less widely considered. Ward et al., (2007), found that the abundance of *C. acutus* and *R. gigas*, particularly the younger stages, was higher in areas where phytoplankton blooms had occurred than in areas of low productivity. Low productivity regions, as typified by P2, do not appear able to sustain such large populations of large calanoids.

At P2, smaller copepods such as *Oithona spp., Ctenocalanus spp.* and *Calanus simillimus* were found to be numerically dominant. *Oithona* is ubiquitous across many oceans and is often reported to be the most abundant copepod genus globally (Bigelow, 1926). It is regularly found to be the most abundant mesozooplankton in the upper layers of the Southern Ocean (Foster, 1987; Fransz, 1988; Fransz & Gonzalez, 1995). Despite this, it was not found to be amongst the most numerically dominant species at P3, suggesting that P3 favours other species to a greater extent. The global distribution of *Oithona* indicates that it is a species capable of thriving in a range of conditions including low productivity regimes. *Oithoina similis*, the most abundant species of *Oithona* in the Southern Ocean, has a life-cycle that is de-coupled from the primary productivity cycle (Atkinson, 1998b), possibly due to its omnivorous diet. An omnivorous diet may allow these copepods to feed on sources such as detritus when chlorophyll levels are low, allowing them to thrive in areas of low productivity such as P2. Further to this, Ward & Hirst (2007) found that *Oithona* reproduction occurred all year round and had no relationship to the chlorophyll levels but egg production did decline with decreasing temperature. This suggests that temperature is a more important factor than primary production in determining the abundance of *Oithona*. In the present study, the two locations are supplied by the same water mass, and have similar sea surface temperatures. If temperature was impacting the abundance of *Oithona*, then it would be expected that the two sites would have similar abundances. In the present study, *Oithona* abundance was found to be ~10 fold lower at P3 than P2 (a combined total of 1212 individuals across the upper 1000 m at P3 and 13112 individuals across the upper 1000 m at P2), suggesting that temperature is not the only factor influencing the abundance of *Oithona* in this region.

These differences in communities at P2 and P3 may have further impacts for the energy flux within the wider ecosystem. In a recent study modelling energy flow through zooplankton communities, it was found that the removal of omnivorous copepods caused a decline in fish biomass of up to 80 % while the removal of carnivorous copepods increased fish biomass by over 70 % in some of the simulated areas (Heneghan et al., 2020). A number of explanations for this were proposed including omnivorous copepods having a higher predator prey mass ratio than carnivorous copepods as well as a high carbon content, enabling carbon to be transferred efficiently to higher trophic levels. In contrast the diet of carnivorous copepods consists of other zooplankton causing feeding chains to be longer and less efficient. These findings suggest that smaller omnivorous copepods have a higher energy transfer efficiency to their predators than larger copepods. In the present context, at P2, where copepod biomass was found to be dominated by smaller omnivorous copepods with fewer larger copepods, fish biomass may be higher than that at P3 where a higher biomass of larger copepods were present. This may be influential in the steeper slopes found at P2 as an increase in fish biomass may manifest itself in the form of steeper spectral slopes as a result of energy being lost from the copepod community into higher trophic levels outside the copepod community. This could have further implications upon higher trophic levels through competition for zooplankton prey or increased prey abundance for higher predators. However, the model of Heneghan et al., (2020) only considers copepods within two groups, smaller omnivores or larger carnivores. As discussed previously, in the present study, a high proportion of the larger copepods were herbivores and therefore may have different functional traits to those used in Heneghan et al., (2020). As seen in this chapter, these copepods appear to increase the energy transfer within the copepod community due to their ability to convert energy from phytoplankton into large lipid and carbon stores. Further to this, Heneghan et al., (2016) also found that fish communities supported by herbivorous zooplankton communities were more resilient to fishing pressure, suggesting that energy flux into higher trophic levels was more efficient via herbivores than carnivorous zooplankton. At P3, where higher herbivorous copepod biomass resulted in comparatively shallower slopes reflecting the higher energy retention within the ecosystem, a similar resilience to external factors may also be apparent. For instance, Tarling et al. (2018) found that the geographic location of copepod communities within this region had not changed over recent decades despite a substantial change in sea surface temperature. While these large herbivorous copepods have a higher prevalence at high latitudes and in areas of relatively high primary productivity, the findings within this chapter highlight that copepod community composition and functional traits of species are important aspects of assessing energy transfer through systems.

2.4.3 Depth and the Copepod Community

Depth in the water column was expected to have an influence on the copepod community structure, with larger individuals and detritivorous species being more abundant within deeper layers. When analysing the multivariate size structure at P2 and P3, three broad clusters emerged within the samples, with depth being the principle driver. On the whole, the groupings consisted of deep samples tightly clustered together to form one group, mid-depth samples clustering slightly further apart and shallow samples grouping together but in a comparatively dispersed formation. The tight clustering of the deep samples suggests that, in line with Ward et al., (2014), there was a degree of homogeneity across P2 and P3 below 500m. The larger dispersion between samples within the shallow cluster indicates that community structure was less homogenous between stations in the upper water column. This separation of the shallow samples appeared to be reflective of the different species present and their relative dominance at the two sites. The upper water layers at P2 consisted of O*ithona* spp., *Ctenocalanus* spp., *Metridia* spp*.* and *C. simillimis*. Within this, *Metridia* had the greatest abundance, but was not notably more abundant than other species in the 5-125 m depth interval. This was not the case in the 125- 250 m interval, where *Metridia* abundance was tenfold higher than any other species. In addition to this, the abundance of all species was far lower in the 125-250m interval than the 5-125m interval at P2, explaining the separation seen within the cluster analysis. At P3, *C. acutus* dominated, with later stages (stages C4 and C5 combined) being twice as abundant as any other species or stage in the top 250 m of the water column. *R. gigas*, *C. simillimis* and *Metridia* were also present in these upper water layers at P3 but had relatively low abundances. In contrast to P2, the depth intervals of 5-125 m and 125-250 m at P3 had similar copepod abundances. Intermediate levels of clustering between samples at mid-depths indicated that this is a transition zone between the spatially different shallow copepod communities and spatially homogenous deep water community.

This shift in copepod community from shallow to deep water can also be seen in the biomass structure. The majority of the copepod biomass was found within the top 500m. This is in line with previous findings, which report that the majority of summer zooplankton biomass is in upper water layers (Ward et al., 1995, 2014). Further to this, the biomass, particularly in the shallow layers, was comprised of large copepods including *C. acutus* and *R. gigas*. This was also reported by Ward et al., (2006b) who found that *R. gigas* accounted for up to 44 % of the total mesozooplankton biomass in some areas, while *C. acutus* contributed up to 8 % of the biomass, with copepod biomass accounting for approximately 70 % of the mesozooplankton biomass. As we move down through the water column, the peaks in biomass shift to smaller individuals such as *Oithona spp.* and *Metridia spp*. At these increased depths, cluster analysis suggests more homogeneity between the two sites, which is reflected in the species compositions. This higher variability in species composition in the surface layers and increased species homogeneity at depth was also reported by Ward et al., (1995) in waters surrounding South Georgia.

The difference in variability between surface and deep samples may be due to copepod physiology or environmental factors. *C. acutus* and *R. gigas* are strong seasonal migrators, spending the winter at depth where they rely on lipid stores and then rising to surface layers to feed during summer months (Atkinson, 1991; Kattner et al., 2004). The present study was undertaken during the austral summer, when it would be expected that individuals would be residing in the surface layers. *R. gigas* featured amongst the most abundant species at 5-125 m and 125-250m depths at P3, suggesting that it was residing in the surface layers. *C. acutus* was found to be relatively dominant throughout the water column at both P2 and P3, but their abundance decreased with depth, suggesting a large proportion of the *C. acutus* population were residing in the surface layers where food abundance is greatest. The decrease with depth was more pronounced at P3 where *C. acutus* heavily dominated the copepod abundance within the surface 250m, further suggesting that food presence is a driver in the vertical positioning of this species at the time of sampling. Furthermore, older stages (CIV and CV) of *C. acutus* increased in prevalence with increasing depth at both locations. Stage specific vertical distribution patterns in copepods have been reported by Atkinson, (1991) who found that older stages of *C. acutus* gradually descend through the water column during summer and autumn. This gradual and asynchronous descent may be an explanation for the vertical distribution seen in the present study. It may also explain the relatively low abundances of *C. acutus* in the upper water layers at P2. While the cue for the descent is currently unknown, it may be that the reduced productivity at P2 causes seasonal migrators to enter diapause earlier. This would reduce their abundance in surface layers in late summer and may explain some of the variability between these shallow samples in the present study.

Vertical distribution of copepods may also be influenced by feeding strategies. As described in section 2.1.3, copepods may position themselves within the water column based upon their prey type. If this is the case it would be expected that herbivores would occupy the shallowest depths, residing in the euphotic zone where phytoplankton is abundant. Detritivores would be found below these depths in order to intercept any sinking matter and carnivorous species may be expected to occupy a wide range of depths in order to prey upon a range of species. In the present study, herbivorous copepods such as *Ctenocalanus*, *C. acutus* and *Calanus simillimus* were found to have higher abundances in the upper layers. *C. simillimus* was found to have high relative abundances in the surface 125m only. This was the case at both locations suggesting that *C. simillimus* is residing high in the water column. Atkinson et al., (1992) also found that *C. simillimus* appeared to reside in the upper water layers with highest gut fullness being found at midnight. It was proposed that *C. similimus* has a high gut evacuation rate, so residing in the chlorophyll maxima may be more beneficial than carrying out migrations over short time scales. Conversely, *C. acutus* and *Ctenocalanus* were found throughout the water column, suggesting that feeding strategy was not the only factor determining vertical distribution in these species.

2.4.4 Application of the Biomass Spectra Theory

The present study found a number of biomass domes along the log weight size categories, reflecting an unequal distribution of biomass with body size through the copepod community. This analytical approach was developed by Thiebaux and& Dickie (1993), who identified biomass domes and troughs as a function of size in plankton communities which they considered to reflect the relative sizes of predators and prey, such that the domes could be considered to represent trophic levels through the size classes. This was taken further by Sprules and& Goyke (1994), who found that the major domes within the biomass spectra represented the grazers and primary carnivores, while the secondary sub-domes were comprised of higher trophic levels that occupied a range of sizes. Applied here, it would suggest that the copepod community has a greater trophic structure at P2 with two trophic levels being present at some depths, demonstrated by primary and secondary biomass peaks within the biomass. The primary peak in this study is likely to consist of *R. gigas*, while the second peaks at larger size classes are likely to be comprised of *Euchaeta*. To satisfy the principle put forward by Thiebeaux and Dickie (1993), the peaks should reflect trophic levels with each dome along the size class (the log C weight categories in the present study) being a trophic level higher than the one before. This was not the case in the present study due to the domes not representing sequential trophic levels. *Euchaeta spp.* tend to prey upon smaller copepods than *R. gigas* (Oresland, 1991), yet there is no dome to represent these smaller copepod prey. *R. gigas* are detritivores and would therefore be at an intermediate trophic level between herbivores and predators. Despite the present study not fully conforming to the Thiebeaux and Dickie (1993) principle, biomass domes may still represent loose trophic levels. The present study further found that the positioning and magnitude of the domes change slightly through the water column, potentially reflecting trophic changes with depth.

Normalised biomass slopes can provide a proxy of the amount of energy that is retained within the community as it passes from smaller to larger organisms. Shallower slopes indicate a greater level of energy retention within the community while steeper slopes infer that more energy is lost. The relatively similar slopes found in the present study show that the energy retention within the ecosystem was fairly consistent across locations, times and depths. However, the variability within the data around these slopes was high, indicating that the slopes may not reflect the small scale patterns within the data. The average regression slope gradient across all samples was found to be -0.56. However, small differences could be seen with depth. In general, the deeper waters (below 625m) were found to have the steepest gradients, indicating energy loss, while the mid-waters (250-625m) had the shallowest gradients, suggesting higher levels of energy retention. This difference in slopes through the water column suggests that energy retention within the Scotia Sea copepod community is highest in the mid-depths, whilst loss is greater in deeper water. Few studies have examined unevenness in energy retention within plankton communities through the water column. However, the steeper slopes found in deeper waters are likely to reflect the simpler biomass structures found at depth. At these depths, it was found that the biomass was made up of smaller omnivorous copepods, with fewer large copepods. This absence of large copepods suggests that energy cannot be retained within larger individuals and is therefore lost from the community.

Although the biomass and species found at the two sites differed, the present study found that size spectral slopes remained similar. This pattern of different species leading to similar spectral slopes was reported by Rodhouse et al., (1994), who suggested that this may be a result of different species occupying the same niches within communities, thereby resulting in the same general structure. Nevertheless, the different productivity regimes may further influence community size structure. Sprules and Munawar (1986) and Iriarte & González (2004) found that oligotrophic areas had steeper slopes than more productive areas within close proximity. This difference resulted from pico- and nanoplankton accounting for a greater proportion of the primary productivity in these less productive areas. This microbial activity increases the proportion of small particles within the system driving a steeper slope. However, others have suggested that productive areas will have the steepest slopes (Zhou et al., 2009). These steep slopes would be a result of the high proportions of herbivorous grazers within productive systems (Zhou, 2006; Zhou & Huntley, 1997), meaning that energy was stored at lower trophic levels. Hence, both shallow and steep slopes have been used as indicators of productive regimes, so the steepness of biomass spectra slopes needs to be viewed with some caution when used to assess a system (Marcolin et al., 2013). In line with this, a recent meta-analysis assessing normalised biomass slopes from a range of locations across seasons found that slopes steepened under both eutrophic and oligotrophic conditions, however, a number of factors may influence the slopes (Atkinson et al., 2020). In the present study, it is probable that a combination of factors has led to similar slopes in both productivity regimes. The exclusive focus on copepods will result in the small particles responsible for the majority of primary production being missed, potentially resulting in a shallower slope than would be seen if the whole plankton community had been analysed. Secondly, a higher abundance of grazers was seen at P3, but these grazers are often too large for the predatory copepods, such as *Euchaeta*, to prey upon. In many systems, sequential biomass domes progress in line with trophic position (Cohen et al., 1993; Sprules & Goyke, 1994), making the Scotia Sea copepod community unusual in this regard.

The Southern Ocean is a highly seasonal environment, requiring specific adaptations for survival, resulting in the presence of a number of endemic copepods. These endemic species include the species thought to account for a large proportion of the biomass in the present study, *C. acutus*, *R. gigas* and *E. antarctica.* Each of these species has developed a different strategy to cope with the short feeding season. The life cycle of *C. acutus* appears to be linked to the primary productivity cycle (Atkinson, 1998). As a herbivorous grazer, feeding and reproduction for this species takes place in summer when phytoplankton levels are high (Atkinson, 1998). During the winter months, when productivity is reduced due to ice cover, cold temperatures and the polar night, *C. acutus* exhibit diapause behaviour allowing them to overwinter (Atkinson, 1998). This life cycle is common to many large *Calanus* species found inhabiting high latitudes and allows survival through the winter months in a non-active state and a multi-year life cycle (Atkinson, 1998). *R. gigas* may also have a multi-year life cycle but is less reliant upon diapause to overwinter (Atkinson, 1998). It is currently unclear to what extent *R. gigas* carries out diapause, with some individuals being non-feeding during winter (Hopkins et al., 1993), while others have contents within their digestive tracts (Marin & Schnack-Schiel, 1993). While there appears to be some debate with regards the life cycle of *R. gigas*, the finding of adult stages in early spring by a number of authors (e.g. Atkinson, 1991; Marin, 1988; Schnack-schiel & Hagen, 1994; Ward et al., 1997) indicates that overwintering occurs. In contrast to *C. acutus*, it is thought that reproduction of *R. gigas* may take place during the winter (Bathmann et al., 1993) allowing nauplii to grow through winter and copepodites to reach large sizes in the spring and summer. The life cycles of the *Euchaeta* species within the Southern Ocean are not well known. However, Ward & Robins (1987) found that spawning occurs in both July and

September around South Georgia, indicating that *Euchaeta antarctica* is active all year round and, similar to *C. acutus* and *R. gigas*, has a multi-year life cycle. Despite the differences in life cycles, all three species need to build up their lipid stores in order to survive the winter. Copepods that exhibit diapause behaviour have been found to have larger lipid stores than those that remain active throughout the year (Cavallo & Peck, 2020), suggesting that these species are able to capitalise on limited resources and lay down lipid reserves during summer, potentially driving the large sizes seen across trophic levels in the Southern Ocean. The presence of large endemic copepods may result in a size structure that does not fit the traditional size-spectra theory as energy is stored within large organisms at many trophic levels.

Despite the potential differences between the Southern Ocean and other regions, the average gradient reported in the present study, -0.56, is much shallower than slopes previously reported for the area (Tarling et al., 2012; Rodhouse et al., 1994). It is also much shallower than the theoretical value of -1.22 proposed by Platt and Denman (1978) for open ocean communities. Previous studies investigating mesozooplankton report slope values between -0.44 and -2.30 (Marcolin et al., 2013), showing a wide range of values dependent upon location and size range and demonstrating that the slope found here falls within the observed range. Tarling et al., (2012) calculated a slope with a gradient of -1.09 for the spring zooplankton community of the Scotia Sea, while Rodhouse et al., (1994) found an average gradient of -0.71 for crustaceans within the Scotia Sea. The shallow slope found in the present study indicates that the energy loss from the copepod fraction of the community is relatively small and, in line with Tarling et al., (2012) and Rodhouse et al., (1994), is due to high biomass within larger size categories. This high biomass within the large size categories may also be a result of the copepod life-cycles mentioned earlier. Many herbivorous copepods inhabiting high latitudes have multi-year life-cycles (Conover, 1988), with physiologies that allow them to over winter using their energy stores. This multi-year life-cycle results in the copepod community being composed of several copepod generations at any one time and may lead to an increase in the proportion of larger copepods within a population when compared to temperate and tropical regions.

The variability seen around the slopes also changed with copepod size. In general, the biomass contained within smaller copepods was greater than the regression slope would predict. An exception to this is the -2.75 log C weight category, where the biomass is consistently below the regression line. However, this may be an artefact of the sampling methodology, with this size range being at the lower catchability limit of the net. When moving into the large size classes, variability remains great but biomass volumes are below regression lines. This suggests that there may be more energy within smaller animals and less in larger animals than the fitted spectral slope indicates. The variability around the regression line does not capture all patterns found within the copepod community. While the normalised spectral slope theory has been widely used to assess energy flows within ecosystems and communities (e.g. Law et al., 2009; Rodhouse et al., 1994; Sprules & Barth, 2016; Tarling et al., 2012), it is rarely applied to a single taxon, as has been done in this study. This high variability surrounding the regression slopes may indicate that the data contained within this study is at the limit of the spectral slope theory proposed by Thibeaux and Dickie (1993). Nevertheless, the fitting of these slopes to a limited data set is still useful in resolving energy flow through this major component of the Southern Ocean ecosystem, particularly with regards the influence of different levels of productivity on size structure.

2.4.5 Evidence for Diel Vertical Migration

Many copepod species within the Southern Ocean are thought to undertake vertical migrations, feeding in the upper water column at night. Therefore, it was expected that there would be a change in the vertical distribution of copepod biomass and abundance across the day and night samples. This study found that, although the composition of species through the water column generally remained the same, there was a redistribution of abundance and biomass between depth intervals. Unexpectedly however, the amount of biomass in the upper depth intervals decreased during the night compared to the day, suggesting a reverse migration was taking place, at least in the dominant species.

It has been previously hypothesised that reverse migration may be a response to the presence of larger invertebrates such as amphipods, cheatognaths and euphausiids (Lampert, 1989; Ohman, 1990; Tarling et al., 2002). The migrations seen in the present study are likely to reflect the large copepods inhabiting the surface waters such as *C. acutus* and *R. gigas*. Previous studies have not found these copepods to display strong migratory behaviours (Ward et al., 1995), however they are prey species for the abundant euphausiids in the area (Atkinson & Snÿder, 1997) and therefore may be responding to their presence. A number of euphausiids are found in the area, and exhibit a range of diets, from predominantly herbivory in *Euphausia superba* to the omnivorous *Thysanoessa spp.* (Atkinson et al., 2012). *Thysanoessa* spp. was found to be present in all but one of the daytime samples in the present study, suggesting that it plays an important role within the respective zooplankton communities. Copepods are often prey for omnivorous euphausiids, such as *Thysanoessa* spp. (Båmstedt & Karlson, 1998; Hopkins & Torres, 1989), and vertical movements may be a response to the presence of these predators. *Thysanoessa* species have been recorded to undertake daily migrations for feeding, rising to the surface mixed layer at night (Nordhausen, 1994; Sameoto, 1980), so increasing predation pressure on copepods during the night time and possibly inducing them to undertake reverse migration.

Another possibility is that midnight sinking has decreased abundance and biomass of copepods in the surface layers during the exact time of sampling. Midnight sinking is a migration pattern of feeding at night but seeking refuge in deeper layers in the middle of the night leading to shorter migrations (Cushing, 1951; Tarling et al., 2002). Midnight sinking may be a product of satiation sinking, in which animals feed in shallow waters until they reach gut fullness before sinking to digest and repeating the migration once digestion is complete (Pearre, 2003; Tarling & Johnson, 2006). These migration patterns involve numerous short migrations into the surface layers to feed, termed forays. As highlighted earlier, migration behaviour is difficult with nets that only sample a single time point and often single depths. Here, the study sampled the upper 1000 m of the water column and broke it down into depth intervals in order to detect any movement between depths between night and day. Despite this, assessing migration patterns is still limited with this method as only synchronous patterns of migrations between the depths can be visualised, with any asynchronous foray behaviour acting to blur this pattern.

2.5 Summary

- Scanned images from the ZooScan were successfully used to assess the size structure of the copepod community at P2 and P3 within the Scotia Sea. Using these images, it was possible to apply a size spectra approach to investigate how the size spectra changes with location and depth within the water column.
- Copepod abundance and biomass was higher at P3, likely due to the higher primary productivity at this location than at P2.
- Larger species and herbivorous species were more prevalent at P3, in line with the higher food availability.
- Depth discrete samples showed that the size spectra remained similar throughout the top 1000m of the water column. This is contrary to the hypothesis that larger

copepods would reside in deeper layers in order to avoid detection and indicates that copepods were not vertically segregated due to size.

- A redistribution of copepod biomass within the upper 500 m of the water column from day to night was found at both locations, suggesting that copepods undertook vertical migrations. However, a traditional vertical migration pattern was not clearly evident and, in fact, reverse migration was more apparent.
- Using a normalised biomass spectra approach, linear regressions were fitted to determine the slope gradients and energy retentions within the community. There was a high degree of variance around the fitted slopes. Shallower slopes were found at P3 than P2, suggesting that energy is retained to a greater extent at P3.
- Energy flow through the community varied slightly with depth with the highest retention being found in the upper mesopelagic depths, while the lowest retention was seen in the lower mesopelagic depths. This suggests that energy is lost from the community as depth increases.
- Overall, the copepod community of the Scotia Sea had a high energy retention and therefore provide a potential source of energy and carbon export within the region. However, to further understand the level of carbon export migratory, behaviours within the copepod community require resolving further.

Chapter 3: Detecting Migrations Using a Novel Motorised Upward and Downward Looking Net

3.1 Introduction

3.1.1 Zooplankton Migrations

Zooplankton have long been known to undertake vertical migrations, the most commonly described being diel vertical migration (DVM) (Cushing, 1951). DVM is a phenomenon in which, classically, zooplankton travel in a synchronised manner to the upper water column at night to feed, but reside in deeper waters during the day (Lampert, 1989). A number of reasons have been suggested for this behaviour, which I have reviewed in Chapter 1. Briefly, although this behaviour is often thought of simply as a feeding strategy synchronised by external light (Pearre, 2003), the diversity of migration patterns that have now been resolved suggests that it may have a number of drivers. For instance, synchronised migration patterns have been shown to be disrupted or cease all together if there is a change in environmental conditions, such as the absence of predators (Gliwicz, 1986). This finding supports the predator-avoidance hypothesis, which is based on the premise that the advantages of migrating to avoid predation outweigh the energetic costs of vertical movement (Stich & Lampert, 1981). An alternative hypothesis is that residing in deeper, colder waters confers a metabolic advantage in reducing overall energetic costs (Enright, 1977). Hunger and satiation have also been found to play a role in DVM, with animals sinking once satiated during the night or remaining at the surface during daylight hours when food is scarce (Pearre, 2003).

Given the numerous observations of migrations that do not fit the classical DVM pattern, it is now thought that zooplankton migrations exhibit considerable variability (e.g. Bayly, 1986; Conroy et al., 2020; Cottier et al., 2006; Tarling et al., 2002). Observations of non-classical DVM behaviour include midnight sinking, a form of bimodal migration resulting in two feeding peaks within the night (Cushing, 1951), reverse migrations, feeding within surface layers during daylight hours and sinking at dusk (Bayly, 1986) and asynchronous migrations within populations (Pearre, 1979). Asynchronous migrations may be a product of foray behaviour, in which zooplankton undertake smaller migrations either throughout the night, or potentially over the whole day. Presently, the reasons for foray behaviour are unknown, however, the hunger-satiation hypothesis has been favoured (Pearre, 2003).

Here, variation between individuals in feeding rates may result in zooplankters reaching satiation and subsequent downward migrations at different times, even if the onset of feeding is synchronised. Hunger may then strike at different times dependent upon metabolic rates and other energy demands whilst digesting, forcing zooplankton to return to food rich layers at varying time intervals (Pearre, 2003).

3.1.2 Zooplankton foray behaviour and carbon flux

The movement of zooplankton through DVM enhances the export of nutrients and carbon from the upper water layers to the deeper layers (known as active flux), supporting the Biological Carbon Pump (BCP) (Turner, 2002). The contribution of this 'active flux' to the total volume of particulate organic carbon (POC) is poorly parameterised but is thought to vary across seasons and oceanic regimes (Boyd et al., 2019; Buesseler & Boyd, 2009), with estimates ranging from 3 % (Hernández-León et al., 2001) to 70 % (Dam et al., 1995) of the total POC export and up to 90 % of dissolved inorganic carbon export (Boyd et al., 2019). Faecal pellets produced by zooplankton may contribute significantly to the downward flux of POC (Cavan et al., 2015; Manno et al., 2015; Turner & Ferrante, 1979). Foray-type behaviour was found to increase the number of faecal pellets produced below 30m (a depth at least 10m below the highest chlorophyll values) when compared to a population displaying no migration patterns (Wallace et al., 2013), suggesting that the presence of foray-type behaviour may act to increase the contribution of active flux to the BCP. Very few studies have considered the contribution that foray behaviour plays in the BCP (e.g. Wallace et al., 2013). However, it is becoming apparent that a greater knowledge of non-classical zooplankton migration behaviour is fundamental to parameterising the BCP more accurately.

In addition to the behaviour of zooplankton, geographical location plays an important role in the volume of carbon transported through the BCP (Henson et al., 2015). High latitudes are thought to be particularly important, with the amount of exported POC being high relative to the rate of primary production (Buesseler, 1998). In particular, the Southern Ocean absorbs approximately 50 % of the current annual oceanic carbon uptake (Keppler & Landschützer, 2019), making it one of the biggest carbon sinks globally. Furthermore, high latitude regions undergo the largest changes in seasonal light regimes (Berge et al., 2015). If light is a cue to synchronise zooplankton migration, it is in these environments that synchronised migration patterns will undergo the greatest seasonal changes.

Furthermore, it may be expected that, during midnight sun conditions, the lack of a synchronisation cue halts synchronised vertical migration (Wallace et al., 2013) but may initiate greater levels of foray type behaviour (Cottier et al., 2006; Wallace et al., 2010), so continuing the process of active flux.

3.1.3 Evidence of Foray Behaviour

To date, most zooplankton sampling methodologies are only capable of detecting synchronous migrations at the population level (Pearre, 1979). These methodologies, generally nets and active underwater acoustics, are unable to detect migrations (or forays) that may be occurring within just parts of a population or at the individual level. Similarly, biogeochemical modelling studies are often unable to incorporate individual zooplankton vertical distribution and migration despite the importance of their role in active flux (e.g. Batchelder et al., 2002; Reiss et al., 2003; Zakardjian et al., 2003).

One study which did develop a technique to test for foray behaviour within near-surface waters used modified plankton traps, and is described in detail in Chapter 1 (Pierson et al., 2009). These nets consisted of z-traps with rigid openings and 2 m long cylindrical or rectangular bodies tapering to a cod end. Traps were deployed in a closed position and opened using mechanical messengers once they had reached the desired trapping depth. After a period of time, an acoustic messenger was sent to close the traps before they were hauled in. The original set up of these traps was to mount two onto the same frame, one in an upward facing orientation the other rotated 180° in a downward orientation. This design captured zooplankton that were either migrating upwards or downwards. However, this design was found to be ineffective at catching zooplankton and the net design was revised. The revised design involved two different nets deployed simultaneously, one that was upward facing (a standard WP2 net equivalent) and another downward facing (an inverted plummet net). The plummet net was modified using a nylon cover to prevent sampling during deployment. Using these paired nets, Pierson et al., (2009) were able to catch and compare zooplankton migrating up and down the water column within Dabob Bay, USA, an inshore bay on the west coast of the USA. However, they reported a number of biases within their catches, which included a selectivity for downward-migrating plankton and a bias towards larger individuals in the upward facing net. Despite these biases, foray foraging behaviour was observed in *Calanus pacificus* and *Metridia pacificus* females, evidenced by the presence of individuals in the upward facing nets throughout the night, indicating that, at any time, a number of zooplankton were migrating downwards. Furthermore, these individuals had increased gut contents compared to those caught swimming upwards.

The present study aims to build upon the work of Pierson et al., (2009) by developing a new net system to detect foray behaviour in open ocean situations. Thus far, foray behaviour has not been detected empirically in any open ocean setting. Detecting it in the Southern Ocean has a particular importance given its major role in global carbon sequestration. In the present study, a novel bi-directional net is deployed for the first time in the Southern Ocean with the intention of capturing zooplankton travelling in both upward and downward directions simultaneously. Simultaneous capture of individuals in both upward and downward looking nets provides evidence that asynchronous migrations are regularly taking place. Further taxonomic analysis of the catches will reveal which zooplankton species/stages are undertaking such vertical movements and hence contribute to active carbon flux.

3.2 Methods

3.2.1 Net Design

The net used in the present study follows the same principle as the original net proposed by Pierson et al. (2009), however, major modifications have been made. The Motion compensated Upward and Downward Looking net (MUDL) was designed by scientists and engineers at the British Antarctic Survey. The MUDL net is comprised of two conical nets mounted on an aluminium frame (Figure 3.1). Both nets have a rigid cylindrical opening with a diameter of 61 cm, with 100 µm nylon netting tapering to cod ends 2 m away. The nets are positioned with one net opening facing up and the other facing down. At the entrance of the cod ends is a spherical valve. This valve is hollow with three circular holes cut into it and is the mechanism which allows the net to start and end sampling. The positioning of the valves determines when sampling occurs. In a closed position, the alignment of the valves results in the cod ends being closed and any water flushed through the net being released through a side opening in the cod end. Sampling commences when the valves rotate to an open position by aligning the holes to create an open passage into the cod ends. After a set time, the valves rotate back into the closed position ensuring no zooplankton are caught during net retrieval. The valves are rotated via arms connected to a motor located in the centre of the frame. Prior to deployment, the motor is programmed to rotate the arms and therefore the valves at set time points. In addition to the motor, a spring loaded motion compensation mechanism sits in the centre of the frame. This allows the net to maintain its vertical position and remain stable within the water column.

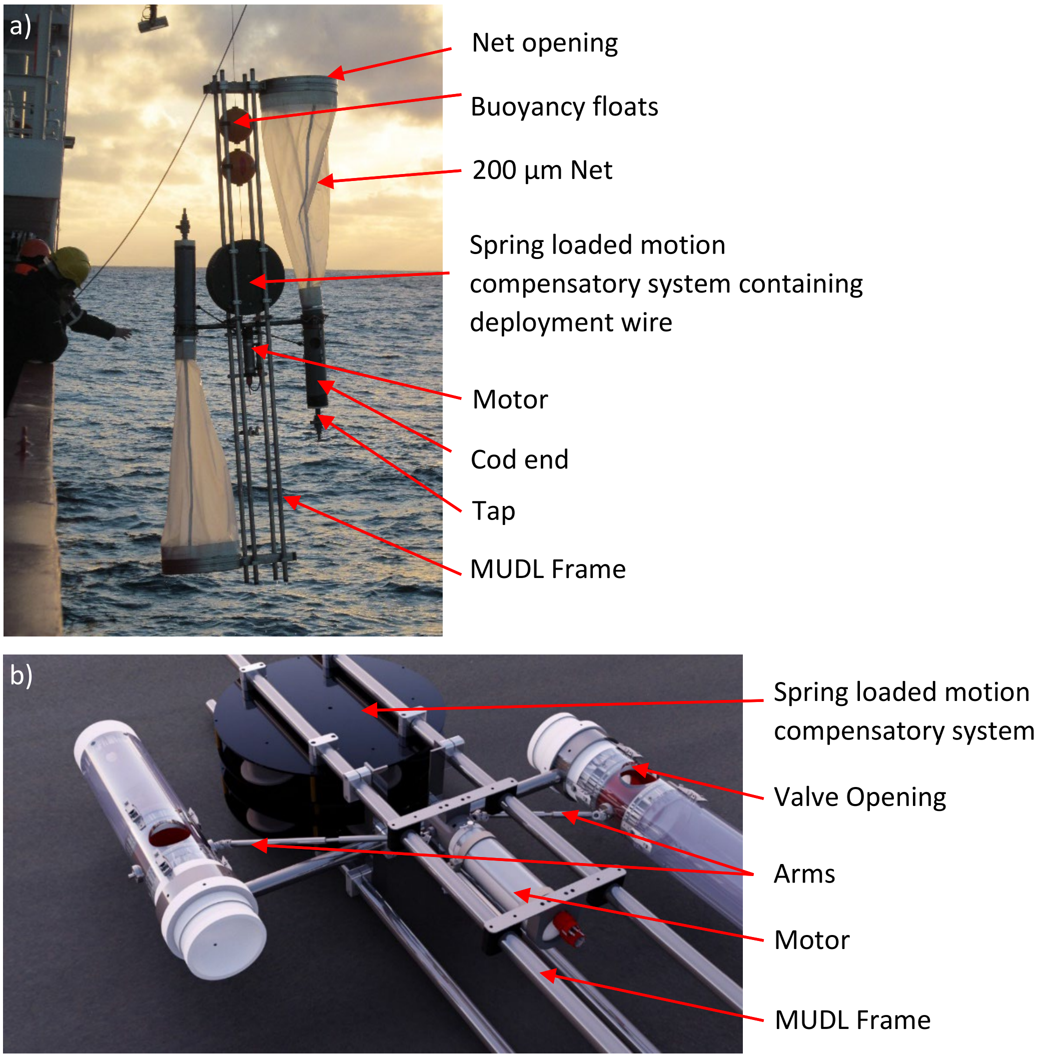


Figure 3. 1 a) MUDL net being deployed from the *RRS James Clark Ross* in the Southern Ocean. The main features of the net can be seen including the motion compensatory system and bi-directional nets. b) close-up of the MUDL system prior to deployment, showing the motion compensatory system, pre-programmed motor and cod ends with the valves in a closed position. Photo credit: GA Tarling.

3.2.2 Field Sampling

Zooplankton sampling was carried out by deploying the MUDL from the *RRS James Clark Ross* as part of the BAS long-term ecosystem monitoring programme off northwest South Georgia. The cruise was undertaken in the austral summer, during December 2016-January 2017 (JR16003). The MUDL net was deployed in multiple locations, including the standard monitoring stations of P2 and P3 (although only a single deployment was possible in the latter) and at several locations around the Antarctic Polar Front (Figure 3.2). These station locations vary in their primary productivity regimes which makes them ideal sites for comparisons of zooplankton behaviour.

Because of the multidisciplinary nature of the cruise and full deployment schedules, only dusk and dawn time slots were consistently available for MUDL deployments. Although these are times when synchronised migrations are most likely to take place, its remains possible to detect asynchronous swimming behaviour if both upward and downward facing nets capture individuals, even if in different relative proportions. Importantly, the dusk and dawn scheduling allowed two very different time points to be sampled at each station. This made comparisons possible where methodological artefacts could be identified and discriminated from true biological variance.

To maintain consistency across the cruise, deployments were always made as close to sunrise and sunset as possible. Where time allowed, two deployments were made at each time point, one to a set depth of 100 m and the second to 10 m below the chlorophyll maximum (typically 60-80 m depth) as determined by a CTD cast (Table 3.2).

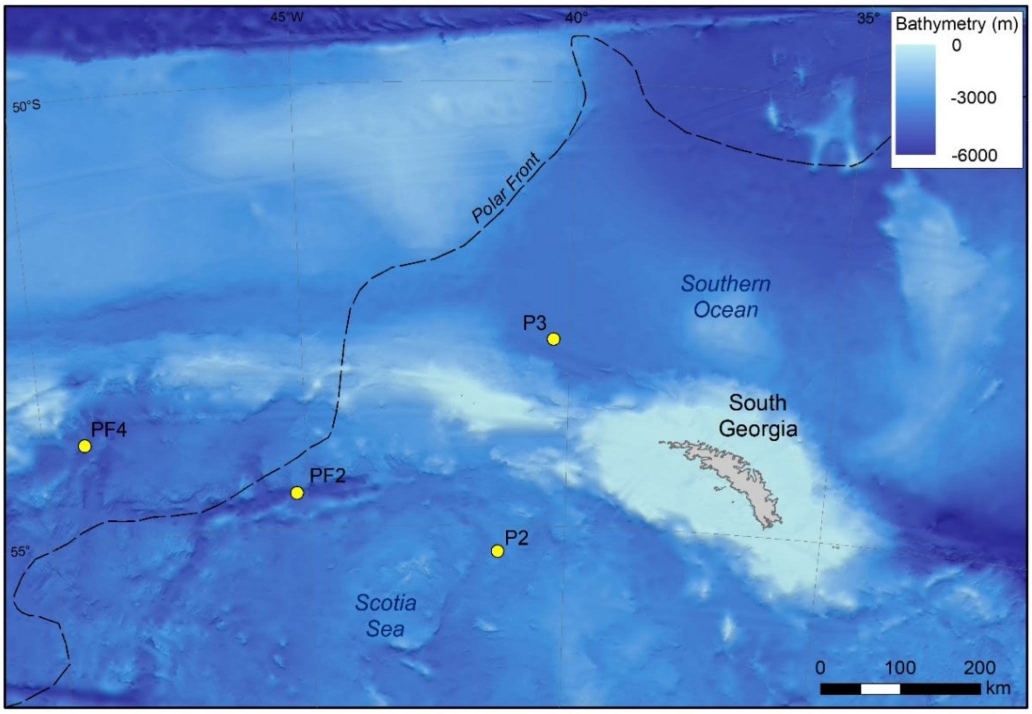


Figure 3. 2: Map of South Georgia study region showing locations of MUDL deployments from *RRS James Clark Ross* during 2016/17 (JR16003). Dashed line shows location of the Polar Front as found by Orsi et al., (1995) and Trathan et al., (2000).

Event Number	Depth (m)	Station	Time	Local Time (GMT -3)
90	100	P3	Dusk	21:13
96	80	P2	Dusk	23:24
97	100	P2	Dusk	00:13
99	80	P2	Dawn	05:09
100	100	P2	Dawn	05:56
117	100	P2	Dawn	07:05
118	60	P2	Dawn	07:55
127	100	PF2	Dusk	22:05
128	80	PF2	Dusk	22:52
131	100	PF2	Dawn	06:19
132	80	PF2	Dawn	07:08
145	100	PF4	Dusk	21:43
148	100	PF4	Dawn	04:41

Table 3. 1: MUDL Deployments during 2016/17 (JR16003), showing ship log event number, depth, location and local time when deployment commenced.

The CTD was deployed prior to MUDL deployments. This consisted of a SBE32 carousel water-sampler, a SBE9Plus CTD, containing a SBE3Plus temperature sensor, a fluorometer (Chelsea Aquatracker mark III) and a photosynthetically active radiation (PAR) sensor. The depth of the chlorophyll maximum was asdetermined from the chlorophyll *a* profile obtained during the downcast (Figure 3.3). Water for use in the respective MUDL deployments was obtained from 100 m and 10 m below the chlorophyll maxima during the up cast of the CTD via Niskin bottles mounted on the CTD frame. Immediately before deploying the MUDL net, the cod ends were filled with water from the target depth of the deployment in order to minimise changes in temperature, salinity and other properties that may prevent water from mixing within the cod end once the net was in position at depth (filling cod-ends with water was also structurally necessary to minimise stress on the cod-ends during deployment). The MUDL net was programmed using customised Hydrobios software, and was set to rotate the valves within the cod ends to an open position after 12 minutes, allowing it to reach the target depth before opening. Deployments were made with the valves in a closed position minimising contamination during this stage. Once the net was at the target depth, the valves rotated to an open position allowing the mixing of water in the cod ends and zooplankters to swim into the cod ends. The valves remained in this open position for 20 minutes, before being closed for retrieval. Whilst open, the MUDL remained at the target depth, and with the aid of the motion compensating mechanism, vertical movement was minimal, decreasing the potential of zooplankton to enter the nets through intermittent vertical motions caused by the effect of oceanic swell. Following a 20-minute open period, the valves were programmed to rotate to reach a closed position. The net was hauled vertically to the surface in the closed position, preventing contamination of the cod-end samples during this phase.

Once the net had been recovered, the cod ends were emptied. This was done by opening a tap valve at the base of the upward looking net, allowing the sample to be collected by placing a large bucket underneath. To collect the sample from the downward looking net, the base of the net was removed and the valve rotated to an open position. Once in an open position, the sample was collected in the same way as the upward looking net. Samples were then passed through a 100 µm mesh cloth, collecting any zooplankton on the cloth. Mesh cloths were then immediately frozen at -80 ˚C for analysis back at the laboratory.

3.2.3 Mini Bongo deployment

In addition to the MUDL net, a mini bongo net was deployed at PF4 to provide a sample to compare with the MUDL samples and assess catch performance. The mini bongo net had an 18 cm mouth diameter with 53 µm meshed net tapering to the cod end. The mini bongo was hauled vertically from 70 m to the surface, collecting all plankton present in the water. Upon retrieval, the sample was filtered and preserved in 95 % ethanol. The preserved sample was sent to Morski Instytut Rybacki, Poland for zooplankton taxonomic analysis, using the following protocol: any organisms larger than 10 mm were removed from the aliquot and recorded before the sample was sorted; the aliquot was then sorted and all plankton identified to the lowest possible taxonomic level; the raw counts of each species were multiplied by the inverse of the sample fraction to give a whole sample count for each species/ stage recorded.

3.2.4 Sample Analysis

Once back at the UK laboratory, frozen samples from the MUDL net deployments were transferred to ethanol or 4 % buffered formaldehyde (within 24 months of collection). Whole samples were analysed and zooplankton were counted and taxonomically identified using a stereo microscope (Olympus SZX16) with a NIKON D750 camera attachment. Photos of zooplankton were taken to enable secondary verification of taxonomic identification. Easily distinguishable zooplankton were identified to species, such as *Rhincalanus gigas, Calanoides acutus* and *Calanus propinquus*. A number were identified to genus level, including *Oithona* spp., *Metridia* spp. and *Thysanoessa* spp. Other zooplankton were identified to groups such as calanoids, pteropods, ostracods, chaetognaths, euphausiid calyptopes and hyperiid amphipods.

3.2.5 Statistical Analysis

Statistical analyses were carried out in SigmaPlot 14 (Systat Software, Inc.). To establish significant differences between samples in the upward and downward facing MUDL nets, a number of statistical tests were performed. A Mann-Whitney U test was carried out to check for significance between the total numbers in samples between the two net directions. Linear regression analysis was undertaken to establish whether the total number of plankton caught in both MUDL nets at each deployment influenced the relative proportions of plankton found in the nets. An ANOVA on Ranks was also carried out to establish whether the number of zooplankton within the MUDL samples varied with location.

To compare species diversity at the various locations, the Shannon Diversity (Shannon & Weaver, 1949) and Simpson's Diversity Index (Simpson, 1949) were calculated. Samples were pooled by location for this analysis with all samples across all depths at each time point pooled to form two locational groups: (1) the Polar Front group and (2) the P2 group. Due to only having one dusk sample from P3, this sample was not included in this analysis. This resulted in four index figures for each location, comprising of an index figure for the upward looking net at dawn, the upward looking net at dusk, the downward looking net at dawn and the downward looking net at dusk. Shannon Diversity Index measures species richness, defined as the number of different species, based on the total number of species found within a population and was calculated using the following equation:

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

(Equation 3.1)

Where p_i is the proportion of individuals belonging to each species and R is the number of species.

The Simpson's Diversity Index takes into account the number of species present, along with the number of individuals in each species, to give a measure of diversity and was calculated using the equation:

$$D = 1 - \frac{\sum n_i(n_i - 1)}{N(N-1)}$$

(Equation 3.2)

Where n is the number of individuals in each species and N is the total number of individuals across all species.

A multivariate analysis was conducted using Primer 7 (version7.0.13, PRIMER-e) (Clarke & Gorley, 2015). Data were imported in a sample-variable matrix, where each net at each deployment was a sample and the taxa were variables. In total, 26 samples were included from 13 net deployments. All samples had corresponding factors of location, time, depth and net direction.

For all analyses, data was fourth root transformed to reduce the influence of highly abundant taxa. Shade plots were used to confirm such taxa had been sufficiently down-weighted before proceeding with further analyses. Subsequently, a resemblance matrix was generated, calculating Bray-Curtis similarities between samples.

To investigate drivers of sample structure, a series of SIMPER (similarity percentage) analyses were carried out. These analyses tested for differences between pairs of samples grouped using the factors of location, depth, time and net direction. A dissimilarity statistic was derived for each pair of groups based on either the relative contribution or the presence/absence of taxa within the samples. This allowed those taxa that contributed most to taxonomic differences in either net direction or time of day to be identified.

A non-metric multidimensional scaling (nMDS) analysis (Kruskal stress formula 1) was carried out to provide further context on similarities and differences between sample sets.

MDS generates ordination plots where the distance between samples is a representation of the multi-dimensional differences in the underpinning resemblance matrix.

Two way crossed chi squared tests (Baltosser & Zar, 1996) were carried out to ascertain whether time of day influenced the abundance of migrating zooplankton. Tests were carried out for locations where a complete set (a dawn and dusk deployment) was available as well as all 2016/17 samples and P2 samples averaged. This resulted in eight sets; all 2016/17 samples, P2, P2 100m, P2 80m, P2 chl+10m (a depth of 10 m deeper than the chlorophyll maximum as determined by a CTD cast), PF4 100m, PF2 100m and PF2 80m. Tests were carried out on the complete taxonomic data sets and on the copepods only. Significant differences were set at P<0.05.

3.3 Results

3.3.1 Environmental conditions

Temperature, salinity and fluorescence profiles show the differing environmental conditions at the stations sampled during the cruise (Figure 3.3). When looking across al CTD profiles, P3 and P2 showed the same general water column structure consisting of a surface mixed layer (0-~80 m), winter water (~80- ~ 200 m) and then upper circumpolar deep water (UCDW) (below ~200 m), while the structure of the water column was less clear at the Polar Front stations as a result of a greater amount of vertical mixing.

At P2 and P3, the temperature profiles provide a good guide to the vertical structure of water masses; the mixed layer at the surface had a temperature of 1.5 to 2 °C, at around 80 m there was a sharp thermocline, between the mixed layer and the winter water, in which the temperature decreased to -0.5-0 °C. A deeper (between 180 and 220 m) thermocline marked the transition to UCDW, where the temperature increased to approximately 2 °C. The Polar Front stations had less strong thermoclines and higher temperatures throughout the water column (top 500 m), with surface maxima of 4 °C and minima of -0.5 °C. Here, a mixed layer of approximately 80 m was present, with temperatures reaching 3.2 °C in this layer at PF4 and 2.5 °C at PF2. Further to this, PF4 had a thin (~10 m) subsurface layer of warm water, where temperatures reached 3.8 °C. Below the mixed layer, temperature dropped by 1-2 °C but was quite variable (range of ±1 °C). However, a general warming trend with depth was observed, resulting in stabilised temperatures of between 2 and 3 °C at 500 m.

Salinity within the surface mixed layer was consistent across all locations at ~33.8. This value increased beyond 80 m, at a greater rate at P2 and P3 than at the Polar Front. Within the winter water layer at P2 and P3, salinity increased gradually with depth, reaching 34.6 by ~300 m. Salinity was relatively unchanged within the UCDW. At the Polar Front, a similar pattern was seen with increases in salinity occurring after 80 m, however the increase was more gradual, with salinity continuing to increase down to 500 m where it reaches 34.4.

Chlorophyll derived from fluorescence measurements reached its maximum value within the surface mixed layer at all locations. The Polar Front and P3 had much higher maxima (0.7 and 0.8 mg m^{-3} respectively) than P2 (~ 0.25 mg m^{-3}). At P3, the maximum chlorophyll was found in the surface 50 m before a sharp decline to negligible levels by 100 m. At P2, a subsurface maximum was present, with the highest values being around 70 m, followed by a sharp decline to negligible levels by ~150 m. The same pattern of chlorophyll presence was seen in the water column at the Polar Front, with subsurface maxima being present in the mixed layer at ~70 m before declining rapidly to negligible levels by 100 m.

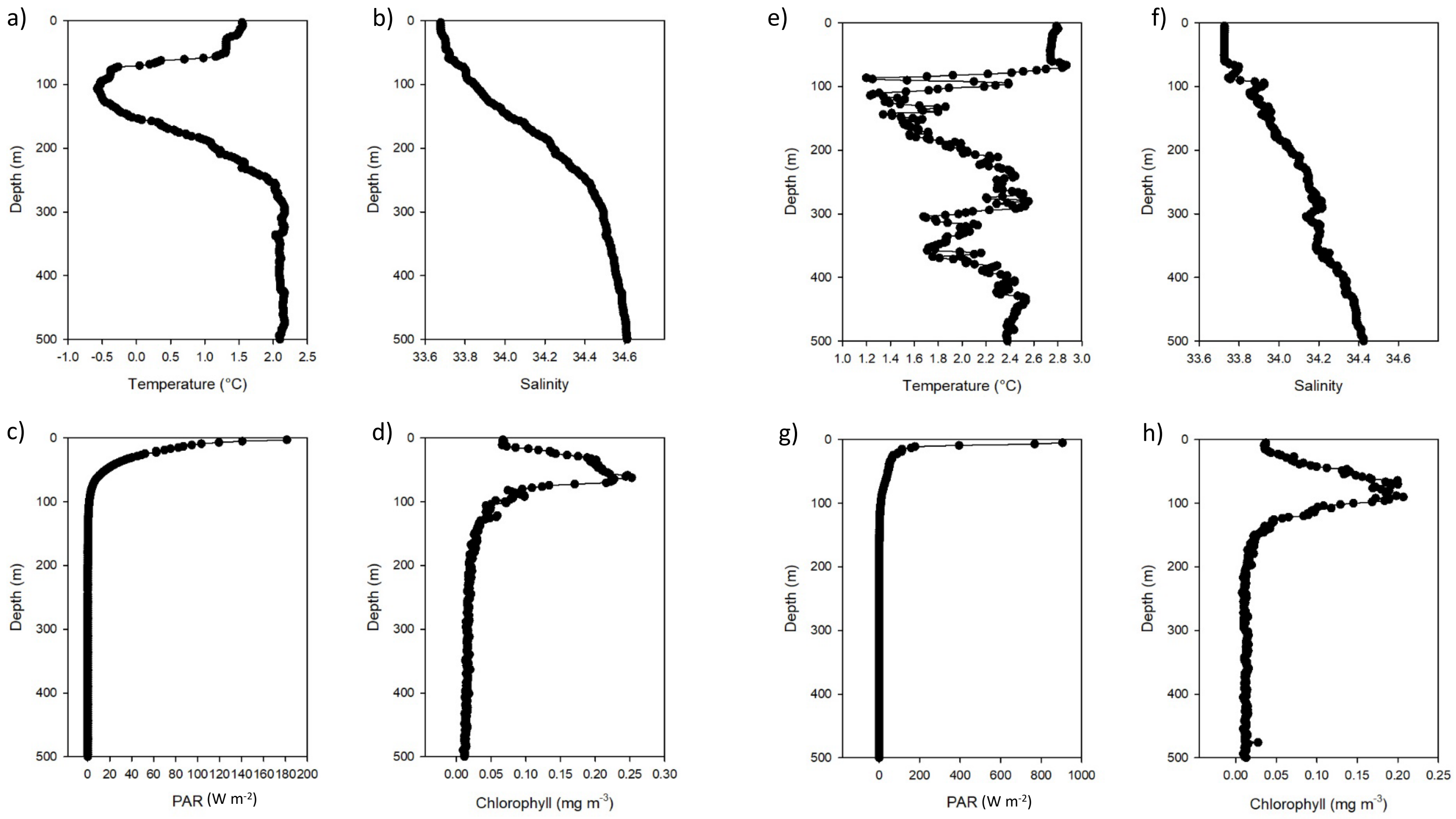


Figure 3. 3: Example profiles of temperature, salinity, PAR and chlorophyll derived from fluorescence with depth as recorded by CTD casts. A) temperature at P2, b) Salinity at P2, c) PAR at P2, d) Chlorophyll at P2, e) temperature at the Polar Front (PF2), f) Salinity at the Polar Front (PF2), g) PAR at the Polar Front (PF2), h) Chlorophyll at the Polar Front (PF2)

3.3.2 Catch Efficiency

Both the MUDL and the mini Bongo net were successful in catching zooplankton, with the mini Bongo having the greatest total catch. When comparing the mini-Bongo with a MUDL sample from the same location, the MUDL net was found to catch approximately 4.5 % and 0.3 % of the total mini Bongo catch in the downward facing and upward facing nets, respectively (Figure 3.4). In terms of the patterns of proportional taxonomic composition of the two net types, catches were broadly similar, with cyclopoid copepods being the most abundant taxa across all samples (Figure 3.5a). However there were some differences in taxonomic composition between the two net types. These were 1) proportional abundances of the dominant taxonomic groups, such as calanoid copepods, differed substantially in being highly dominant in the MUDL samples (accounting for almost 40 % and 30 % of the total catch in the downward and upward facing nets), but making up less than 20 % of the total abundance in the mini Bongo sample (Figure 3.5b); 2) certain taxa were absent from the MUDL, including annelids, appendicularians and tunicates; 3) harpacticoid copepods had lower abundances in the MUDL samples, whilst the abundances of ostracods was higher in the downward facing MUDL.

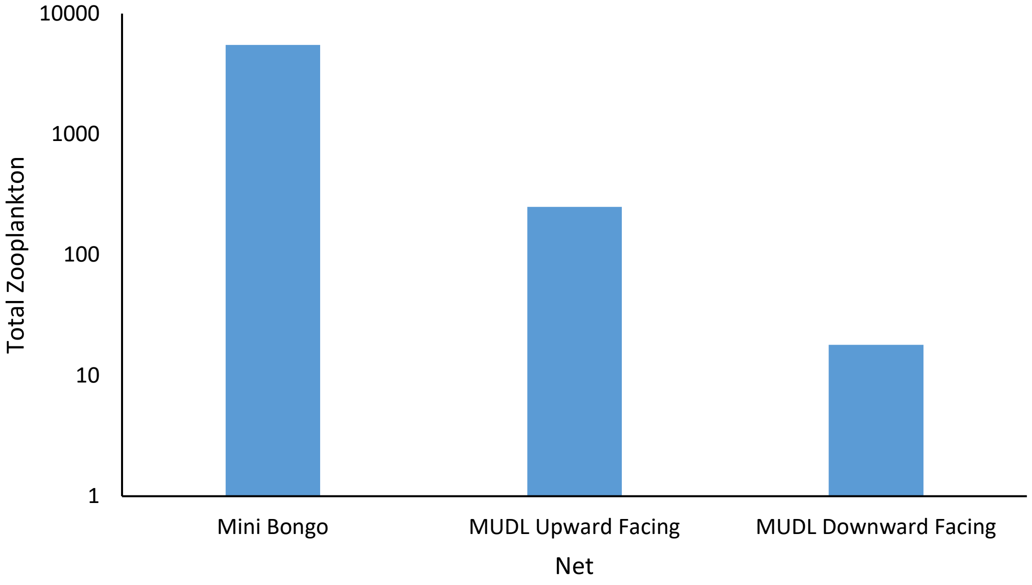
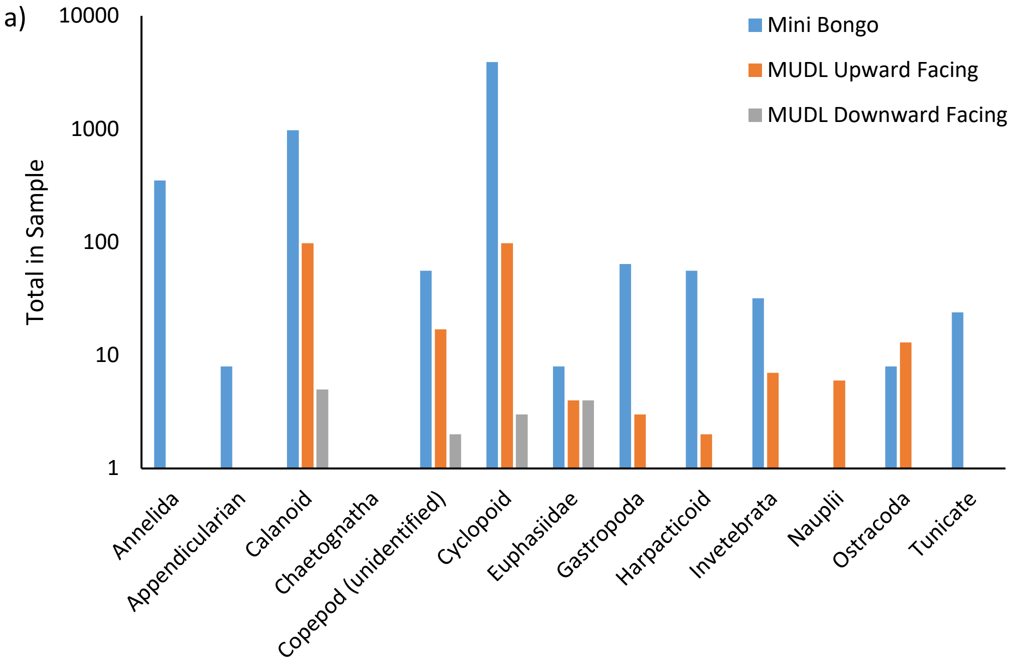


Figure 3. 4: Total number of zooplankton caught in each of the mini-Bongo, upward and downward facing nets at dusk at PF4. The mini- Bongo net was vertically hauled to the surface from 70 m, while the MUDL net only sampled whilst stationary at 100 m.



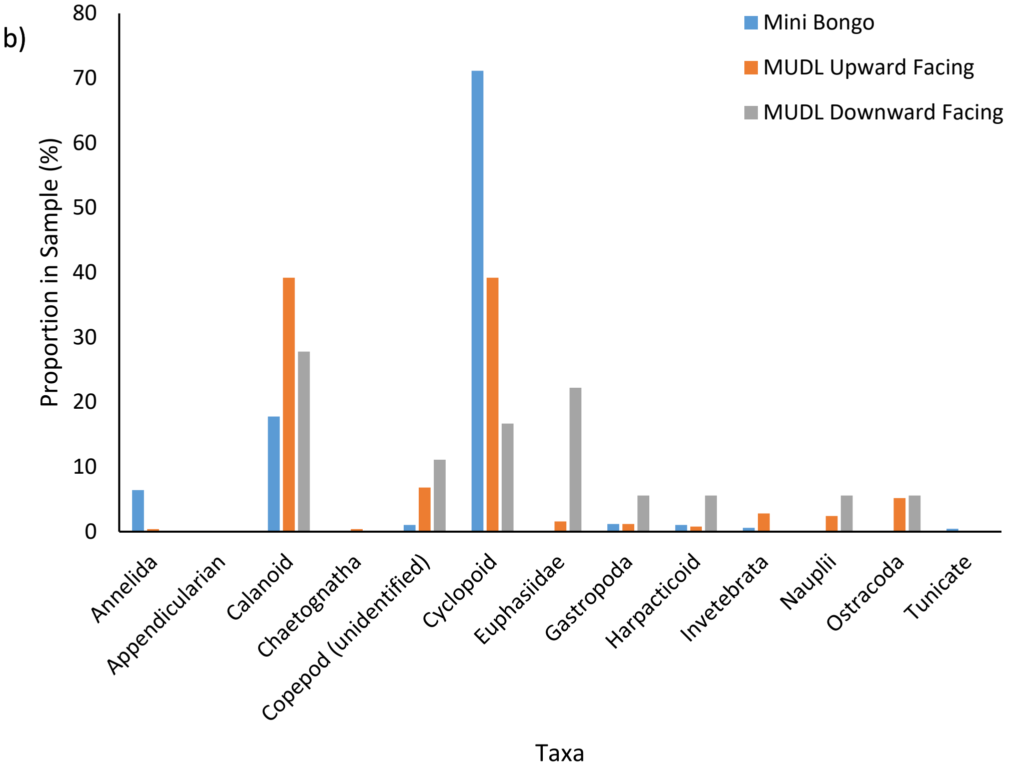


Figure 3. 5: Comparisons of MUDL (event number 145) and mini Bongo nets (event number 144) at dusk at PF4. a) total abundance of zooplankton in each taxa found in the mini Bongo (blue), the upward looking MUDL net (orange) and the downward looking MUDL net (grey), b) relative proportions of each zooplankton taxa found within each of the net samples for the mini Bongo (blue), the upward looking MUDL net (orange) and the downward looking MUDL net (grey).

3.3.3 Comparison of upward and downward facing nets

All MUDL deployments resulted in zooplankton being caught in both nets, indicating that the net was effective in catching both upward and downward swimming zooplankton. However, the upward facing net caught significantly more than the downward facing net (Mann-Whitney U test, $P<0.001$) (Figure 3.6).

In addition to this, there was high variability with location. The Polar Front stations had the greatest abundance of zooplankton in both upward- and downward-facing nets, whilst P2 had the lowest abundances on average (Figure 3.6). The proportions caught in each net were also highly variable with the downward facing net catching from 7 % to 100 % of the total catch in the corresponding upward facing sample. The percentage of organisms caught in either net was not influenced by the overall number of organisms caught in both nets (linear regression, $P=0.26$; Figure 3.7) or deployment location (ANOVA on Ranks $H_{3,10}=5.4$, $P=0.15$).

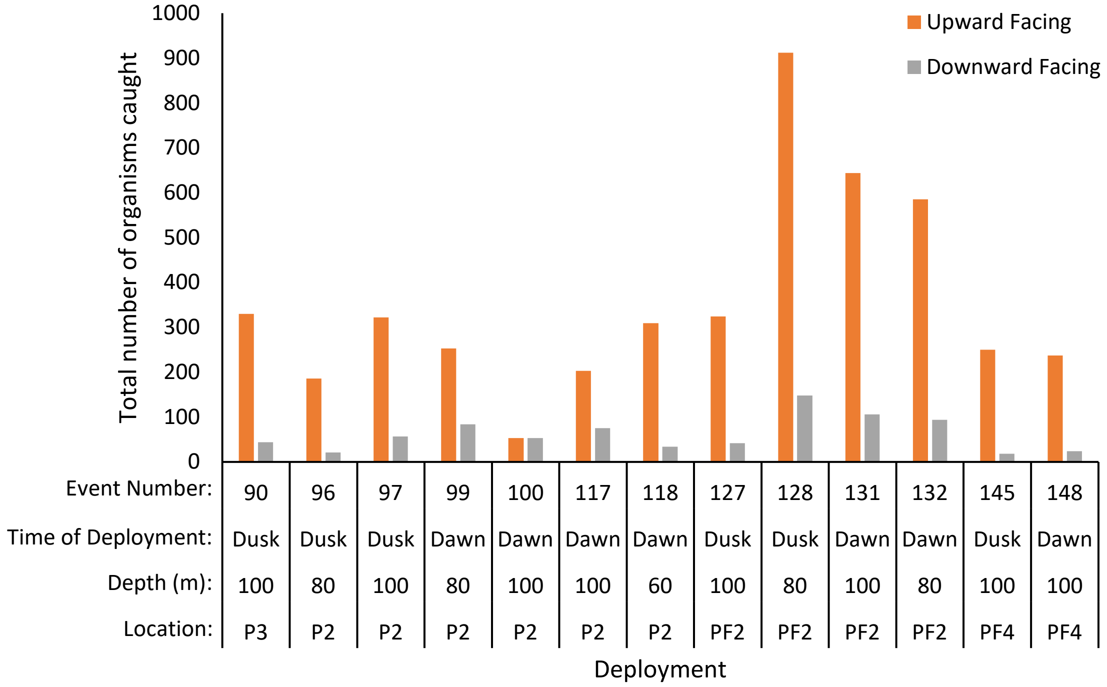


Figure 3. 6: Total number of organisms identified in each net from MUDL deployments carried out during 2016/17 (JR16003). Orange bars show organisms caught in the upward facing nets, grey bars show those found in the downward facing nets. Horizontal axis label displays, from top to bottom: ship log event number, time of deployment, net depth and location.

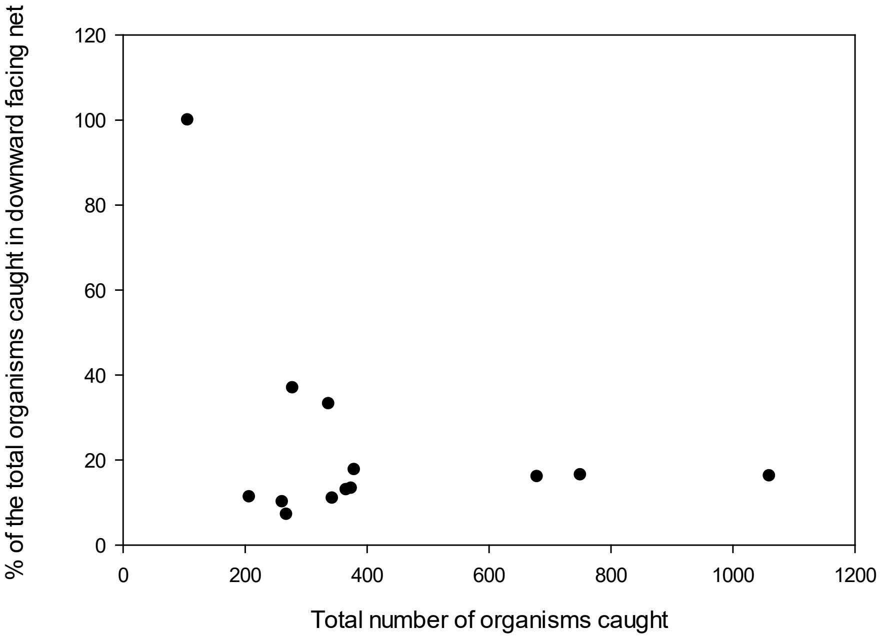


Figure 3. 7: Number of organisms in the downward facing net expressed as a percentage of the total number of organisms caught by the downward and upward facing nets.

3.3.4 Species Contributions

Copepods were found to be the most abundant taxonomic grouping across all samples, with cyclopoids (mainly *Oithona spp*.) and calanoids being dominant. With regards to calanoids, the greatest abundance was at PF2 while P3 and P2 had low abundances (Figure 3.8a). However, the cyclopoids displayed a different pattern since although PF2 had the highest abundance, the relative numbers of cyclopoids caught at P2 and P3 were higher compared to the Polar Front stations. Both cyclopoids and calanoids were more prevalent in the upward facing nets than the downward facing nets across all deployments, with the exception of event number 100 (80 m dawn P2 sample) for the cyclopoids (Figure 3.8b).

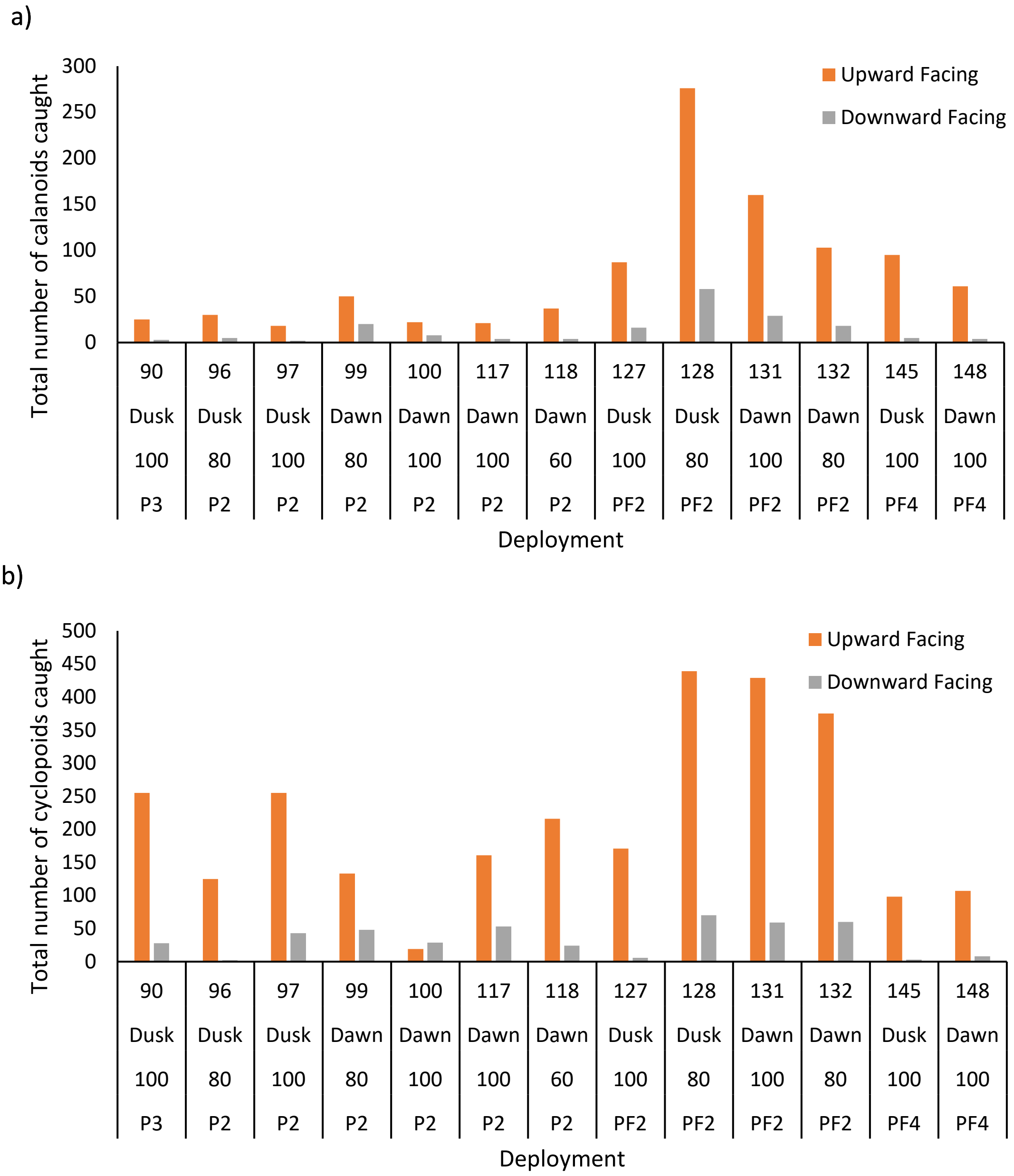


Figure 3. 8: Number of copepods caught in the upward facing net (orange) and downward facing net (grey) across all MUDL deployments carried out in 2016/17. Separated by copepod type, a) shows calanoid copepods with b) showing cyclopoid copepods

Across all stations, *Oithona spp.* was the most numerically dominant taxa overall followed by calanoid copepods (Figure 3.9). The Shannon Diversity index varied slightly with time of day and location (Table 3.2).

Merging all Polar Stations into one group (PF), it was apparent that the community moving at dusk had a greater diversity than at dawn; however, this was not the case at P2 (Figure 3.10). Here, dawn samples had marginally higher Shannon Diversity indices than samples collected at dusk. At dusk there appeared to be a difference in the diversity between the different nets. Across all locations at dusk, the downward looking net had a greater diversity than the upward looking net, suggesting that the upward swimming community involved more taxa than the community travelling downwards at this time. The diversity indices were almost the same across the different nets at dawn, indicating that the communities travelling in both directions were similar.

H'		
P2	Dusk	Dawn
Upward Facing	1.22	1.52
Downward Facing	1.42	1.44

H’		
PF	Dusk	Dawn
Upward Facing	2.13	1.72
Downward Facing	2.24	1.84

D		
P2	Dusk	Dawn
Upward Facing	0.46	0.61
Downward Facing	0.61	0.61

D		
PF	Dusk	Dawn
Upward Facing	0.80	0.65
Downward Facing	0.90	0.74

Table 3. 2: Biodiversity indices for P2 and Polar Front (PF) MUDL samples. Top tables show Shannon Diversity indices’ for upward and downward facing samples for dawn and dusk at P2 and PF. Bottom table shows Simpson’s Index of Diversity for upward and downward facing samples for dawn and dusk at P2 and PF.

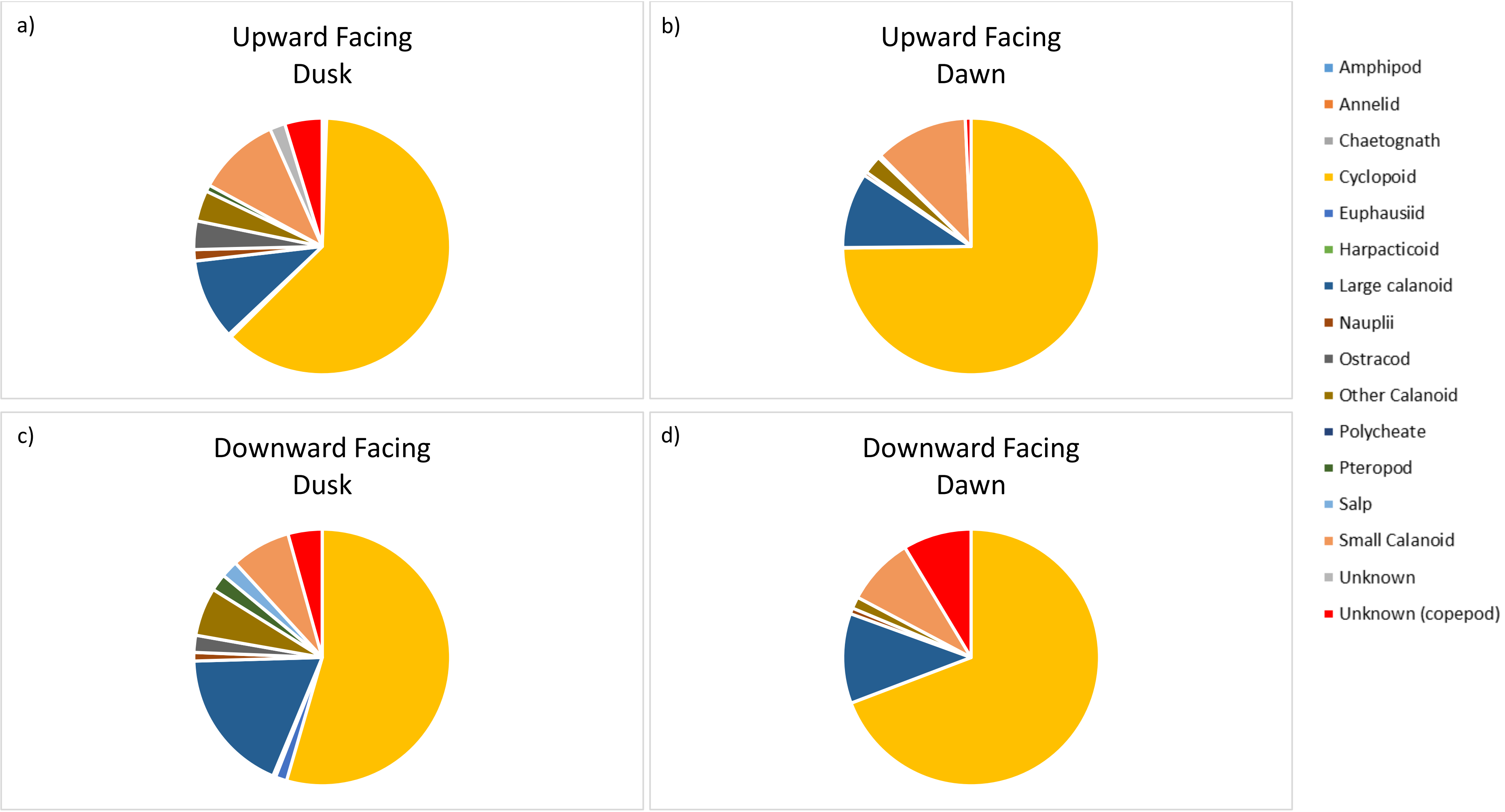


Figure 3. 9: Proportional abundance of respective taxa across all MUDL deployments during 2016/17. Charts represent all deployments grouped together based on deployment time irrespective of location or depth. A) upwards facing nets at dusk, B) upwards facing nets at dawn, C) downwards facing nets at dusk, D) downwards facing nets at dawn.

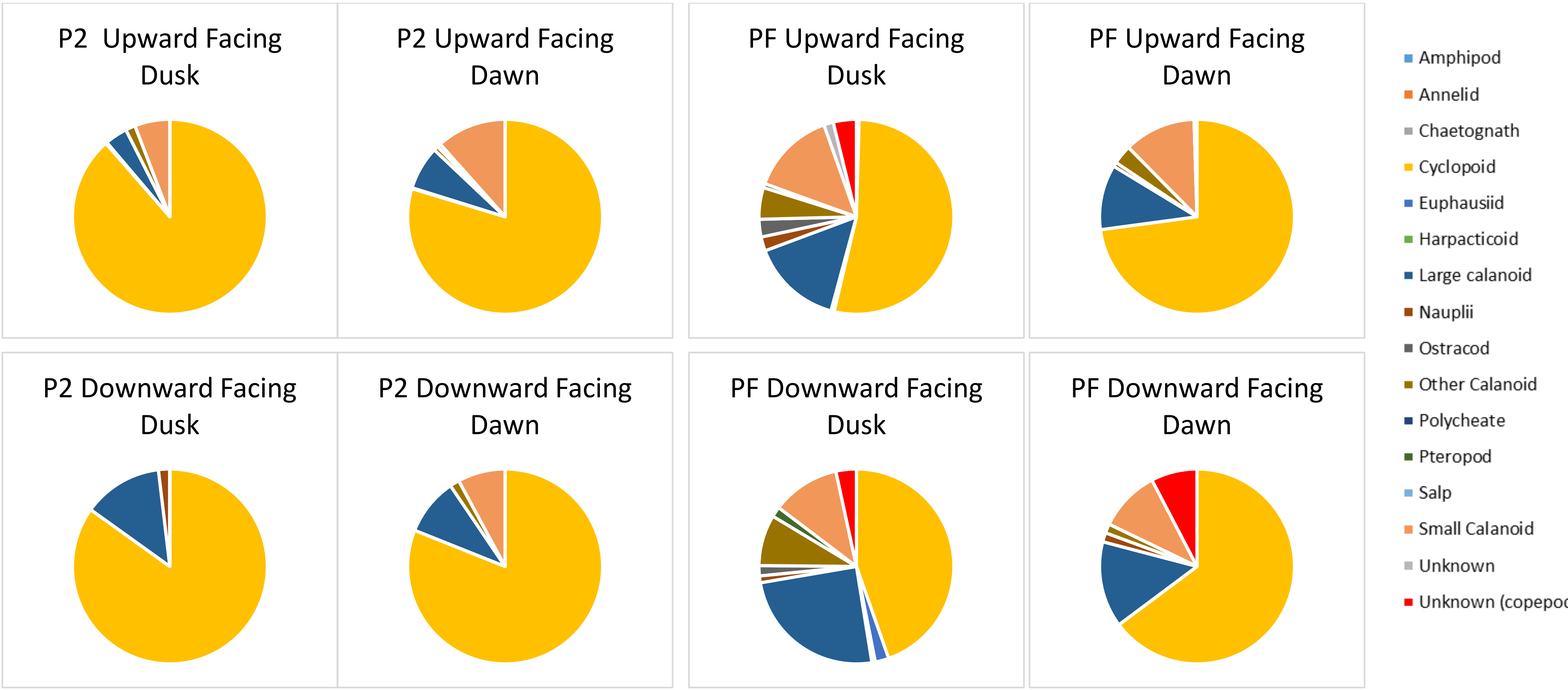


Figure 3. 10: Proportional abundance of respective taxa across all MUDL deployments at P2 (left panel of four plots) and PF stations (right panel of four plots). Colours within the plots represent different taxa found to be present within the net samples. Upward facing nets are shown on the top row with downward facing nets on the second row. The first and third column show dusk deployments and the second and fourth rows, dawn deployments.

SIMPER analysis found location to have the greatest influence on taxonomic composition as shown by dissimilarity statistics, based on the level of underlying similarities within the data (Table 3.3), a dissimilarity of 0 % would indicate identical samples while 100% indicates total dissimilarity . P3 vs PF2 had the greatest level of dissimilarity (55 %) followed closely by P2 vs PF2 (53 %). P3 vs P2 had the lowest dissimilarity level (48 %), with PF2 vs PF4 also being similarly low (48 %). This result indicates that different oceanographic regions (i.e. PF, Scotia Sea [P2,P3]) had greater influence on taxonomic composition than location within an oceanographic region.

In addition to location, net direction, time of day and depth were also found to influence dissimilarities between samples. Net direction had the greatest dissimilarity (53 %) mostly due to differences in abundance rather than species compositions. Samples from dawn and dusk had slightly different species compositions and a dissimilarity of 51. When considering depth, all dissimilarity statistics were found to be around 50 (Table 3.3), suggesting some degree of difference in taxonomic composition was dependent on the depth of the MUDL net.

When looking at the taxonomic contributions, a high degree of overlap was found between samples at different times of day and net directions (Table 3.3). In total, 14 of the 56 taxonomic groups were found to contribute ≥ 50 % cumulatively to the dissimilarities in both net direction and time of day in SIMPER comparisons (Table 3.4). *Oithona spp.* made the greatest contribution, accounting for 6.25 % and 5.11 % of total dissimilarity between net directions and times of day respectively. *Ctenocalanus* spp. and *Metridia* spp. made the second and third greatest contributions, respectively each accounting for 4-5 % of total dissimilarity between net directions and times of day .

In terms of taxa contributing to levels of dissimilarity, the top 14 taxa were the same with regards both net direction and time of day, with the exception of *C. propinquus* CIV (Table 3.4) which did contribute to net direction but not time of day, with all but one of these specimens being caught in the dawn deployments.

Comparison	Dissimilarity (%)
P3* v PF2	55.20
P2 v PF2	53.25
Upward Facing v Downward Facing	53
P2 v PF4	51.56
60 m (P2) v 80 m (P2)	51.12
Dusk v Dawn	51.02
60m v 100m	50.06
80m v 100m	49.78
P3 v PF4	48.41
PF2 v PF4	47.95
P3 v P2	47.71

Table 3. 3: Dissimilarity statistics from SIMPER analysis. Analysis was run on all taxonomic data collected from all MUDL deployments. Each row shows a separate comparison within the SIMPER analysis, with the top rows showing comparisons found to have the greatest dissimilarities.

Direction	Contrib%	Time	Contrib%
Oithona spp.	6.25	*Oithona spp.*	5.11
Ctenocalanus spp.	4.87	*Ctenocalanus spp.*	4.49
Metridia spp.	4.13	*Metridia spp.*	4.46
Clausocalanus spp.	4.07	Pteropod	4.23
calanoid	3.96	Unknown	4.06
Pteropod	3.8	calanoid	4.05
Triconia spp.	3.64	*Triconia spp.*	3.83
Unknown	3.55	*Clausocalanus spp.*	3.51
Unknown (copepod)	2.96	*C. prop CIV*	3.37
Euphausiid	2.89	Ostracod	3.19
Calyptopus (Euphausiid*)*	2.87	*Calyptopus (*Euphausiid*)*	3.17
Nauplii (Copepod)	2.84	nauplii (Copepod)	2.81
Ostracod	2.84	*Euphausiid*	2.79
Eucheata spp.	2.66	*Eucheata spp.*	2.74

Table 3. 4: Taxa/ groups identified as contributing ≥ 50 % cumulative dissimilarity between SIMPER groups. Direction refers to SIMPER comparison between upward and downward facing nets. Time refers to SIMPER analysis between Dawn and Dusk samples. Contrib% shows the % contribution to the dissimilarity between the SIMPER groups for each taxa/group.

Multivariate analysis of all samples collected during 2016/17 showed two broad clusters in the nMDS plots (Figure 3.11), separating the downward facing samples from the upward facing samples. Furthermore, the upward facing samples clustered closer together than the downward facing samples, indicating a greater degree of variation in the latter. In addition to this, the dawn samples appeared to be clustered closer together than the dusk samples, indicating that dawn samples were more similar to each other than the dusk samples were. However, there was a large degree of overlap within the groupings suggesting high variability and a sharing of taxa across all samples. Location and depth did not have a major influence on the clustering patterns.

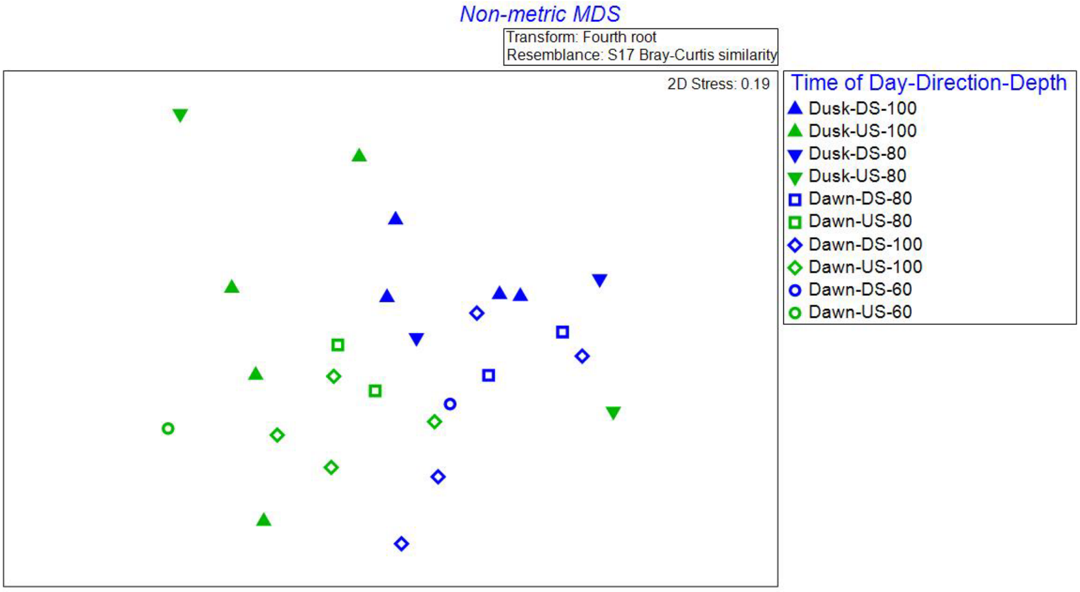


Figure 3. 11: nMDS of all MUDL samples from 2016/17. Spacing between samples indicates the level of similarity with those being located closest together having the greatest similarity. Blue symbols denote samples caught travelling in a downward direction; green symbols, travelling in an upward direction. Symbol shape differs according to the specific deployment type, i.e. the combination of time of day and depth. Solid symbols represent dusk samples, unfilled symbols, dawn samples.

Chi-squared analysis found that, at some locations, the number of zooplankton caught by the MUDL nets was dependent upon the time of deployment (Table 3.5). This was found to be the case at P2, with the numbers of zooplankton and copepods caught travelling upwards relative to those moving downwards differing at dawn and dusk across all depths.

However, this was not the case at the Polar Front where the ratio of zooplankton and copepods moving upwards to those moving downwards was independent of the time of day at all depths sampled.

		X^2	
Location	Depth	Whole sample	Copepods only
All	all	5.83	5.79
P2	all	8.45	32.68
P2	100 m	24.45	15.31
P2	80 m	17.05	30.99
P2	chl max +10 m	8.86	18.39
PF4	100 m	0.80*	1.06*
PF2	100 m	1.29*	4.80*
PF2	80 m	0.00*	0.01*

Table 3. 5: Chi squared values testing whether the proportion of organisms caught in each net was dependent on time of deployment. * denotes significance ($P<0.05$) indicating that the proportions of organisms caught in the nets was independent of the deployment time. Tests were carried out on the whole samples encompassing all taxa and on copepods only.

Examining just the zooplankton caught moving upwards in the water column (i.e. those caught in the downward facing net), there was a pattern of numbers being higher at dawn than at dusk (Figure 3.12), suggesting a pattern of reverse migration. This was the case for all locations with the exception of the 80 m deployment at PF2, where a large number of pteropods were captured swimming downwards at dusk. This pattern remained when only examining copepods and the most abundant captured copepod, *Oithona spp.*, showing that *Oithona spp.* and other copepods were moving within the water column. However, there was some inconsistency between stations with regards the reverse migration pattern of *Oithona spp.* with, for instance, a clear pattern of greater numbers moving upwards at dawn than at dusk in the 80 m PF2 sample but not in the 100 m deployment at P2 (Figure 3.12). This was possibly a result of high inter-sample variability in numbers captured, particularly in the multiple samples collected at P2 (Figure 3.6). Nevertheless, across all locations, there was a general pattern of higher relative numbers of *Oithona spp.* swimming up at dawn than at dusk.

In contrast, no patterns were discernible with regards zooplankton caught swimming downwards (i.e. caught in the upward facing net). The numbers of zooplankton, copepods and *Oithona spp.* caught swimming in this direction were highly variable across times and depths, suggesting a lack of synchronicity in downward migrations.

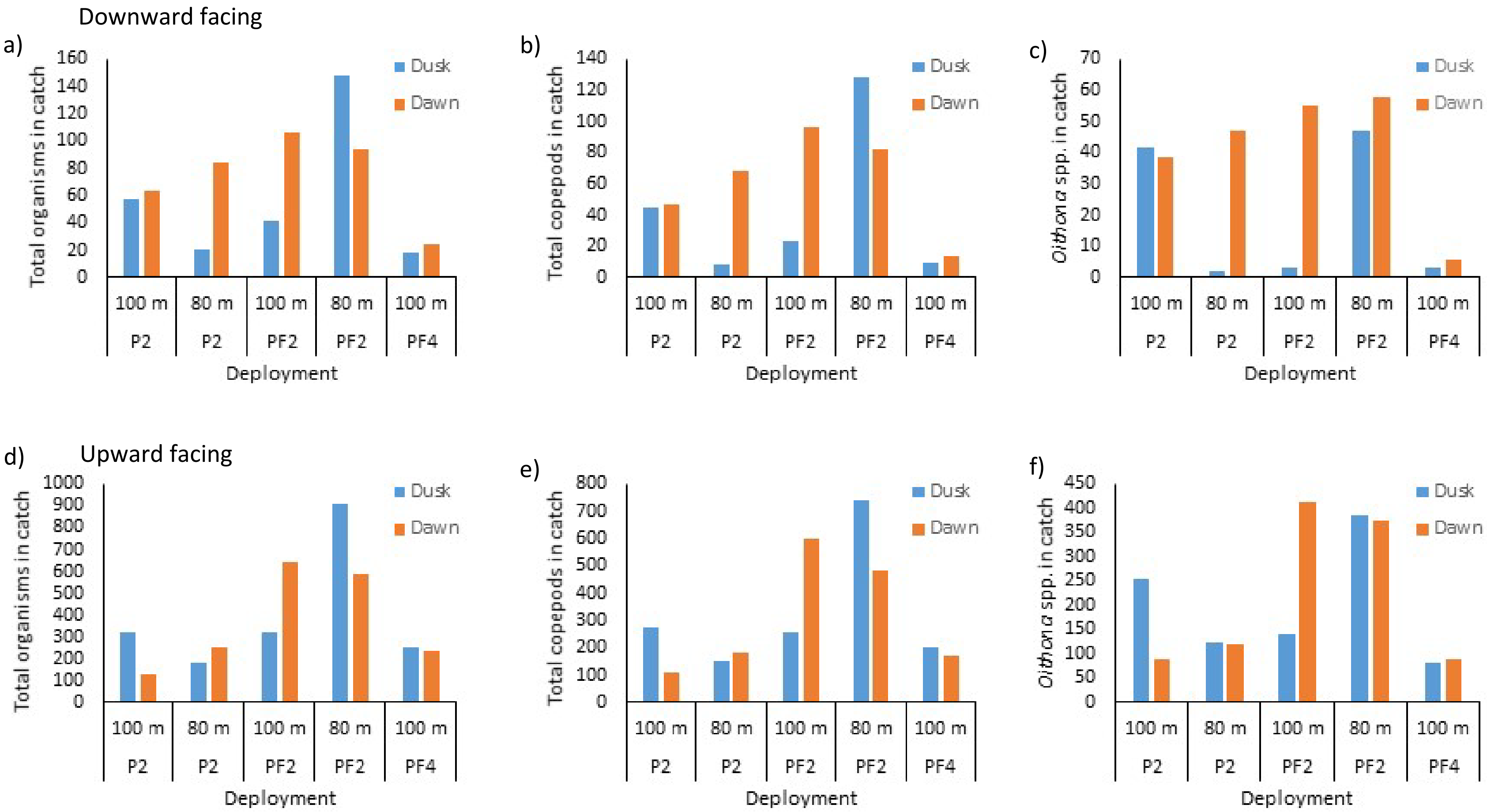


Figure 3. 12: Zooplankton caught in nets that were downward facing (hence upward swimming) and upward facing (hence downward swimming) at dawn (orange) and dusk (blue). a) Total number of zooplankton caught in the downward facing net, b) number of copepods caught in the downward facing net, c) number of *Oithona* spp. caught in the downward facing net, d) Total number of zooplankton caught in the upward facing net, e) number of copepods caught in the upward facing net, f) number of *Oithona* spp. caught in the upward facing net. 100 m refers to the sample being obtained from 100 m, 80 m refers to the sample being obtained from 80 m. P2, PF2 and PF4 show the location the sample was collected from.

3.4 Discussion

3.4.1 Influence of net direction on capture efficiency

The MUDL net system was successful in capturing a range of zooplankton taxa, swimming both upwards and downwards, at a range of depths within and below the mixed layer. Upward and downward swimming organism were captured at both dusk and dawn across a range of stations that were geographically separated and sited within contrasting environmental conditions.

When considering net direction, the samples loosely formed two clusters. Samples from the upward looking net formed one cluster whilst the other cluster was formed of a majority of samples from the downwards looking net. However, these clusters were broad, with overlap suggesting that net direction alone was not driving the sample structure. Furthermore, this broad clustering may be a result of the net capture efficiency differing across the nets. The MUDL net consistently caught a larger number of downward moving than upward moving zooplankton, with the downward looking net catching between 7 and 100 % of the corresponding upward looking net catch. It is not clear why this was the case, however, this is consistent with Pierson et al., (2009) who also caught larger numbers of downward travelling individuals when using net traps similar to those used in the present study. Pierson et al., (2009) suggested a number of reasons, including differences in behavioural and sensory responses of migrating organisms. For instance, upward swimming organisms may encounter the side panels of the net as they enter and respond by swimming downwards. If this is the case in the present study, animals that come into contact with the net at any point during their upward migration may not enter the cod end and would therefore avoid capture within the MUDL. Animals migrating downwards may be doing so in a passive sinking manner, as would be expected within the hunger/satiation hypothesis, and may be less inclined to swim upwards and out of the net on encountering any side panels. In addition to this, if the main response to sensing the equipment is to swim down, then this will only act to increase the funnelling of naturally downward swimming organisms into the cod end, resulting in a bias in numbers in catches by the upward facing net.

Alternatively, Pierson et al., (2009) suggested light attenuation caused by the net may be a factor in reducing the capture efficiency of downward facing nets. As zooplankton migrate upwards, the net may block or alter the light signal they receive from the surface. This alteration may result in avoidance behaviour by the zooplankton reducing the capture efficiency of the downward facing net. If this is the case, a greater difference between the nets during daylight hours would be observed. Due to the deployments in this study occurring at dawn and dusk, it is not possible to resolve this, as light levels would be similar at both time points. Irrespective of the different capture efficiency rates, it is clear from this study that zooplankton are travelling in both directions at all sampled times.

3.4.2 Evidence of Foray Behaviour

The second variable found to be driving the community structure within the samples was time of deployment. In the nMDS analysis, dawn samples were concentrated together, forming a broad grouping, suggesting that all samples taken at dawn were similar to each other (Figure 3.11). The majority of dusk samples were positioned in a large, well-spaced group with some overlap with the dawn samples. Hence, while the dawn samples were comparatively similar to each other, there was a much greater variability within dusk samples.

A further major influence on variability in net catch composition was net direction. In most locations, a greater number of zooplankton were travelling upwards at dawn than at dusk. By contrast, no discernible pattern was found across the downward moving samples. The increase in upward moving plankton at dawn and lack of any pattern in downward moving plankton at this time does not support the traditional DVM theory, but does suggest the presence of asynchronous migrations.

A number of theories have been proposed to explain this asynchronous pattern in migrations. Cushing (1951) proposed a five phase pattern of zooplankton migration. This included a departure from the surface during the night following an initial ascent at dusk, termed midnight sinking. This is then followed by a secondary ascent just before dawn. The upward migrations seen in the present study would appear to align with this pattern in that dusk sampling may be capturing an initial ascent, whilst dawn sampling may be catching zooplankton returning to the surface having already undertaken a dusk migration. Midnight sinking has been previously recorded in a range of species including copepods (e.g. Durbin et al., 1995; Simard et al., 1985; Tarling et al., 2002), and a number of reasons have been proposed. Tarling et al., (2002) attributed the midnight sinking found within *Calanus finmarchicus* to the arrival of a predatory krill species; suggesting that the sinking was a predator avoidance response. However, due to the wide range of taxa seen to be moving in the present study, it is unlikely that predator avoidance was the only driver behind the patterns observed.

As an alternative, Pearre (1970, 1973, 1979, 2003) proposed that midnight sinking is a product of the hunger satiation hypothesis, in which plankton undertake migrations in line with their feeding and digestion rates. This theory has also been linked to foray behaviour, with zooplankton feeding and digesting several times within the course of a night and therefore undertaking a number of shorter forays into food rich surface layers. If the hunger satiation theory is driving vertical migrations, it would be expected that movements would be asynchronous due to individual differences in feeding rates (Pearre, 2003).

The present study found migrations in both directions at both dawn and dusk, implying that migrations were asynchronous and occurring throughout a daily cycle, supporting the presence of foray behaviour. Very few studies have successfully detected foray behaviour due to difficulties in detecting individual zooplankton movements (Pearre, 2003). However, Pierson et al., (2009, 2013) were able to demonstrate foray behaviour in the copepods *Calanus pacifica* and *Metridia pacifica*. This was evidenced by vertical migrations throughout the night, with those individuals migrating downwards having fuller guts than those migrating upwards, suggesting satiation associated downward migration, as would be hypothesised by the hunger satiation theory. Gut contents of individuals caught by the MUDL were not measured in the present study, so direct attribution to hunger and satiation processes cannot be made. However, the similarity in migration patterns seen within this study to those carried out by Pierson et al., (2009, 2013) suggests that similar mechanisms may be responsible.

The presence of downward migrating zooplankton at dusk suggests that a number of zooplankton were in the surface waters during the day. A number of studies have found vertically migrating zooplankton to be present in the upper water column during daylight hours (e.g. Irigoien et al., 2004; Ohman et al., 1983; Pearre, 1970, 1973; Sims et al., 2005). Lampert (1989) and Ohman (1990) argue that a flexibility in vertical migration and potentially a reverse migration is due to the presence of larger invertebrate predators such as chaetognaths and euphausiids. Predatory chaetognaths and euphausiids were caught in the MUDL, showing that these taxa were also undergoing vertical migrations and may be exerting predation pressure upon the zooplankton community.

Primary productivity may also influence migration behaviours. Pearre (1979, 2003) suggested that zooplankton may stay in lit waters during times of low food abundance since if food availability is low then zooplankton will need to spend longer feeding before reaching satiation. A number of studies have shown that *C. finmarchicus* spent more time in surface layers when food was low than when it was high (Bohrer, 1980; Braarud, 1934; Durbin et al., 1995 in Pearre, 2003), suggesting that residence time in surface layers is linked to food availability. The present study sampled zooplankton in a number of locations with contrasting levels of food availability, including a nutrient rich area (P3), a nutrient poor area (P2) and an area of high turbidity (PF2 and PF4). Nevertheless, evidence that this had an influence on surface residence time is equivocal since, for instance, downward swimming at dusk is prevalent at comparable levels across all of these stations.

Oithona spp. were found to be the most dominant taxa across all locations but they had greater dominance at P2 (Figure 3.9). This high abundance is in line with previous sampling efforts within the Scotia Sea (Atkinson & Sinclair, 2000; Ward et al., 2012b). The ratio of directional movement of zooplankton at P2 was found to be dependent upon time, and *Oithona spp.*, as the most abundant zooplankton taxa, often drive these community level patterns in the vertical movements. Often regarded as the most ubiquitous copepod in many oceans (Bigelow, 1926), *Oithona spp.* are an important component of the zooplankton community and exhibit an omnivorous diet (Ward & Hirst, 2007). However, little is known about vertical migration behaviour in *Oithona spp*. Tanimura et al., (2008) investigated the vertical positioning of *Oithona similis* under sea ice in mid-Summer. During 24-hour daylight *O. similis* undertook a reverse migration, inhabiting surface waters during the day and migrating to slightly deeper waters at night (Tanimura et al., 2008). However, a number of authors report no vertical migration in *Oithona spp.* species over daily (Bogorov, 1946; Irigoien et al., 2004) or seasonal cycles (Ashjian et al., 2003; Atkinson, 1998). The present study shows that *Oithona spp.* are undertaking at least foray style vertical migrations in the water column. Further studies of these migrations are required to gain an understanding of the importance of this behaviour within the zooplankton community.

Oithona spp. are ambush predators, detecting prey particles from hydrodynamic signals (Paffenhöfer & Mazzocchi, 2002; Saiz et al., 2003; Svensen & Kiørboe, 2000). However, it has been reported that signals can only be perceived by stationary *Oithona spp.* (Paffenhöfer & Mazzocchi, 2002), with individuals passively sinking until prey is detected at which point they undertake an active ‘jump’ in order to catch motile and non-motile prey (Kiørboe, 2007). This feeding strategy indicates that vertical movements within the water column are a necessary part of *Oithona spp.* feeding behaviour and may lead to the observed foray behaviour. The present study found that, in contrast to previous studies, *Oithona spp.* were not vertically stable but were moving vertically within the water column at both dawn and dusk, further underlining the presence of foray behaviour. *Oithona similis* have been found to have a passive sinking speed of 0.0237 ± 0.0042 cm s^{-1} and a mean swimming velocity of 0.051 ± 0.030 cm s^{-1} (Hubareva & Svetlichny, 2016). Using these speeds, it would take *O. similis* between 2 and 3 hours to passively sink the 2 m distance from the top of the upward facing net to the cod end, but they may be able to swim the distance in 40 minutes. While this would indicate that *Oithona* could not traverse the 2 m length of the net during the 20 min in which the net was open, those that were already within the net system, i.e. at the depth where the MUDL came to rest, would be able to travel into the cod ends. In addition to this, as passive sinking is slower than active swimming, the high numbers of *Oithona spp.* caught in the present study are likely to have been actively swimming in either an upward or downward direction, showing that *Oithona spp.* must be undertaking vertical migrations.

The presence of high numbers of *Oithona spp.* in both the downward and upward facing nets at dawn and dusk suggests that migrations are not synchronised but occur at all times, lending further support to the existence of foray behaviour. Due to their omnivorous feeding strategy, *Oithona spp.* may be able to find food sources throughout the water column and vertically migrate to areas of high food intensity. In this study, primary productivity, represented by chlorophyll levels, was greatest at depths shallower than the sampling depths and therefore it would be expected that copepods would be migrating upwards to feed, with downwards movement being a result of satiation sinking or passive sinking whilst feeding. The finding of copepods undertaking movements in both directions at all sampling times suggests that *Oithona spp.* are migrating to feed during both daylight and darkness, disputing the idea of a single daily migration at dawn and dusk, but rather undertaking more migrations into food rich areas throughout the day.

Alternatively, the vertical movements seen in *Oithona spp.* in the present study may relate to predator avoidance. *Oithona spp.* are small copepods and are preyed upon by a number of larger zooplankton including carnivorous copepods and chaetognaths (Oresland, 1991; Saito & Kiørboe, 2001). While these predators were not found in high numbers in the present study, a small number were present, particularly *Euchaeta* spp. *Euchaeta spp*. feed on *Oithona spp.* within Antarctic waters (Oresland, 1991) and may influence their vertical distribution. If *Euchaeta* spp. and other predatory species are more active at dusk and during the night, predator avoidance would drive prey species to forage at other times, potentially leading to migrations throughout the daylight hours when predators are less active. The presence of these predators in surface waters throughout the night may also drive foray behaviour in prey species. Prey species may only spend the time required to reach satiation in surface waters before moving to a deeper area of safety to digest. This may then need to be repeated throughout the night leading to short forays being undertaken.

This study provides strong evidence that *Oithona spp.* are vertically mobile within the water column at different times within a 24-hour cycle. This is an important finding given their ubiquitous nature and the major position they occupy within global zooplankton communities and linked processes, including the biological carbon pump.

3.4.3 Implications for carbon flux

The present study reveals the existence of widespread foray behaviour in the zooplankton communities of the Scotia Sea and Polar Front. By migrating from the upper water column to deeper waters, zooplankton transport carbon (as well as nutrients) deeper in the water column, so contributing to the biological carbon pump. Using a 1D model of Pacific regions, Bianchi et al., (2013) estimated that carbon transported through zooplankton migrations may contribute up to 30 % of the total particulate flux. Wallace et al., (2013) used a model to simulate the volume of carbon exported in faecal pellets from polar copepods undergoing different migration patterns, including foray behaviour. These authors found that, in the absence of any vertical migrations, all faecal pellets were produced in the top 50 m of the water column and the resulting carbon export would be minimal. When vertical migration, including synchronised diel vertical migration and foray behaviour, were simulated, faecal pellet production occurred deeper within the water column, increasing carbon export to depth. This model study suggests that the asynchronous migrations reported in the present study may play a large role in the carbon flux in the Scotia Sea.

In the Scotia Sea, particulate organic carbon contributes up to 22.91 mg C m^{-2} d^{-1} at 2000 m, with much of this being in the form of faecal pellets (Manno et al., 2014), highlighting the importance of zooplankton migrations in this region. However, it is currently not possible to calculate what proportion of faecal pellets caught at depth by sediment traps were generated from organisms only feeding in the surface layers rather than at depth. Greater resolution of this issue necessitates further taxonomic analysis of detrital matter, something that may be possible in future with emerging molecular techniques.

Vertically migrating organisms may further transport C to depth through respiration, generating Dissolved Inorganic Carbon (DIC). To understand the role zooplankton play in the BCP more completely, in the next chapter I will explore how copepod metabolic carbon contribution to the BCP varies with depth.

3.5 Chapter Summary

- This chapter shows the successful use of a novel net. The MUDL net was proven to be a reliable net in which zooplankton moving within the water column were caught. This methodology has the potential to open further avenues of research within the field of zooplankton migration.
- A greater number of zooplankton were captured in the upward facing net than the downward facing net irrespective of time and location.
- It was found that both upward and downward vertical movements were present within the copepod community at all sampled times, suggesting that smaller vertical movements, possibly forays, are common.
- A greater number of zooplankton were found to be moving upwards at dawn than at dusk, suggesting that reverse migration and/or foray behaviour may be prevalent in the sample area.
- Copepods are the most dominant mesozooplankton within the study area, with *Oithona spp*. being the most common within the samples showing that, contrary to previous studies, *Oithona spp*. undertake vertical movements. This finding may have far reaching implications due to the global abundance of *Oithona spp.* and their potential role in the transport of carbon to deeper layers through migrations.
- The finding of vertical movements of copepods in both directions may have implications for the active flux of carbon. The high abundance and biomass of copepods in many zooplankton communities means that they are likely to have a large influence on zooplankton mediated carbon flux. Many biogeochemical models do not parameterise the acceleration of carbon to depth as a result of copepods (and other zooplankton) mediated processes mainly because robust parameterisations are lacking. This process needs further investigation in order to build a sufficient body of evidence to warrant their inclusion in future carbon cycle models.

4. Chapter 4: Depth-specific variations in the respiration rate of a vertically migrating copepod, *Metridia longa*, in the Arctic Ocean

4.1 Introduction

4.1.1 Zooplankton Vertical Migration and Carbon Flux

Vertical carbon flux is crucial within the ocean's mesopelagic zone (~200 to 1000 m) to facilitate carbon sequestration. Here, primary production is limited such that carbon and nutrients that fuel the operation of this carbon flux need to be sourced from regions above. Marine zooplankton play a role in the delivery of these materials through augmenting the biological carbon pump (BCP) via a number of processes that are associated with their widespread vertical migration behaviour. One way in which they do this is through feeding at the surface and migrating to deep waters to digest and produce faecal pellets. However, gut clearance times tend to be short, with many crustaceans having gut passage times of less than 45 minutes (Dagg & Wyman, 1983; Landry et al., 1994; Morales et al., 1991; Schnetzer & Steinberg, 2002; Wlodarczyk et al., 1992), suggesting that egestion may occur before the zooplankton reach deep waters and therefore the contribution of egestion to the carbon flux may be relatively low (Longhurst & Harrison, 1989). Longhurst and Harrison (1989) suggested that respiration may also provide a mechanism for zooplankton to transport carbon through the water column (Longhurst et al., 1990). The premise is that zooplankton ingest organic matter within the upper water layers before undertaking their downward vertical migration to regions below the mixed layer, where they respire and produce CO_2, contributing to the pool of dissolved inorganic carbon (DIC). Following this suggestion, Longhurst et al., (1990) estimated that respiratory carbon flux may constitute 13-58 % of DIC reaching depths below the pycnocline (~1000 m). Steinberg et al., (2002) found that the combined respiratory carbon and DOC transported by zooplankton migraters reached up to 38.6 % of the POC flux at 150 m and 71.4 % at 300 m within the Sargasso Sea. Hannides et al., (2015) investigated zooplankton respiration within the mesopelagic zone with a view to understanding whether respiration accounted for the loss in particulate carbon, nitrogen and phosphorous within the mesopelagic zone. These authors found that zooplankton respiratory carbon demand was 4-6 times higher than POC loss, with nitrogen and phosphorus demand being 0.5 times and 1.0 times, respectively higher than the attenuation within this zone. These studies indicate that zooplankton respiration is vital for the vertical nutrient flux within our oceans. Furthermore, a recent study found that the respiratory flux from migrators was 23-71 % of the total organic carbon flux measured at 160 m near the Canary Islands (Ariza et al., 2015).

Oceanic respiration is extremely variable, with surface layer respiration estimates ranging from 32 Gt C yr^{-1} to 42 Gt C yr^{-1} and photic zone estimates of 37 ± 5 Gt C yr^{-1} (Del Giorgio & Duarte, 2002). These estimates suggest that oceanic respiration may consume more organic matter than is produced through primary production (Del Giorgio & Duarte, 2002). Zooplankton respiration may account for ~3 Pg C yr^{-1} (Del Giorgio & Duarte, 2002), or 13 Pg C yr^{-1} when including carnivorous feeding (Hernández-León & Ikeda, 2005a). This latter estimate indicates that more than a third of the organic carbon flux is through mesozooplankton, of which respiration accounts for ~17-32 % (Hernández-León & Ikeda, 2005a). However, these estimates rely on specific respiration rates, which can vary across a range of spatial and temporal scales, as well as accurate measurements of biomass, which is often inherently patchy (Hernández-León & Ikeda, 2005a). High latitude oceanic regions, such as the Arctic, are considered to be major sinks of atmospheric carbon in which the BCP is believed to play a major role (Hauck et al., 2015). Estimates of zooplankton biomass and taxon specific respiration rates in the Arctic are particularly difficult to obtain at the appropriate spatial and temporal scales due to large seasonal variations in environmental conditions that restrict ship-based surveys (Hernández-León & Ikeda, 2005a).

4.1.2 Metabolism and vertical migration

In order to better understand the role zooplankton respiration plays in the BCP, metabolic rates during vertical migration need to be further investigated for all taxa and ontogenetic stages within species. Metabolism is the product of all cellular processes that provide an organism with energy to survive, grow, feed, digest, move and reproduce. Metabolic rates vary with changing physical and chemical conditions and will therefore alter as zooplankton undergo vertical migrations. Metabolic processes are difficult to measure at a cellular level and therefore oxygen consumption rate is often used as a measure to reflect metabolic rates for organisms that require oxygen to undergo aerobic processes (Lampert, 1984). The majority of zooplankton respiration occurs within the epipelagic zone (0-150 m), with the contribution to global ocean respiration estimated to be in the order of 10.44 Pg C yr^{-1} (Hernández-León & Ikeda, 2005b).

Respiration rates of zooplankton found in the mesopelagic zone are problematic to measure due to their patchy distribution and difficulties in obtaining healthy intact organisms from deeper in the water column (Hernández-León et al., 2001; Hernández-León & Ikeda, 2005a). However, the contribution to global respiration from zooplankton within the mesopelagic zone has been estimated to be 21 % of that from the epipelagic zone (Hernández-León & Ikeda, 2005a). While a large number of studies have investigated changes in respiration rates across temperature gradients, (e.g. Almeda et al., 2011; Castellani et al., 2005b; Lehette et al., 2016; Tande, 1988), very few studies have assessed how respiration rates change with depth within the water column. A meta analysis covering 32 studies and over 50 copepod species found that a 1 °C increase in temperature resulted in a 7 % increase in respiration rate, showing that temperature is an important factor when assessing metabolic rates (Heine et al., 2019). One attempt to assess how metabolic rates may change throughout the water column was by Hernández-León et al., (2001) who investigated the vertical distribution of zooplankton biomass and metabolic rates around the Canary Islands. Metabolic rates were calculated by measuring the electron transfer system (ETS), an enzyme system that initiates respiration at the cellular level (Packard, 1985). Here, it was found that zooplankton caught between 200 and 500 m had a slightly, but not significantly, higher respiration than those caught below 500 m. This higher respiration rate was attributed to higher water temperatures.

Changes in temperature and respiration rates within the water column may confer a metabolic advantage to migrating zooplankton. Herbivorous zooplankton need to enter the warm, upper layers of the water column to feed, but by migrating to deeper, colder water they may be able to reduce their metabolism (McLaren, 1963), and therefore minimise energy losses whilst not feeding (Geller, 1986). This may be particularly so in Arctic Ocean regions which can experience intense thermal stratification. Furthermore, the alteration of respiration rate with depth over the course of DVM may be an important consideration when quantifying the role of zooplankton respiration within the BCP at high latitudes.

4.1.3 The Fram Strait

Within the Arctic Ocean, the Fram Strait is an area of open ocean at the boundary of the North Atlantic and Arctic Ocean between Greenland and Svalbard (Figure 4.1). It is the only deep water connection between these oceans, allowing an exchange of water masses (Müller et al., 2009; Werner et al., 2014). The area is characterised by a number of water masses; The West Spitsbergen Current (WSC) carries warm Atlantic water northwards, entering the Fram Strait west of Svalbard (Manley, 1995). As the WSC moves northwards, it cools and freshens as a result of an exchange with sea ice and glacial melt water (Rudels et al., 2005), with temperatures averaging 3.1 °C (Beszczynska-Möller et al., 2012). At 78-80 °N, the WSC splits into three. The divide results in a Svalbard branch, which flows along the edge of Svalbard, the Yermak branch, which flows along the western and northern edges of the Yermak plateau and a third branch which is re-circulated in the return Atlantic current (RAC) (Beszczynska-Möller et al., 2012). To the west of the Fram Strait, cooler, fresher Arctic water flows at the surface, southwards in the East Greenland Current (EGC). Hydrographic domains are separated by frontal systems (Hirche et al., 1991). The Arctic Front separates Atlantic water from the Arctic water in the Greenland Sea gyres (Hirche et al., 1991), whilst the eastern and western currents are separated by the East Greenland polar front (EGPF), which generates a Marginal Ice Zone (MIZ) (Bergmann et al., 2016). The western part is often covered in permanent sea ice, whilst central and northeast areas have seasonal variations in sea ice cover and the south eastern region of the Fram Strait is permanently ice-free (Bergmann et al., 2016). This hydrography results in some of the most dramatic water mass transitions in the oceans (Beszczynska-Möller et al., 2012), and provides different regimes across the Strait, strongly influencing the biology found in the region (Hirche et al., 1991; Svensen et al., 2011). Further to this, a topographical feature, the Molloy Deep, which is an area of deep bathymetry (up to 5607 m) located close to the east coast of Svalbard (Thiede et al., 1990). The Molloy Deep causes stationary and propagating eddies within the MIZ (Smith et al., 1984). These eddies may enhance the primary productivity within the region as a result of them driving the upwelling of nitrate rich waters (Smith et al., 1985).

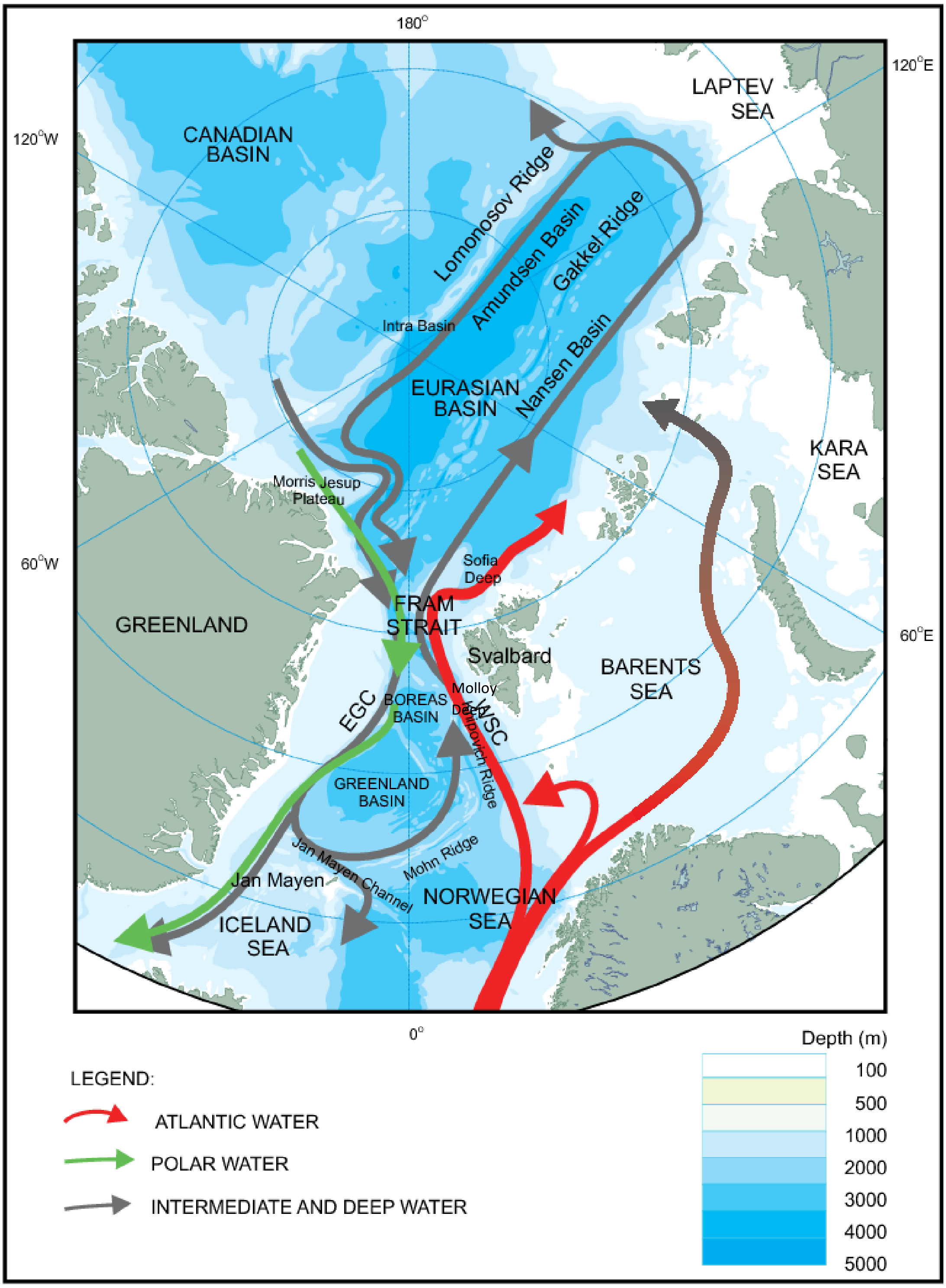


Figure 4. 1: Map of the Fram Strait and Arctic Ocean. Red and green arrows represent the ocean currents transporting warm Atlantic and cold Arctic water masses, respectively. Figure from Langehaug and Falck, (2012).

4.1.4 Zooplankton community of the Fram Strait

The different hydrographic regimes across the Fram Strait give rise to three biogeographic zones; the Arctic (Polar Water), Subarctic (Arctic Water) and the Boreal (Atlantic Water) (Hirche et al., 1991), with differing zooplankton communities (Svensen et al., 2011). The zooplankton community of the Fram Strait has been studied since the beginning of the 20th century (Nansen, 1902). However, there have been relatively few comprehensive studies of zooplankton species ecology and their role in pelagic ecosystem dynamics (Nöthig et al., 2015). Similarities in the zooplankton species compositions of the North Atlantic and the Arctic Ocean have been recognised (Mumm et al., 1999), suggesting some overlap in their respective communities . A number of studies indicated that this overlap in species composition may be increasing with Atlantic origin species becoming more abundant in the Arctic, for which the term 'Arctic Atlantification' has been coined (Kraft et al., 2013; Møller & Nielsen, 2020). The pelagic community of the Arctic Ocean is dominated by the copepods *Calanus finmarchicus*, *Calanus glacialis*, *Calanus hyperboreus* and *Metridia spp.* which together make up two-thirds to three quarters of zooplankton biomass (Hirche et al., 1991; Mumm et al., 1999). Within the Fram Strait, Nöthig et al., (2015) found *Calanus* copepods and the amphipod *Themisto spp*. to be dominant although this does alter between the different water masses within the Strait (Møller et al., 2006). In the Atlantic water entering in the east, *Calanus finmarchicus* is the most important copepod (Wiborg, 1954), whilst in Arctic waters further west, *Calanus hyperboreus* and *Calanus glacialis* are more abundant (Smith, 1988).

The Arctic Ocean also exhibits strong thermal gradients within the water column (Grainger, 1989). Arctic water characterises the top 200-300 m, with warm Atlantic water reaching from 200-900 m and, beyond this, cold Arctic bottom water. Many studies report that highest zooplankton biomass are found in the Arctic water surface layers (Grainger, 1989; Mumm et al., 1999) and that vertical zooplankton community structure is strongly influenced by the vertical positioning of water masses. For instance, in the central Arctic Ocean and West Spitsbergen Current, Mumm et al., (1998) found that *Calanus spp*. dominated zooplankton biomass in the top 100 m of the water column while *Metridia spp.* was found to have greater abundance below 100 m.

4.1.5 Metridia

The Arctic Ocean has strong seasonal light regimes, with short periods of primary productivity leading to a short feeding season for herbivorous zooplankton. The dominant *Calanus spp.* in the Arctic Ocean have adapted to this by entering into diapause, a form of hibernation, which allows them to survive the food limited winter months (Hirche, 1996). However, *Metridia spp*. are also highly abundant in this area and do not display diapause behaviour (Osgood & Frost, 1994a), but are thought to display omnivorous behaviour (Arashkevich, 1969) along with strong vertical migrations throughout the year (Foxton, 1972).

In this study, I will focus on *Metridia longa* which is one of 18 known copepod species in the family Metridinidae (Boltovskoy, 1999). It has a wide global distribution pattern occurring in all oceans including the high Arctic, and Antarctic Continent (Boltovskoy, 1999). However it is most dominant in the high Arctic where other Metridian species are absent (Auel & Hagen, 2002; Mumm et al., 1999). *M. longa* is a moderately sized copepod, with females (3.7-5.0 mm) attaining a greater size than males (1.8-2.2 mm) (Hopcroft, 2009).

Metridians are known to undergo pronounced daily vertical migrations between the upper mesopelagic layer and the surface layers year round. Berge et al., (2012), for instance, reported that *Metridia* species undertook a distinct diel vertical migration (DVM) during the polar night in the Arctic. Hays (1995) found that night time samples contained 95 % of *M. longa* collected during a CPR survey in the North Atlantic and North Sea, supporting a strong vertical migration. Dagg et al., (1998) also found that the *M. lucens* population within Dabob Bay (an enclosed bay within Puget Sound, North East Pacific) performed strong migrations with the population residing mostly in waters between 50 and 108 m during the day and above 50 m during the evening/night. However, a substantial proportion of the population (20 %) remained at depth during the night. Osgood and Frost (1994a) reported that the vertical migration pattern of *M. lucens* in Dabob Bay varied between genders and across development stages. For example, the majority of adult females exhibited strong DVM behaviour, being found between 75 and 125 m during the day and between 0 and 10 m at night. In contrast, males occurred predominantly between 75 and 200 m during both day and night, with no vertical migrations to the surface layers evident.

Given the pronounced DVM behaviour of *Metridia* spp., they are likely to be a key group in the operation of the Arctic/sub-Arctic BCP (Morales, 1999). Kobari et al., (2008) calculated the total active flux of carbon through the DVM of *Metridia pacifica* to be up to 16.6 mg C m^{-2} d^{-1} in the Western Subarctic Gyre. Similar values were found for *Metridia spp*. in the Oyashio region of the subarctic North Pacific, where an annual mean flux of 8 mg C m^{-2} d^{-1} was estimated, which accounted for up to 96 % of the POC flux during some seasons (Takahashi et al., 2009). Further to this, Takahashi et al., (2009) found that the contribution to the downward carbon export by *Metridia spp*. was greater during non-blooming seasons (summer-winter), when other calanoid species are less active, suggesting that *Metridia spp.* play a pivotal role in carbon export throughout the year.

Metridia spp. are likely to experience pronounced changes in thermal environments during DVM and may therefore alter their metabolism in response, making them an ideal species to investigate variations in respiration rates across vertical migrations. To date, studies investigating the contribution of *Metridia spp*. to carbon drawdown have not taken into account different metabolic rates over the course of a migration, or differences related to sex and ontogeny. However, these differences may be important when estimating the respiratory component of active flux. The purpose of this study is to examine whether respiration rates and body composition of *M. longa* differs between those caught in deep water and those found in the upper water column within the Fram Strait (Arctic Ocean). Specifically, I aim to:

- Investigate whether depth or sex plays a role in respiration rates of adult *M. longa.*
- Relate any respiratory rate differences to carbon, hydrogen and nitrogen content (elemental composition analysis) to examine the effect of body condition on metabolic rates.
- Consider relationships between body condition and migration behaviour.
- Examine whether laboratory measured respiration rates are representative of those that occur *in situ.*
- Add to the current body of knowledge regarding the behaviour and life cycles of biomass dominant copepods that are likely to be major contributors to respiratory carbon flux within the BCP.

4.2 Methods

4.2.1 Field Sampling

Respiration incubations were carried out on board the *RRS James Clark Ross* during a CAO (Changing Arctic Ocean) research cruise for project DIAPOD (Mechanistic understanding of the role of diatoms in the success of the Arctic complex and implications for a warmer Arctic). Specimens of *Metridia longa* were collected on board RRS *James Clark Ross* (JR17005) during summer (May-June) 2018. Net sampling was focussed upon eleven station locations within the Fram Strait in the Atlantic sector of the Arctic Ocean (Figure 4.2). All sampling took place during the daytime. The copepods were collected from differing depths of the water column, using either a 1 m^2 Multiple Opening and Closing Net with an Environmental Sensing System (MOCNESS), a Bongo net (57 cm diameter opening and 200 µm mesh), or a ring net (57 cm diameter opening 200 µm mesh). The MOCNESS net was deployed (ice conditions and sea floor depth permitting) to obtain depth-discrete samples from the deeper parts of the water column not reachable with vertically hauled Bongo, or ring nets. The MOCNESS was equipped with 9 nets of 330 µm mesh that could be opened and closed on command and was configured to sample the water column in 125 m depth-strata between 0 and 1000 m. The net system was trawled obliquely at a speed of ~2 knots with each net open for a vertical depth range of 125 m for a duration of ~10 mins. We selected *M. longa* samples from 375-500 m (or 450-600 m at station NT11), as these were considered representative of individuals in a deep dwelling (upper mesopelagic) phase. Copepods residing in waters in the surface layers were collected by Bongo nets that were deployed to a maximum depth of 200 m and hauled vertically to the surface. On one occasion, a ring net was deployed instead of the Bongo net at station F2 (Figure 4.2). This net was deployed in a similar manner, resulting in copepods from the upper 100 m of the water column being collected. In locations where *M. longa* could not be collected from a Bongo or a ring net, specimens were taken from the surface net (5 to 125 m) of the MOCNESS. Once on-board, net samples were taken immediately to a temperature controlled room (2 °C) and adult *M. longa* specimens were selected randomly, using soft tweezers, from sub-samples for on-board incubations and respiration measurements.

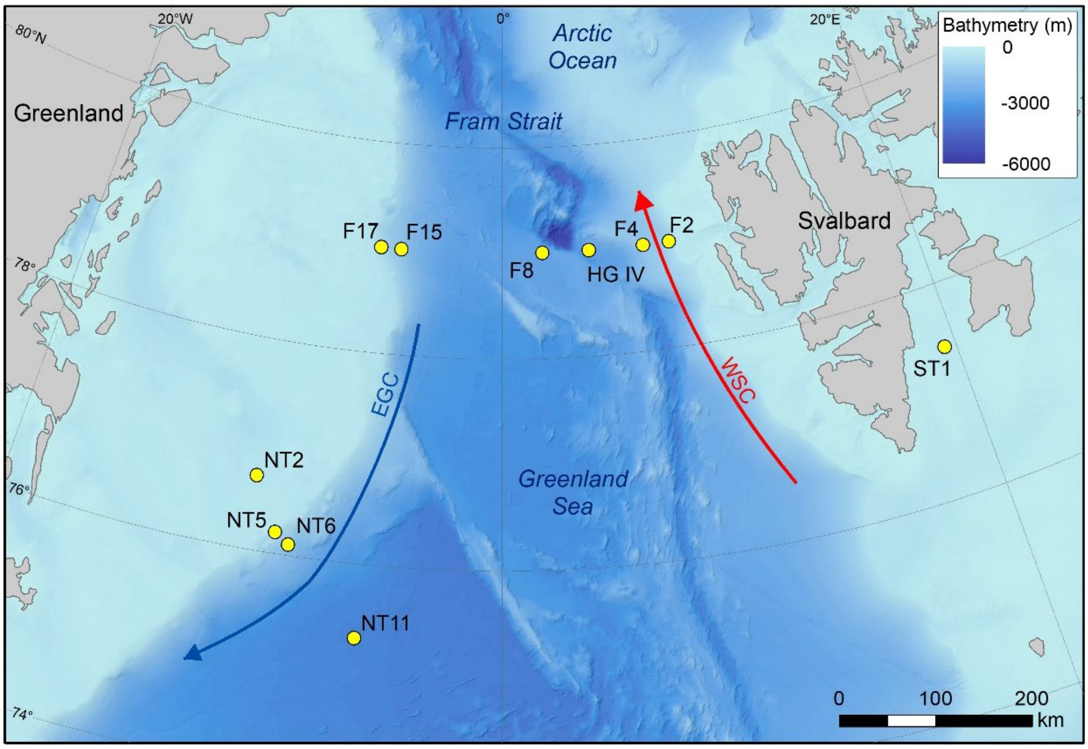


Figure 4.2: Map of Fram Strait study area showing locations from which *Metridia longa* were collected during summer 2018 using nets deployed from *RRS James Clark Ross*. Red arrow represents the West Spitsbergen current carrying warm water northwards; the blue arrow represents the East Greenland Current transporting cold Arctic water southwards.

A CTD was deployed prior to net deployments at each station. This consisted of a SBE32 carousel water-sampler plus a SBE9Plus CTD containing a SBE3Plus temperature sensor. Temperature was measured every ~1 m on the downcast. All temperature values recorded within each depth integral at each station were averaged to give one temperature value for every net collection.

A total of 186 *M. longa* specimens were obtained from a number of stations across the Fram Strait, encompassing a range of water masses and thermal environments. Specimens of the shallow-water (0-200 m) copepod community were collected at 12 stations, whilst deep-water (375-500 m) specimens were collected from 5 locations. On one occasion (station NT11), deep water copepods were also collected from 450-600 m. Overall, respiration incubations were performed on almost three times as many copepods collected from the upper layers as the deeper layers (138 shallow copepods versus 48 deep copepods).

4.2.2 Measuring Oxygen Consumption

Oxygen consumption of *M. longa* was measured on board using a non-invasive Loligo microrespiration system (Loligo Systems, Viborg, Denmark). This system consists of a sealed glass microplate with a planar oxygen ruthenium-complex disk fitted to the base of each 500 µl well. The microplate sits on a 24-channel fluorescence-based respirometry system (SDR Sensor Dish Reader) (PreSens Precision Sensing GmbH, Regensburg, Germany), which allows the oxygen content of the 24 wells to be read simultaneously. The concentration of dissolved oxygen was measured every three minutes using oxygen-dependent fluorescence of the disks at the base of each well. These measurements were recorded via an attached computer, from which oxygen consumption and therefore aerobic respiration can be calculated. This system was secured in an incubator which maintained a temperature of 2 ± 0.5 ˚C for all respiration incubations. The reader, plate and sample water (0.2 µm filtered surface seawater) were placed inside the incubator 24 h prior to respiration experiments to allow all temperatures to equilibrate. Before respiration incubations, filtered seawater was placed into all wells to wet the sensor spots. This water was then removed and replaced with filtered sample water that had been acclimated to 2 ˚C for a minimum of 12 hours, referred to as sample water, immediately before the wells were populated with *M. longa*. All wells were part filled with sample water and inspected for the presence of air bubbles. An individual *M. longa* was placed into each of twenty wells, leaving four wells empty as controls in each incubation. Where possible, equal numbers of adult male and female copepods were used along with equal numbers of copepods from deep and shallow water. Once the plate was populated, each well was overfilled with sample water and inspected for air bubbles and to confirm that the copepods had remained in the wells. The wells were then sealed with parafilm and re-inspected. Any wells containing bubbles were refilled and the parafilm seal re-applied. A layer of silicone was placed on top of the microplate, with a weighted block sitting on the silicone for further sealing. The microplate was then placed on top of the SDR reader in the thermal incubator (Figure 4.3). The reader was set to take oxygen readings (% air saturation) every three minutes for the duration of the trial. Loading of the microplate was carried out in a temperature-controlled room; however, well plate temperature readings were consistently higher than the temperature of the incubator at the beginning of each incubation (reaching a maximum of 5°C). As a result, early oxygen readings within each incubation were discounted. Well plate temperature was recorded throughout all incubations and only when temperature stabilisation had been reached were oxygen consumption measurements considered acceptable for analysis. Incubations were run for a maximum of 24 h, before being removed from the incubator. At the end of each incubation, copepods were removed and photographed under a microscope, before being placed in a tin capsule and stored at -80 ˚C.

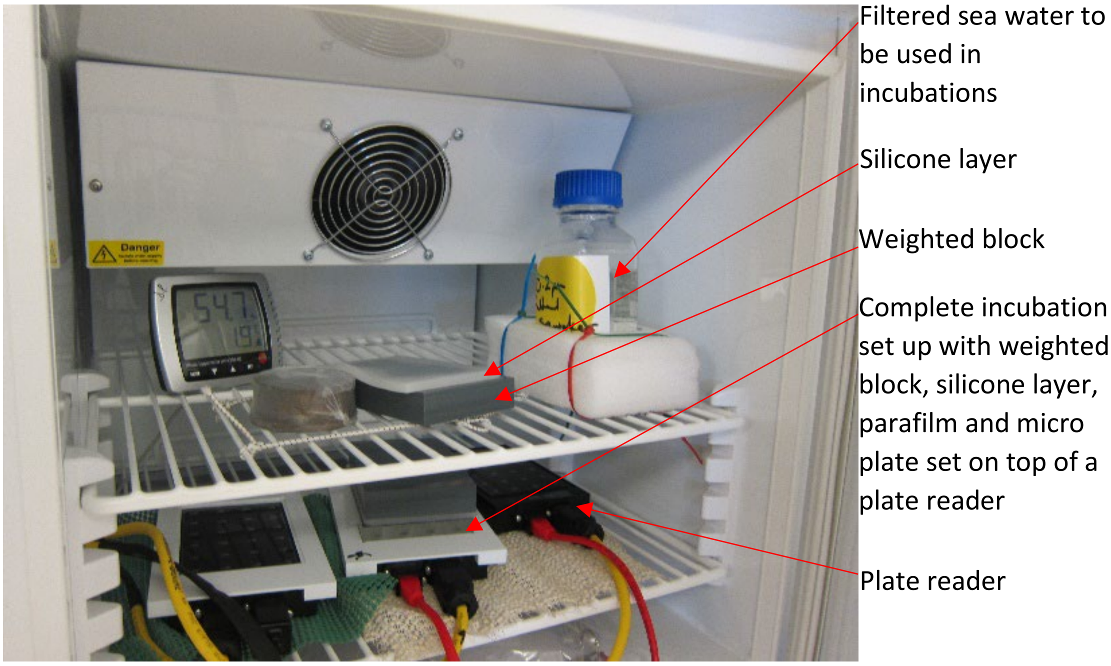


Figure 4. 3: Loligo respirometer set up inside the incubator onboard the *RRS James Clark Ross*. Labels show each section of the respirometer including the microplate and reader. Photo credit: S. Reed.

Prior to use, the sensor spots were calibrated in accordance with the user manual. This was done by using a 1 % sodium sulphite solution to achieve 0 % oxygen saturated water. Half the wells were filled with deoxygenated water and sealed with parafilm. The remaining wells were filled with filtered water and left unsealed in order to achieve an air saturation of 100 %. Oxygen measurements were then recorded overnight and the values used to create a new calibration dataset within the Loligo software. This calibration dataset required determination of the air pressure and water salinity, taken from the on-board sensors in order to standardise across all respiration incubations.

Following respiration incubations, *M. longa* were transferred to individual tin capsules and transported to the British Antarctic Survey at -80˚C. Once in the on shore laboratory, the tin capsules containing *M. longa* were placed at 60˚C overnight to dry out before being placed in a CE440 Elemental Analyser (Exeter Analytical Limited) for CHN measurements. The analyser was prepared using a benzoic acid organic blank to check nitrogen content prior to any analyses being carried out. All subsequent runs used an acetanilide standard. Empty tin capsules were analysed at regular intervals to provide blanks and assess the data. The system used a horizontal injection system utilising nickel carrier sleeves to transport tin capsules to the combustion chamber. Tin capsules were pre-combusted at 950 ˚C for an hour to remove any CHN impurities. Combustion of material was achieved with bursts of oxygen (N5 grade, 99.999 % minimum) and the carrier gas used was helium (N4.6 grade 99.996 % minimum). Capsules were stored in sealed 96 well plates in a glass jar containing silica gel between drying and CHN analysis.

4.2.3 Data Treatment

4.2.3.1 Data Validation and Assessment of Loligo cell behaviour

Oxygen data were downloaded as percentage air saturation and O_2 content (µmol/l) from the Loligo software (PreSens version SDR v4.0.0) after each trial in .csv format. From initial scrutiny, any wells with abnormal behaviour during incubations were rejected before absolute oxygen consumption rates were calculated. This procedure was conducted as follows (see Table 4.1 for equation parameter definitions):

Step 1: determine overall % oxygen saturation (G) across all wells and incubations at the start point using the equation:

$$G = \frac{\sum_{for\ c=1,i=1}^{c=M,i=N} AS_{0,m,n}}{M \times N}$$

(Equation 4.1)

Step 2: determine average % oxygen saturation (H_m) for each individual well across all incubations as:

$$H_m = \frac{\sum_{i=1}^{i=N} AS_{0,m}}{N}$$

(Equation 4.2)

Step 3: examine the performance of individual wells relative to the overall performance of all wells ($K_{m,n}$) using the equation:

$$K_{m,n} = AS_{60,m,n} - J_m$$

(Equation 4.3)

Where J_m is:

$$J_m = H_m - G$$

(Equation 4.4)

Step 4: set the threshold at which to reject wells based on their performance as:

$$Reject\ if K_{m,n} < 50\%$$

Term	Description	Unit
AS	Oxygen saturation	% O_2 saturation
c	Individual well	
i	Incubation	
m	Well	
n	Incubation	
M	Total number of wells (24)	
N	Total number of incubations (12)	
0	Start of temperature stabilisation	Mins
60	Start of temperature stabilisation + 60 minutes	Mins

Table 4. 1: Table defining symbols in above equations

4.2.3.2 Oxygen Consumption Rates

Within the present study, respiration rates are assumed to be the oxygen consumption rates measured. Initial data analyses were carried out in units of mg O_2 l^{-1}. Raw data sets were truncated to include only readings taken within a 60-minute period after temperature stabilisation was reached. A linear regression was calculated for each well in every incubation, using the equation *f=y0+a*x*. As a further data validation step, if the R^2 value of the fitted regression was below 0.75, the data were excluded from further analysis.

The regression gradient, *a*, gave an O_2 loss rate in mg l^{-1} for each well. This was then multiplied by the cell volume (500 µl) and converted to give an O_2 consumption for each copepod per hour (R_{IND}, µg O_2 h^{-1} ind^{-1}). R_{IND} was then normalised by the carbon weight of the copepods and converted to give a weight specific respiration rate (R_{SP}, µg O_2 h^{-1} µg C^{-1}).

4.2.3.3 Extrapolation of Environmental Oxygen Consumption

After obtaining an oxygen consumption rate for each copepod during the respiration incubation, values were extrapolated to give an indicative respiration value for the respective *in situ* water temperature. This was done using the following equation:

$$R_{SP2} = R_{SP1}\, Q_{10}^{\frac{T_2 - T_1}{10}}$$

(Equation 4.5)

Where R_{SP} is weight specific respiration rate, with R_{SP1} being the oxygen consumption rate measured within the present study, R_{SP2} being the extrapolated respiration rate and T is temperature. Here T_1 is the average temperature recorded by the well plate across the incubation and T_2 is an average *in situ* temperature averaged over the net collection depth-interval. Q_{10} is the temperature coefficient and represents the factor of the rate of change as a consequence of a 10 ˚C temperature change. Q_{10} values used within this study were taken from published literature on either *Metridia* species or general copepod syntheses (Table 4.2), with the minimum, median, average and maximum of reported Q_{10} values being used to produce a range of predicted respiration rates.

4.2.4 Allometric Scaling

To enable weight specific comparisons to be made between copepods, respiration rates were standardised to body mass using allometric scaling factors. Allometric scaling refers to changes in processes such as respiration change in relation to proportional body size. Hernandez-Leon and Ikeda (2005b) found that most planktonic organisms had allometric scaling factors between 0.7 and 0.9. Therefore, scaling factors of 0.7, 0.8 and 0.9 were applied in order to encompass the range of factors that may be applicable to *M. longa. M. longa* were separated into three groups: females, shallow males and deep males. These groups were selected for the present analysis in order to establish whether differences in their respiration rates were a result of varying body mass and/or sex. As will be made evident in the Results section*,* the deep and shallow female categories were combined since no statistical differences in respiration rates were found between depths. Scaling was done by calculating the average respiration rate and carbon content for each of the three remaining groups (all females, shallow males, deep males). Once the average values had been calculated, the data were log transformed and plotted (log respiration versus log carbon). Separate plots were drawn for each of the allometric scaling factors (0.7, 0.8 and 0.9) and a fitted regression line added for each of the three *M. longa* groups.

4.2.5 Statistical Analysis

Following data validation and treatment, all statistical analyses were performed in SigmaPlot v14 (Systat Software Inc.). A non-parametric analysis of variance on ranks was carried out to determine whether respiration rates were significantly different between males and females from deep and shallow water layers. Mann-Whitney U tests were performed to assess for differences between deep and shallow copepods of the same sex.

4.2.6 Validation of Oxygen Consumption Rates

4.2.6.1 Oxygen Consumption Rates

Following the data validation procedures, only 12 copepods were rejected due to the oxygen saturation of the well dropping to <50 % of the initial oxygen saturation over the 60 minute incubation period (Figure 4.4). All rejected data points at this stage were female copepods collected at stations F2 and F4, with the majority (11 out of 12) caught in the upper 200 m zone.

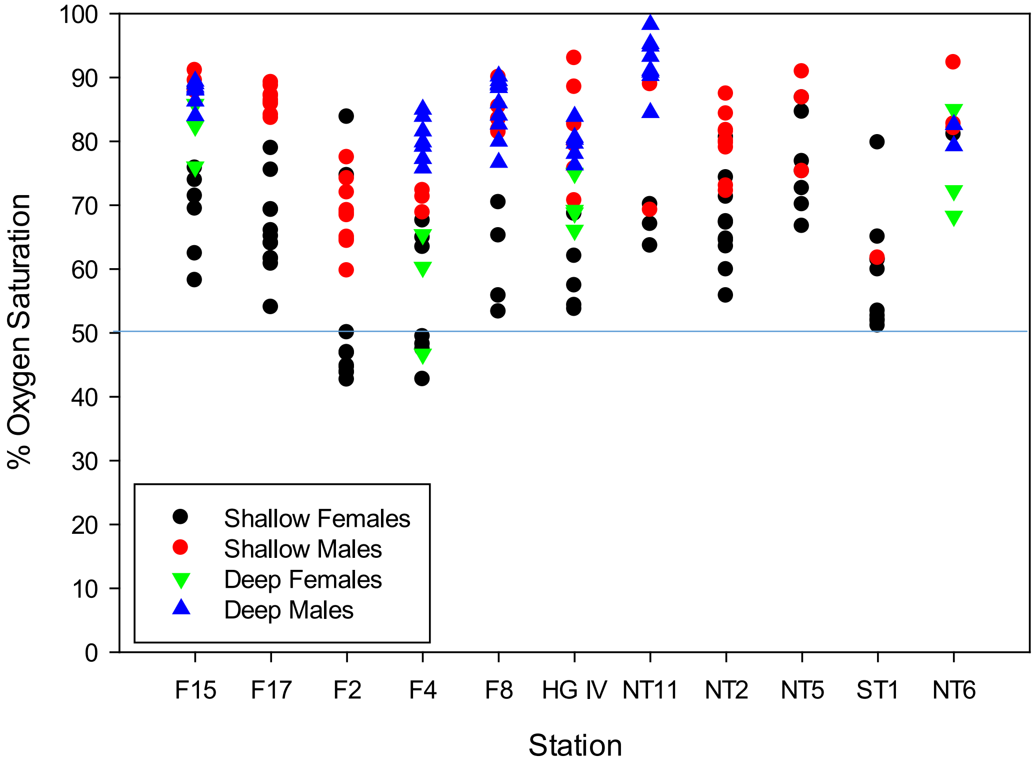


Figure 4. 4: % Oxygen saturation of wells following 60 minute respiration incubation once validation steps 1-4 (outlined in methods) had been carried out. Values represent the percentage of oxygen saturation present in each well at 60 minutes after temperature stabilisation as a proportion of the oxygen saturation at the time of temperature stabilisation in each well. Blue line shows validation cut-off with data below being removed before any further analysis.

The next stage in data validation was to assess the regression slope of the oxygen consumption over 60 minutes following temperature stabilisation. At this point, R^2 values were used to determine the inclusion of data. A cut off of an R^2 value of 0.75 was chosen since this was a reasonable threshold to identify those with non-linear and irregular responses to incubation. This cut off eliminated a further eight copepods (Figure 4.5). In contrast to the previous data validation step, a relatively low proportion of discarded data were from near surface females, the majority being either near surface males or deep females.

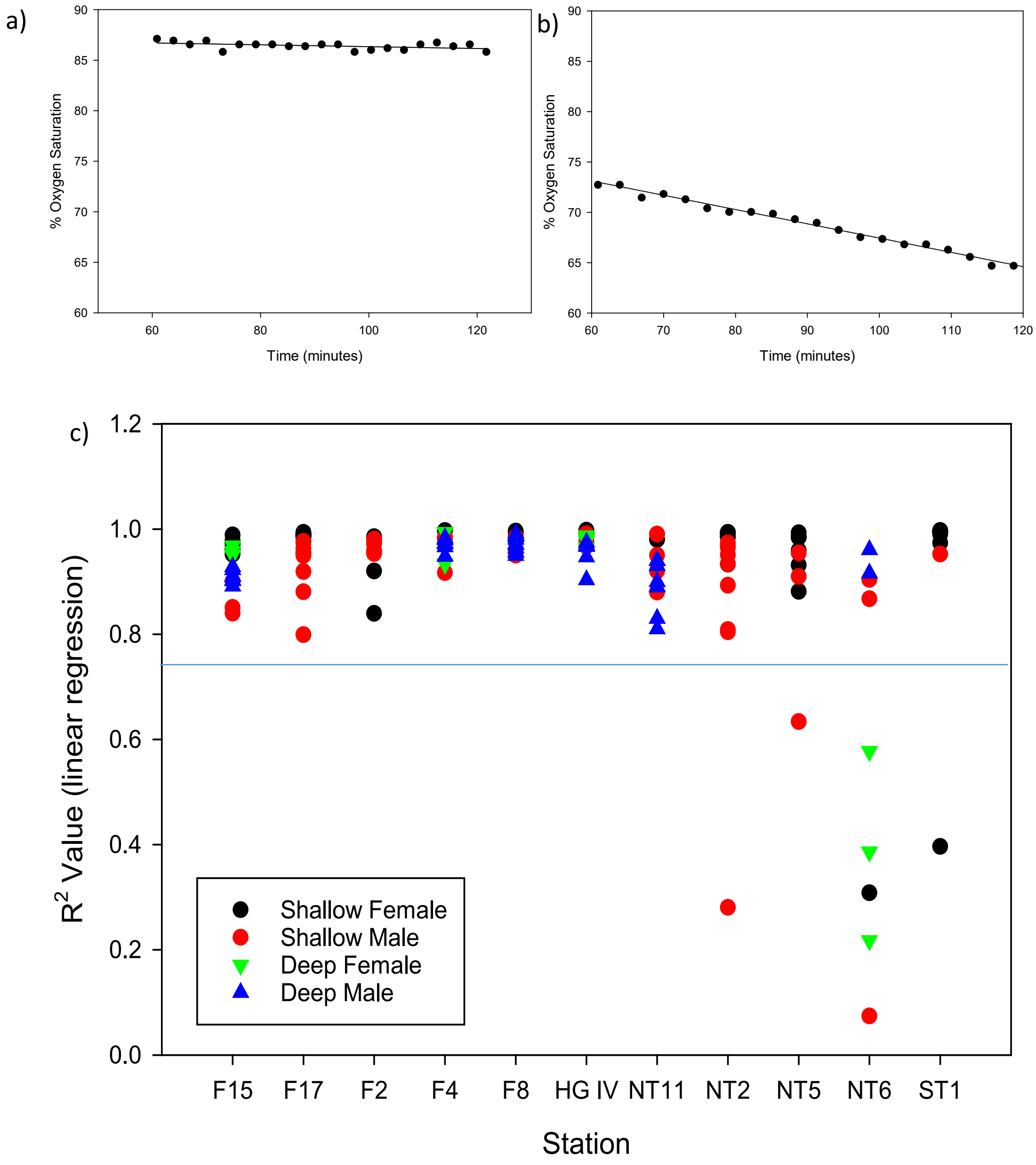


Figure 4. 5: R^2 validation steps. A) an example of an incubation with a low R^2 (0.22) resulting in rejection from further analysis, b) an example of an incubation with a high R^2 (1.00) value allowing data to be included in further analysis c) R^2 values for all incubations carried out that had passed the previous data validation steps. The blue line marks the 0.75 cut off, any incubations below this line were removed prior to any further analysis.

Following the above steps, a further shallow female from NT2 was rejected due to a negative oxygen consumption rate. Also, a deep male from F8 was removed due to data quality issues with the subsequent elemental composition analysis. This left a total of 164 copepod respiration incubations; 9 deep females, 64 shallow females, 39 deep males and 52 shallow males.

4.3 Results

4.3.1 Environmental Temperature

Over the study region, copepods experienced a greater temperature range in the surface layers than in the deeper layers (Figure 4.6). Surface temperatures in the upper 200 m of the water column ranged from -1.75 °C to 4.5 °C across all study sites, temperatures in the deep zone (~375 to 600 m) ranged between -0.25 °C and 2.25 °C.

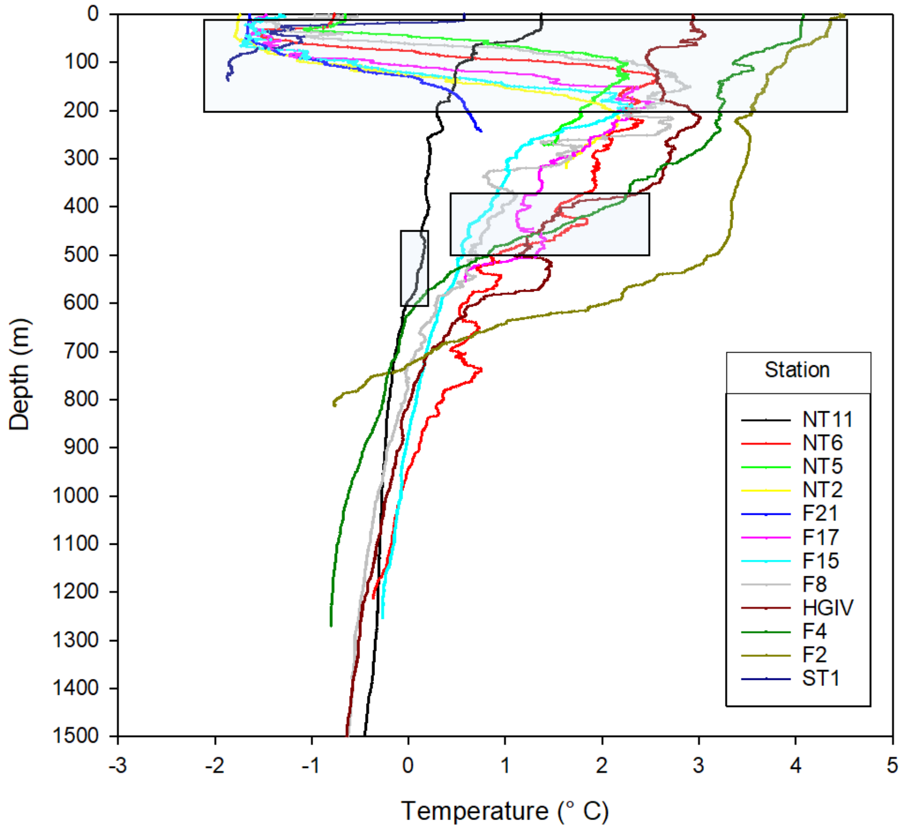


Figure 4. 6: Temperature profiles from the stations where *Metridia longa* were collected. Shaded boxes show depths and profiles from which copepods were taken.

In total, oxygen consumption was analysed for 162 copepods. Oxygen consumption rates ranged from 0.14 to 9.14 µg O_2 h^{-1} ind^{-1}, with an average of 0.89 ± SE 0.12 µg O_2 h^{-1} ind^{-1}. This range demonstrates the high variability in respiration rate between copepods and likely reflects differences in sex and locations. Oxygen consumption rates within females spanned the overall range, with an average of 1.02 ± SE 0.18O_2 µg O_2 h^{-1} ind^{-1}. Males had a smaller range of 0.14 to 7.02 O_2 µg O_2 h^{-1} ind^{-1}, with an average rate of 0.01 ± SE 0.00 O_2 µg O_2 h^{-1} ind^{-1}.

Location within the water column was found to influence oxygen consumption rates of *M. longa* (Figure 4.7). Deep residing copepods had an oxygen consumption of 0.39± SE 0.02 O_2 µg O_2 h^{-1} ind^{-11}. The rate was three times higher in shallow residing *M. longa* (1.26± SE 0.2 µg O_2 h^{-1} ind^{-1}). Station location was also influential, with station F2 having the highest rates (5.48 ± SE 0.50 µg O_2 h^{-1} ind^{-1}) and NT6 had the lowest average oxygen consumption (0.19± SE 0.03 µg O_2 h^{-1} ind^{-1}). However, it must be noted that differences between stations also integrates any inter-station differences in the proportions of copepods of each sex and collection depth used in the incubations. At F2, it was only possible to collect copepods from the shallow layers, increasing the average respiration rate. Further to this, F2 was located to the east of the Fram Strait (Figure 4.2) and had the highest recorded temperature (Figure 4.6) as a result of its positioning within the West Spitsbergen current and close to the coast of Svalbard. This high temperature likely accounts for the high respiration rates observed in *M. longa* caught at F2.

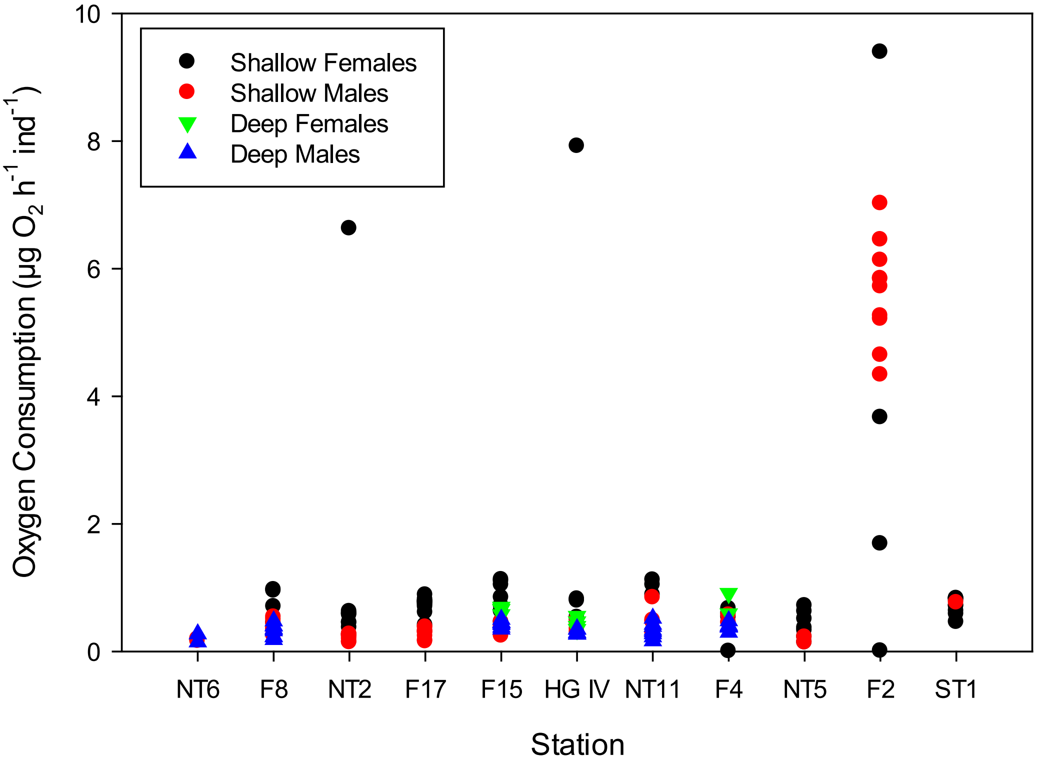


Figure 4. 7: Oxygen consumption rates of *Metridia longa* following the removal of all data that failed prior validation steps (outlined in Methods). Data points placed in boxes were deemed outliers and removed from further analysis.

4.3.2 Physiology of *Metridia longa*

In terms of elemental composition, the carbon content of the copepods ranged from 12.1 µg to 227.2 µg C ind^{-1}, showing the large size range within the male and female populations. Further analyses found that females differed from males across all elements analysed (Figure 4.8), likely representing sexual dimorphism. These differences were found to be significant, with females having higher carbon (135.81 ± SE 5.12 µg in females, 61.89 ± SE 3.81 µg in males; Mann-Whitney U test, U[$n_{females}$=71, n_{males}=91]=637.00, P<0.001), hydrogen (17.56 ± SE 0.75 µg in females, 7.14 ± SE 0.54 µg in males; Mann-Whitney U test. U[$n_{females}$=71, n_{males}=91]=669.50, P<0.001) and nitrogen (29.85 ± SE 0.91 µg in females, 10.00 ± SE 0.47 µg in males; Mann-Whitney U test, U[$n_{females}$=71, n_{males}=91]=227.00, P<0.001), which is consistent with the general size-related sexual dimorphism exhibited in this species. Males had a significantly greater carbon to nitrogen ratio than females (males: 5.96 ±SE 0.20, females: 4.5 ± SE 0.10; Mann-Whitney U test. U[$n_{females}$=71, n_{males}=91]=1680.00, P<0.001) (Figure 4.8 d). No significant differences, across all elements, were found between deep and shallow residing females (Mann-Whitney U tests: nitrogen U[n_{deep}=9, $n_{shallow}$=62]=224.00, P=0.35, C:N ratio U[n_{deep}=9, $n_{shallow}$=62]=223.50 P=0.34; Student's t-tests: carbon t_{69}=0.91 P=0.37, hydrogen t_{69}=0.89, P=0.38). In contrast, deep-dwelling males had an increased carbon content (66.02 ± SE 5.31 µg C in deep males, 58.80 ± SE 5.35 µg C in shallow males, Mann-Whitney U, U[n_{deep}=39, $n_{shallow}$=52]= 835.00, P=0.15), but lower nitrogen content compared to their shallow-dwelling counterparts (9.51 ± SE 0.47 in deep males, 10.37 ± SE 0.73 in shallow males, Mann-Whitney U, U[n_{deep}=39, $n_{shallow}$=52]=1006.00, P=0.95), such that there was a significant difference in carbon to nitrogen ratios in males between depth zone (Mann-Whitney U, U[n_{deep}=39, $n_{shallow}$=52]=590.50, P<0.001).

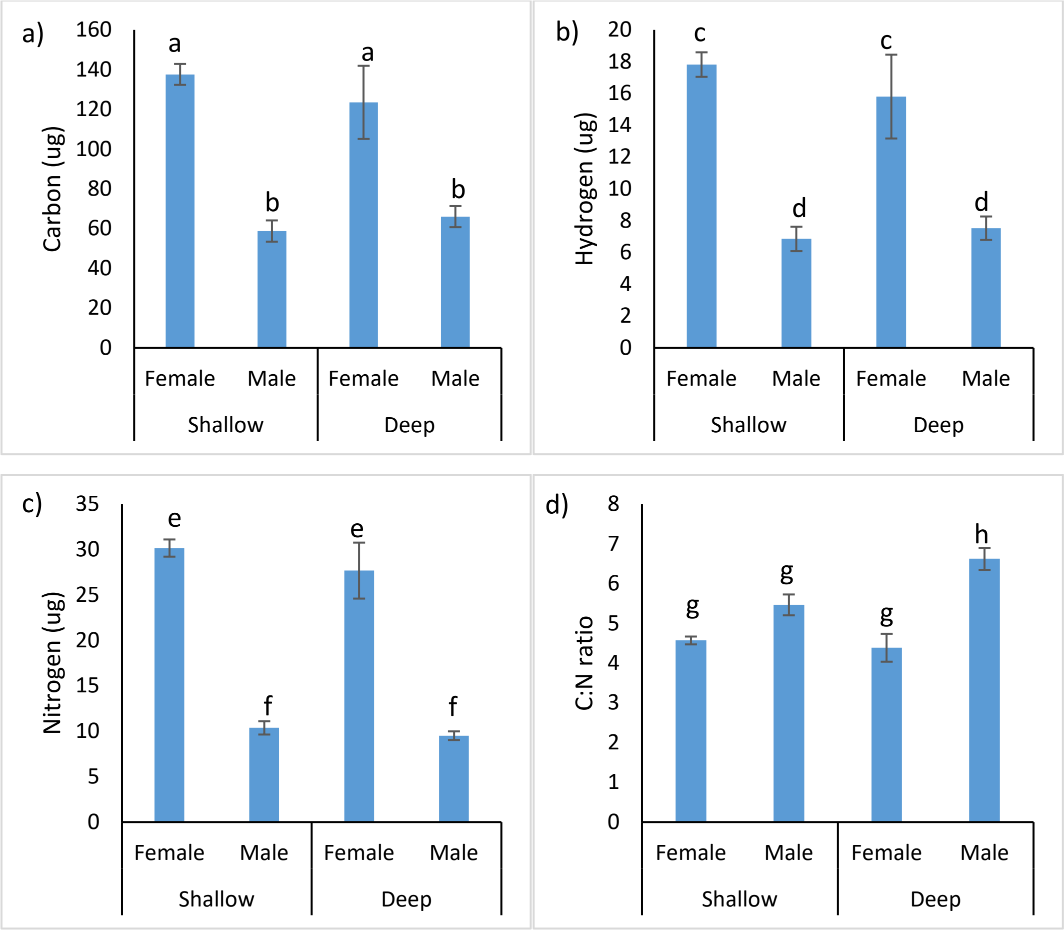


Figure 4. 8: Elemental composition graphs for *Metrida longa*. Graphs display average content found per individual in each of the four groups, shallow female, shallow male, deep female, deep male. Each graph depicts a different nutrient: a) carbon content, b) hydrogen content c) nitrogen content d) C:N ratio. Error bars denote standard error. Letters denote significance as found by Dunn's pairwise tests following a one way ANOVA on Ranks. ANOVAs were carried out on each elemental composition to find significant differences between *M. longa* groups.

Due to the large variation in size across the sampled populations, respiration rates were normalised by carbon content to give weight specific respiration rates. In contrast to total respiration per individual, weight specific respiration rates in males were found to be higher (0.013 ± SE 0.002 µg O_2 h^{-1} µg C^{-1}) than in females (0.01 ± SE 0.001 µg O_2 h^{-1} µg C^{-1}). Rates were also higher in shallow residing copepods (0.012 ± SE 0.002 µg O_2 h^{-1} µg C^{-1}) than in deep residing copepods (0.007 ± SE 0.001 µg O_2 h^{-1} µg C^{-1}).

Weight specific respiration rates further varied between sexes and depths (Figure 4.9). Deep residing females were found to have the lowest weight specific respiration rates, on average (0.006 ± SE 0.001 µg O_2 h^{-1} µg C^{-1}) but were similar to those of females in the near-surface (0.007 ± SE 0.001 µg O_2 h^{-1} µg C^{-1}) as well as to deep residing males (0.007 ± SE

0.001 O_2 µg O_2 h^{-1} µg C^{-1}). However, rates in shallow residing males were three times higher than those of these other categories (0.018 ± SE 0.003 µg O_2 h^{-1} µg C^{-1}), which was significant (ANOVA on ranks $F_{3,161}$=29.05, P< 0.001).

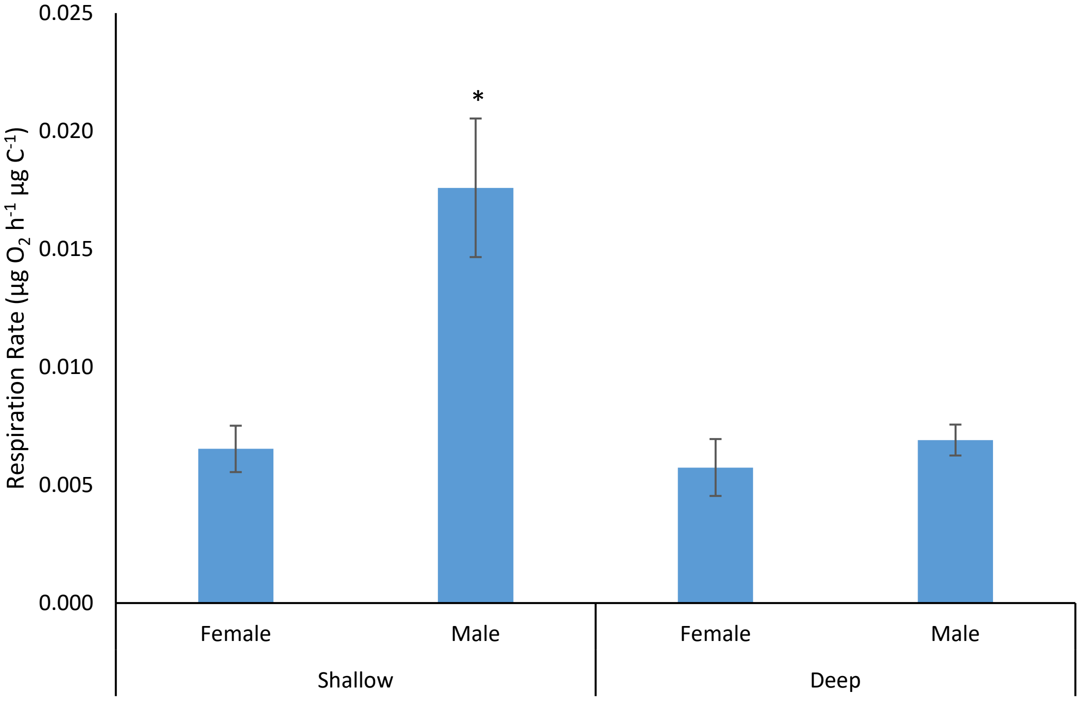


Figure 4. 9: Average measured weight specific respiration rate at 2 °C using the Loligo respirometer for *Metridia longa* collected from near surface and deeper layers. Error bars denote standard error, * denotes significant difference as found by ANOVA on Ranks.

To assess whether respiration rates observed within the incubations were reflective of those that may be observed within the water column, respiration rates were extrapolated to *in situ* temperatures using Q_{10} values, and water temperature readings from the locations and depths from which the copepods were collected. Q_{10} values were taken from the literature (Table 4.2), from which minimum (2.1), maximum (3.7), average (2.6) and median (2.4) Q_{10} values were derived.

Species	Calculation methodology	Study Region	Authors	Q_{10} value
M. lucens Females	Optode measurements of bottles containing 4-6 individuals at temperatures of 9, 13 and 19 °C	Southern Atlantic (Northern Benguela upwelling system, Namibia)	Bode 2011 (masters thesis)	3.7
M. longa	Radiometer probe, 3-5 individuals per bottle. Temperature range of 0-5 °C	Greenland Sea	Hirche 1987	2.09
M.lucens	Calculated using parameters from respiration experiments in Carlotti and Nival (1992)	North Atlantic	Batcheldor and Williams 1995	2.5
Temora longicornis	Modelled parameters from gut clearance experiments to calculate Q_{10}, temperature range: 0-17°C	Long Island Sound	Dam and Peterson 1988	2.16
Temora longicornis	Linear regression of values within literature, temperature range: -1 - 19°C		Dam and Peterson 1988	2.21
Boreal species	Values calculated from respiration experiments using water bottle method and Winkler titrations to determine O_2.	Bering Sea	Ikeda 1970	3.3 (0.1 mg body dry weight) 2.3 (1.0 mg body dry weight)

Species	Calculation methodology	Study Region	Authors	Q_{10} value
Broad casting adult copepods	Literature search of growth and egg production rates of food saturated adult copepods		Hirst and Bunker 2003	2.7
M. pacifica Females	O_2 measurements from sealed bottles containing individual copepods. Temperature range: 0-24 °C	Southern Japan Sea	Ikeda et al. 2002	2.6
M. lucens	O_2 determined by Winkler method, 15 individuals per bottle. Experiments carried out at 5°C	Gulf of Maine and Cape Cod	Haq 1967	2.29

Table 4. 2: Q_{10} values found for copepods within the literature used to provide a range of Q_{10} values for application within the present study.

Figure 4.10 shows that extrapolation of laboratory measured respiration rates (at ~2°C) to rates expected at *in situ* temperatures resulted in a slight reduction in respiration rates in female *M. longa* from near surface and deep water layers and males from deep water layers. However, the same extrapolation resulted in *in situ* respiration rates of near surface males being slightly higher than those measured within the incubations. All extrapolations resulted in a relatively small change in respiration rate, indicating that ~2°C was a reasonable choice of temperature for the incubations. Furthermore, these differences in respiration rates between copepod groupings remained relatively unchanged once converted to *in situ* temperatures.

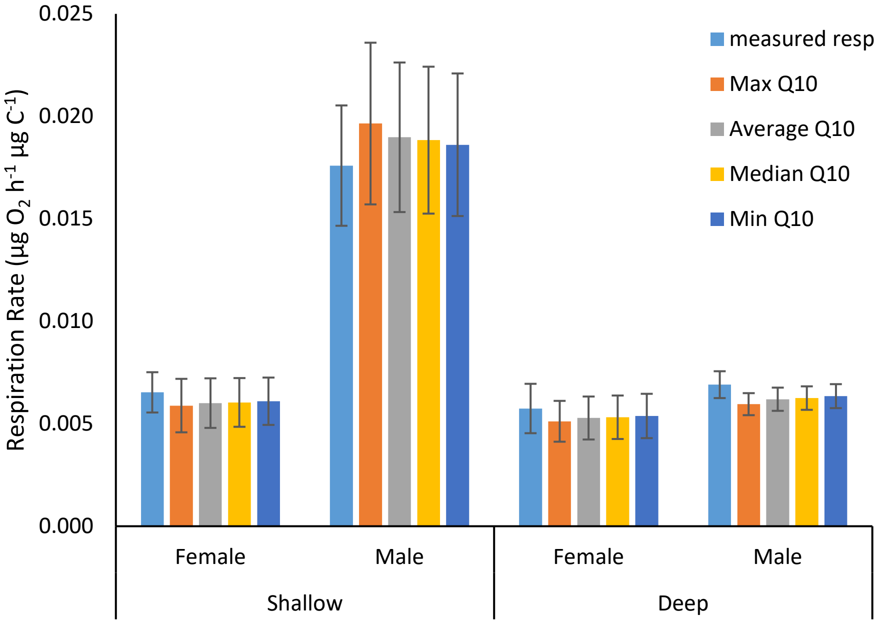
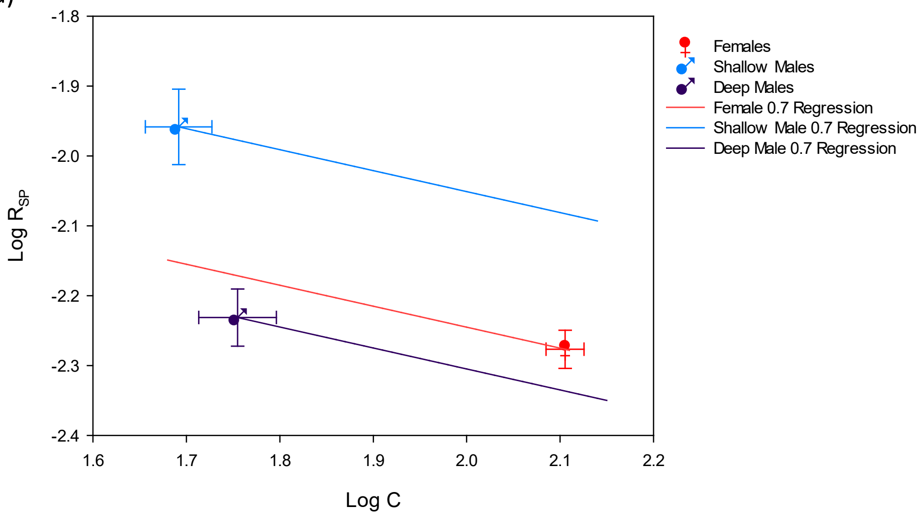


Figure 4. 10: Weight specific respiration rates extrapolated to in situ temperatures using literature-based Q_{10} values. The first bar of each cluster represents the laboratory-based measurement at 2 ˚C. The subsequent four bars in each cluster were extrapolations from this temperature to the best estimate of *in situ* temperature using a range of Q_{10} values which were: Max = 3.7, Average= 2.6, Median= 2.4, Min= 2.1. Error bars denote standard error.

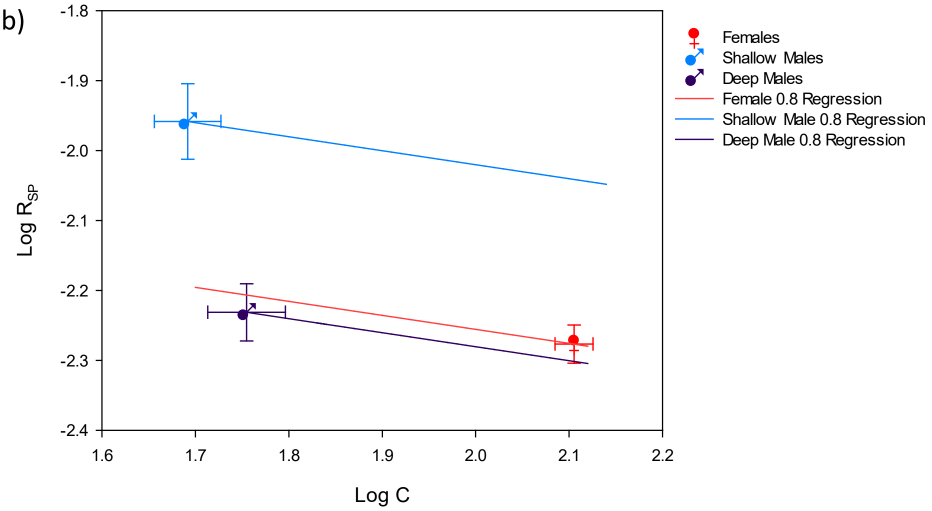
4.3.3 Respiration rates and Physiology

Based on results above, deep and shallow females were combined in the following analysis given similarities in their respiration rates. Scaling coefficients were applied to test the hypothesis that differences between sexes and depths can be accounted for by differences in C weights of these categories. When using a 0.7 scaling coefficient, all three groups remain separate indicating that, at this scaling coefficient, C weight does account for differences between their respective weight specific respiration rates (Figure 4.11). However, when applying scaling coefficients of 0.8 (Figure 4.11b) and 0.9 (Figure 4.11c) females lie close to the regression slope for males caught in deeper layers and vice versa indicating that differences in their weight specific respiration rates (R_{SP}) can be accounted for by their different C weights. In contrast, males caught in shallower layers remain on a separate line indicating that their weight specific respiration rate would remain significantly higher when scaled to the C weight of females or males caught in deeper waters. Across all three potential allometric functions therefore, there is clear evidence that shallow males have a significantly different respiration rate to all other categories.

a)


-1.8
-1.9
-2.0
-2.1
-2.2
-2.3
-2.4
Log R_{SP}
1.6
1.7
1.8
1.9
2.0
2.1
2.2
Log C
Females
Shallow Males
Deep Males
Female 0.7 Regression
Shallow Male 0.7 Regression
Deep Male 0.7 Regression

b)


-1.8
-1.9
-2.0
-2.1
-2.2
-2.3
-2.4
Log R_{SP}
1.6
1.7
1.8
1.9
2.0
2.1
2.2
Log C
Females
Shallow Males
Deep Males
Female 0.8 Regression
Shallow Male 0.8 Regression
Deep Male 0.8 Regression

c)

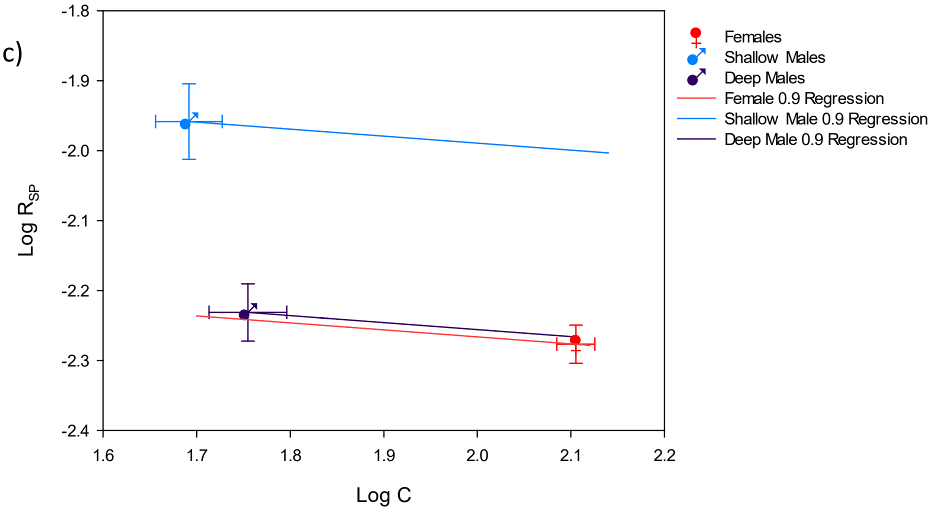

-1.8
-1.9
-2.0
-2.1
-2.2
-2.3
-2.4
Log R_{SP}
1.6
1.7
1.8
1.9
2.0
2.1
2.2
Log C
Females
Shallow Males
Deep Males
Female 0.9 Regression
Shallow Male 0.9 Regression
Deep Male 0.9 Regression

Figure 4. 11: Body mass scaling of *Metridia longa* respiration. Each regression line shows the scaling for a different group of *M. longa*. Each graphs shows a different scaling coefficient assuming R_{IND}= aM^b (a refers to the normalisation component, M is the mass and *b* the scaling coefficient), a) *b*= 0.7, b) *b*= 0.8 and c) *b*= 0.9.

4.4 Discussion

4.4.1 Environmental temperature versus behaviour and body state

This study found that respiration rates of *Metridia longa* varied with sex and differences in vertical distribution, and/or vertical migration behaviour which were more than just a response to temperature changes. Temperature in itself already has a major influence the in situ respiration rates of the species in this environment given the contrasting thermal environments present in Fram Strait. Spatial and vertical variations in temperature result from the influence of the Atlantic water moving northwards to the east, and cold Arctic water flowing south in the west (Bergmann et al., 2016). Consequently, organisms experienced a thermal range of between -1.75 °C to 4.5 °C in the study region, with the species subjected to both short-term (hours) and longer-term (days-months) variations in temperature throughout its life cycle. Based on an average literature-based Q_{10} value of 2.6, respiration rate would almost double between these two thermal extremes. The sex and depth of specimens may then be responsible for a further 30 to 40 % difference in respiration rate between individuals when controlled for body-mass scaling effects. The findings of this study highlights the need to better quantify ontogenetic and DVM-related changes in physiology and respiration of key zooplankton species in relation to their different thermal habitats, and is explored further in this discussion.

4.4.2 Temperature and Oxygen Consumption Rates

The environmental temperature of the water in which the copepods resided varied according to both location and depth. The near surface layers had a greater variability in temperatures across the study site (ranging from -1.75 °C to 4.5 °C) than the deeper layers (ranging from -0.25 °C to 2.25 °C). However, at the majority of locations in which the copepods were found, the near surface temperatures were lower than those found in the deeper layers, suggesting that temperature alone was not the main mechanism driving the vertical differences in respiration in the males. We found that this pattern still prevailed once the respiration data were standardised for ambient temperature. Unfortunately, due to the technical limitations of the available ship-board equipment, it was not possible to incubate copepods at their exact environmental temperatures. As a result, all incubations were carried out at a nominal temperature of 2 °C. In order to understand whether this factor influenced the measured copepod respiration rates, our respiration data were scaled to a range of probable thermal scenarios using previously published Q_{10} values. When extrapolated to *in situ* temperatures, the differences in respiration rates between sex and depth categories remained, indicating that the fixed experimental temperature did not overly influence the comparative approach taken in the present analysis.

In poikilotherms, it is widely accepted that, as temperature increases, metabolism increases. This has been found to be true in a number of Arctic copepods, such as *Metridia longa, Calanus finmarchicus, Calanus glacialis and Calanus hyperboreus* (Hirche, 1987). It is therefore noteworthy that, in the present study, the opposite was true in the case of *M. longa* males, with those in the deeper, warmer layer having a significantly lower respiration rate. This was not the case in female *M. longa* and may be explained, in part, by differing life strategies of the two sexes, as is explored further in the present discussion.

4.4.3 Body Mass Scaling

Body mass is one of the most important biological factors in determining respiration rates (Hernández-León & Ikeda, 2005b), with metabolism scaling allometrically with body size such that, as body mass increases, weight specific respiration decreases. This trend has been reported in a number of zooplankton species (Ikeda, 1970), although variation in the metabolic scaling relationships is evident. Very few studies have examined how respiration scales with body size in *M. longa.* Haq (1967) was the first to do so and reported a scaling coefficient of 0.48. However, this estimate is much lower than the recent scaling coefficients reported for other calanoid copepods (Kiørboe & Hirst, 2014), so we utilised a range of coefficients (*b*) between 0.7 and 0.9 to apply to our data to reflect the level of inherent variation reported in pelagic organisms (Hernández-León & Ikeda, 2005b). Using these values, regression slopes were produced for each of the three *M. longa* groups (shallow males, deep males and females; females were not separated due to no differences being found between the depths sampled). It was found that the trajectories resulted in the values for deep males and females being the similar to each other at equivalent weights when using a scaling coefficient of 0.8 and 0.9. In contrast, the males collected from the shallower waters remained very separate from the other categories, irrespective of the *b* value used. This separation, even when scaling for body mass effects, indicates that other factors appear to influence respiration rates in shallow males compared to the rest of the *Metridia* population, as I explore further below.

While carbon, hydrogen and nitrogen content did not differ significantly between the two male *M. longa* groups, the C:N ratio was significantly different, with males collected from the deeper layers having a higher ratio. This suggests that the two groups of males may have been in different physiological states, which is broadly consistent with copepod studies elsewhere. For example, Hays et al., (2001), found that *Metridia pacifica* individuals that resided in the deeper waters of Dabob Bay also had a higher C:N ratio than those residing in the surface layers. A higher C:N ratio is indicative of individuals having a larger lipid sac than their low C:N ratio counterparts (Ohman et al., 1989). For a number of calanoid copepods, this higher ratio may also be indicative of diapause behaviour, whereby individuals enter a state of dormancy during overwintering, surviving on their lipid stores (Hirche, 1996). In the calanoid *Calanus finmarchicus*, for example, diapause is pronounced and it is thought that body condition plays an important role when *C. finmarchicus* enter diapause, with those entering the state having larger lipid sacs (Jónasdóttir, 1999). In contrast with *C. finmarchicus*, metridians are believed not to enter a pronounced period of diapause, otherwise remaining active throughout the year (Ohman et al., 1998; Osgood & Frost, 1994a). The elemental composition of *M. longa* measured in the present study suggests that *M. longa* in polar environments may have the physiological capacity to prepare for periods of diapause, at least in the case of males.

The feasibility of enduring a period of diapause also depends on the rate of energy consumption while at depth, when the accumulation of any further energy reserves is minimal. Hays et al., (2001) calculated the length of time a deep residing *M. pacifica* could remain at depth before losing condition to equal that of shallow copepods. Applying a respiration rate of 1.5-4.5 µg C^{-1} ind^{-1} day^{-1} (Batchelder, 1986), it took *M. pacifica* deep residing individuals, with a C content of 51 µg C ind^{-1}, 3 to 9 days to decrease to the typical C content of a shallow residing individual (38 µg C ind^{-1}). This rudimentary calculation determined that *M. pacifica* could remain in the deeper layers for 3 to 9 days, suggesting that *M. pacifica* were not able to reside at depth for weeks or months and were therefore not entering into diapause. However, the respiration rates measured by Batcheldor (1986) were from female and stage five (CV) copepods collected within the surface 100 m. In the present study, deep male *M. longa* show a marked reduction in respiration rates when compared to their shallow water counterparts. When applying the same calculation as found in Hays et al., (1991) to the data collected in the present study, males residing at depth would deplete their carbon content to be in line with their shallow counterparts between 0.5 to 2 days (using deep male respiration rate: 0.15- 0.52 µg C^{-1} h^{-1} ind^{-1}, deep male carbon content: 66 µg C, shallow male carbon content: 58.79 µg C). This would suggest that this group may deplete energy reserves at a faster rate than suggested by Hays et al., (2001), reducing residence times at depth. However, the potential to survive on lipid stores while reducing metabolic rate indicates that polar metridians may carry out vertical migrations over longer timescales as a key life cycle strategy to succeed in these environments.

4.4.4 Specific Dynamic Action

A further potential source of variation in respiration rates is difference in feeding conditions. Feeding and digestion increases zooplankton respiration, whilst starvation causes a reduction in respiration (Hernández-León & Ikeda, 2005b). This alteration in respiration as a result of feeding state, termed specific dynamic action (SDA) (Burns, 1953), corresponds to the additional energy expenditure required for ingestion, digestion and incorporation of food into body proteins (Secor, 2009). Two copepod species in which SDA has been studied in detail are *Acartia tonsa* (Kiørboe et al., 1985; Thor, 2000) and *Calanus finmarchicus* (Thor, 2000, 2002). *A. tonsa* feeding in food saturation conditions were found to have a respiration rate four times higher than starved individuals (Kiorboe et al., 1985). However, when a protein synthesis inhibitor, cycloheximide, was present, feeding-associated increases in respiration were diminished substantially, lending support to the notion that SDA is strongly linked to protein synthesis. Normalised respiration rates in starving copepods were also found to be three times higher in *A. tonsa* than *C. finmarchicus* (Thor, 2000). It was thought that this was due to the different physiologies of the copepods; *C. finmarchicus* deposits proteins in storage lipids (Conover, 1988), whilst *A. tonsa* has a high protein content (Berggreen et al., 1988) and lays down protein storage during somatic growth, demanding high levels of protein. While it was not possible to determine the extent of feeding in copepods prior to capture in the present study, it is likely that those caught in the near surface layers had fed more recently than those in deeper layers. Therefore, the higher respiration rates in males found in these shallow layers would be in line with the theory of SDA. In contrast to the males, no difference in respiration was found in females from different depths, suggesting SDA is not consistent across all components of the population. However, it is probable that, as found by Osgood and Frost (1994b), females were undertaking more vertical migrations than males, and therefore the populations at both depths were likely to be composed of recently fed and digesting copepods, potentially masking any SDA. Further to this, Thor (2000) found that the higher SDA in *A. tonsa* compared to *C. finmarchicus* most likely reflected their higher protein content. In the present study, males were found to have a higher C:N ratio than females, indicating a greater proportion of protein in the latter. Nevertheless, the greatest variation in respiration was found in males with lower proportion of protein. SDA is therefore unlikely to be a major cause of the lower respiration rate in deep males found by the present study.

4.4.5 Sex dependent vertical segregation

Metridians are well known to have pronounced daily vertical migrations, however our study suggests that this behaviour differs with sex and other physiological processes in *M. longa.* Females were found to have similar respiration rates and physiology, irrespective of collection depth, indicating that females were well mixed through the water column. Males, by contrast, appeared to exhibit a distinct segregation between shallower and deeper populations with deep males having a lower respiration rate and a higher C:N ratio than shallow males. Interestingly, deep males also had a significantly higher C:N ratio than any other part of the male and female populations. The present study was only able to ascertain respiration rates during the day time and therefore it is not clear whether the vertical exchange of females occurred daily. However, with regards males, it is most likely that the deep portion remained stationary at their residence depths, with little exchange occurring with shallow males over short (daily to weekly) timescales.

It is not clear why *M. longa* migration behaviour varies with sex but such behaviour has been reported in other studies of the species elsewhere. Osgood and Frost (1994b) found that, in Dabob Bay, male *M. lucens*, in contrast to females, did not carry out DVM. Marlowe and Miller (1975) also found that copepodite stages remained in the surface waters, whilst males stayed at depth and females undertook vertical migrations in the North Pacific. Similarly, Batcheldor (1985) found that males in the North Pacific remained below 250 m throughout the diurnal cycle. Batcheldor (1985) hypothesised that, because females are significantly larger than males, the two sexes may be subjected to different levels of predator pressure. Visual predation was thought to be driving different migration behaviours in *M. lucens* within Dabob Bay (Osgood & Frost, 1994b). Given the greater visibility of larger individuals, one would expect that females would spend less time in the better lit surface layers than males, which would drive a more pronounced DVM behaviour. Males appear to adopt a different strategy of either occupying the surface layers for extended periods or remaining at depth.

4.4.6 Seasonality Effects

Another factor that must be taken into account when investigating the differences in respiration rates is seasonality. Zooplankton respiration is strongly affected by the spring phytoplankton bloom (Clarke & Peck, 1991) and differs from season to season (Ikeda et al., 2001). This is specifically true of epipelagic copepods inhabiting high latitudes (Ikeda et al., 2001), with highest rates during the spring bloom and lowest rates in winter. This is likely to be influenced by the fact that many calanoid copepods diapause overwinter, reducing activity and metabolic rate. However, metridians have been found to remain active during the winter but still display a reduced respiration rate during this time (Haq, 1967). In the Gulf of Maine, *M. lucens* winter oxygen consumption rates were found to be approximately 30 % of the spring rate, with a dramatic rise from 12.8 µl mg dry wt^{-1} day^{-1} in January to 34.4 12.8 µl mg dry wt^{-1} day^{-1} in February as the spring bloom occurred (Haq, 1967). It was also noted that, during the summer months (June –August), *M. lucens* were scarce in surface waters, appearing to be confined to deeper waters, possibly influencing respiration rates. There are few studies assessing how respiration rates change with seasons in metridians in high latitude areas due to the difficulties in accessing these remote ice covered regions. However, Seuthe et al., (2007), were able to measure respiration rates of *Metridia longa* in the Beaufort Sea during the winter-spring transition. It was found that prior to and encompassing the beginning of the spring bloom, little variation was seen in *M. longa* respiration. This was in contrast to the ingestion of phytoplankton, calculated using faecal pellet carbon, which increased with the onset of the bloom. However, lipid volume remained constant in *M. longa* suggesting that omnivorous feeding was taking place in order to maintain energy reserves during periods of low primary productivity (Seuthe et al., 2007). The omnivorous nature of *Metridia* species may mean that they are not as tightly coupled to the primary productivity cycle as other calanoid species and therefore seasonal differences in respiration may not be as pronounced. The present study was carried out during the spring phytoplankton bloom (May-June 2018) and therefore represents the highest annual respiration rates. The differences seen between *M. longa* categories at this time indicates that different behaviours and potentially different adult life-cycle stages were present simultaneously in the population.

4.4.7 Vertical Segregation and Reproductive Strategy

Developmental stage or reproductive state also plays a role in respiration rates. Reproduction and gametogenesis can lead to increases in metabolic rates. In the calanoid copepod *Neolovenula alluaudi*, higher oxygen consumption rates were found in egg carrying females than in non-egg carrying females (Parra et al., 2003), showing the increased metabolic demand of egg production. Information regarding the energetic demand, in terms of metabolism, of egg production in calanoid copepods is sparse, with no definitive studies to date looking at the oxygen consumption rates of reproductive *M. longa*. Calanoid copepods, including metridians, are often broadcast spawners, releasing eggs into the water column (Kiørboe & Sabatini, 1994). In Arctic waters, *Metridia longa*, have a single annual spawning period in May when phytoplankton abundance levels off (Båmstedt & Tande, 1988; Grønvik & Hopkins, 1984). This coincides with the period of the present field sampling, and reproductive efforts by *M. longa* may impact measured respiration rates. Båmstedt & Tande (1988) found that adult female *M. longa* in fjords in Sweden and Norway displayed an increased metabolic rate at the onset of spring bloom when spawning activity was also high. However, they could not discern whether the higher metabolic rates were due to increased feeding activity as a result of the bloom or the spawning activity. In the present study it was found that males caught in shallow layers had the highest respiration rate with females having a rate comparable to males caught in deeper layers. This would indicate that if an increase in respiration does occur in female *M. longa* during the spring months, it may not be limited to females and therefore not as a consequence of egg production but either a response to spawning behaviour or higher feeding activity.

Further to this, male behaviour may also be linked to reproductive cycles. The present study found that males segregated into two behavioural groups; active males in the near surface waters and less active males in the deeper layers. Very few studies have examined the life cycle and behavioural traits of male metridians, and those that have considered them have focussed upon their vertical migration behaviour. A number of authors have reported that males remain at depth while females undertake DVM (Batchelder, 1985; Marlowe & Miller, 1975; Osgood & Frost, 1994b; Padmavati et al., 2004). Padmavati et al., (2004), studied the occurrence of all stages of *M. pacifica* throughout a 12-month period in the subarctic Oyashio region. They found that, whilst all stages were present at all sampling times, suggesting reproduction occurred throughout the annual cycle, there were peaks in abundances of copepodite and female stages, suggesting loose seasonality in reproduction (Padmavati et al., 2004). Adult male abundance remained relatively constant throughout the year with relative proportions increasing between December to February. The relative proportion of females in the population increased from January to April, suggesting that males and females matured at different rates. Laboratory experiments investigating maturation rates of *M. pacifica* found that temperature played a role in developmental time with males reaching maturity from hatching in 161 days at 5 °C and 123 days when reared at 8 °C (Padmavati & Ikeda, 2002). Females had a longer development time of 167 days at 5 °C but a shorter maturation time of 112 days at 8 °C. This study suggests that temperature influences male and female metridian development to different extents but decreases in temperature increase development times in both sexes. At higher latitudes, temperatures remain below 5 °C, therefore it would be expected that generation times are longer than the 5-6 months reported in Padmavati and Ikeda (2002). However, the influence of temperature may mean that copepods would mature at different rates dependent upon spawning time, potentially leading to the presence of two generations of adult copepods. This may explain the two groupings of males in the present study. Males caught in the deeper layers may be from an earlier spawning event than those found in the near surface layers but, due to the colder temperatures in the winter months, had a longer development time. This longer time to maturation may have led to these males reaching adulthood shortly before the next generation but would have done so during the spring phytoplankton bloom. This would have allowed them to feed throughout the bloom building up lipid stores before descending to the darker waters. If this is the case, it would be expected that the males caught in the near surface waters had recently reached the adult stage and were still building up energy reserves necessary before descent.

An alternative hypothesis to the simultaneous presence of different male categories may relate to the interception of females for mating. Halsband-Lenk (2005) found that, in contrast to previous studies, male *M. pacifica* in Dabob Bay did migrate to near surface waters at certain times throughout the study period. It was suggested that this migration may be the result of males tracking vertically migrating females in order to mate or that they were attached to females for copulation and were carried by the females. It may also be that males employ different mating strategies. Males in the near surface layers had a greater respiration rate than those found in deeper layers suggesting they were more active. These males may be actively pursuing females within the near surface layers in order to mate. Males in the deeper layers may employ a sit and wait strategy, residing in the deeper waters waiting for females to return in order to encounter them. This aspect of metridian behaviour has not yet been studied. However, it is likely that both life history strategy and environmental factors play important roles in the physiological patterns of *M. longa* reported in this study.

4.5 Chapter Summary

- When measured at the same temperature, weight specific respiration rates of *Metridia longa* adults in the Fram Strait varied between sexes and depth zones. Female *M. longa* had, on average, a higher weight specific respiration rate than males.
- Weight specific respiration rates were similar in females in the near-surface and the deep. There was also no statistical difference between females and deep males. However, rates in shallow males were around three times higher.
- Accounting for differences between incubation and environmental temperatures, and for body size (C content) differences between categories did not alter the above patterns.
- Deep males had significantly higher C:N ratios compared to females and shallow males, indicating that they were storing more C, most likely as lipid.
- The respiration rates and elemental composition of *M. longa* suggest that there was regular vertical exchange between near-surface and deep females, but this did not occur to the same extent in males.
- This chapter provides new insights into the interaction between life-cycle and behaviour of *M. longa*, an abundant but lesser studied Arctic copepod species. The study further illustrates the complexity of determining levels of respiratory carbon flux generated by these migrating species. These will be important aspects to integrate into future efforts to determine the contribution of such species to active carbon flux and sequestration.

Chapter 5: Discussion

5.1 Thesis Overview

This thesis set out to explore zooplankton migration patterns within high latitudes. The high latitude regions are responsible for a large proportion of the oceanic carbon sequestration (Takahashi et al., 2002), making these areas of great importance when considering carbon cycles. Zooplankton play a vital role within carbon sequestration, with some estimating that over 70 % of sinking particulate organic carbon (POC) is a result of zooplankton mediated processes (Turner, 2002). These processes are numerous and include export via migrations. However, migration patterns are not yet fully understood. From an initial view of vertical migration, where zooplankton spend daylight hours deep in the water column and feed in surface layers during the night (e.g. Bayly, 1986; Hutchinson, 1967; Pearre, 1973, 2003; Ringelberg, 1995), there is now a growing body of evidence suggesting that migration patterns are more complex and exhibit variability over a range of temporal and spatial scales (e.g. Ohman et al., 1983; Parra et al., 2019; Pearre, 2003; Pierson et al., 2013, 2009; Tarling et al., 2002). As a result of this uncertainty, the role that zooplankton migration plays in the biological carbon pump is poorly parameterised and may even be overlooked in certain biogeochemical and ecosystem models (Everett et al., 2017). Here, I set out to determine how vertical movements of zooplankton, and their corresponding physiology, impact the carbon flux within high latitude areas. My research focussed upon copepods because they have a relatively high biomass in both Arctic and Antarctic zooplankton communities and are a crucial component of the pelagic ecosystems in these regions (Hirche et al., 1991; Shreeve et al., 2005). They are likely to play a crucial role in the carbon cycle in these regions, particularly in the functioning of the Biological Carbon Pump (BCP), making them an exemplar group for improving our understanding of how zooplankton vertical migrations influence high latitude carbon flux. In order to address crucial knowledge gaps in this area of research, I used: (i) size based analysis, combined with taxonomy, to evaluate differences within the copepod community through the water column (0-1000m) over a daily cycle across two different productivity regimes in the Scotia Sea; (ii) a novel net system to investigate the complexity in zooplankton migrations at various locations within the Scotia Sea; and (iii) physiological analyses to determine the effect of temperature changes on the levels of respiration flux by the biomass dominant and highly migratory Arctic copepod, *Metridia longa*. Collectively, my results provided new insight into the vertical ecology of zooplankton and its role in the BCP at high latitudes, as discussed below.

5.2 Energy Retention in pelagic copepod communities: evidence of greater energy retention at high latitudes

The influence that primary productivity has on the copepod community, and the energy flow within this community, was explored in Chapter 2 of this thesis. This seasonality within high latitude areas shapes their community structure and productivity. Productivity within plankton communities is determined by growth of individuals and abundance, which in turn is driven by food availability and the size structure of the consumer community (Zhou, 2006). An underlying determinant of copepod productivity and energy retention within a copepod community is therefore primary productivity. Polar Regions undergo a dramatic seasonal change in primary productivity, with phytoplankton blooms occurring in spring and summer, whilst little primary productivity occurs throughout the dark winter months. Levels of primary productivity are also very heterogeneous within the Southern Ocean, principally driven by the spatially limited availability of iron, with some areas exhibiting blooms extending over many months and others with very limited levels of productivity (Park et al., 2010).

In this thesis, I studied two sites in the Scotia Sea (P2 and P3) with different levels of seasonal primary productivity to examine how this affected regional copepod community structure, particularly with regards to the distribution of biomass between copepod size categories. I tested the hypothesis that regions with higher levels of primary productivity result in size structures with comparatively higher levels of biomass in larger size classes. Considered in another way, I set out to determine whether the levels of energy flowing from the smaller to the larger size classes accumulate to a greater extent in the larger size classes in more productive environments. At P3, the site with higher rates of primary productivity, a higher copepod biomass was found compared to the less productive site, P2. The P3 community also had a greater proportion of larger organisms. Compared to other oceanic regions, the copepod communities at both P2 and P3 were found to have biomass size structures that implied relatively high levels of energy retention throughout the upper 1000 m of the water column.

Normalised biomass size spectral slopes are commonly used to assess the level of energy retention within a community. Each community is defined by a slope that is steep if there is high energy loss or shallow if energy is retained within the community. Platt and Denman (1977) proposed that communities in equilibrium would have a theoretical slope of -1.22. The average value for the slopes found within this thesis was -0.56, with all slopes being shallower than -1.22 (Figure 2.17). Following the hypothesis of Platt and Denman (1977), this would indicate that the copepod community sampled in this thesis were not in equilibrium but had a much higher energy retention than theoretically expected. However, this study is not the first to report shallower slopes for copepod communities. San Martin et al., (2006) reported normalised biomass size spectra slopes ranging from -0.93 to -1.26 in the Atlantic Ocean and Thompson et al., (2013) found values between -0.6 to -1.0 for the copepod community in the southwestern Atlantic Ocean. While these slopes are also shallower than the theoretical value of -1.22 proposed by Platt and Denman (1977), they are steeper than the values found within this thesis, indicating energy retention is higher within the copepod community sampled in the present study than within other areas of the Atlantic Ocean.

The relative similarity in the normalised biomass size spectral slopes between the two sites, P2 and P3, where primary productivity level were very different, suggests that primary productivity does not have a dominating influence on levels of energy retention within the copepod communities. This was also found by San Martin et al., (2006) when looking at communities spanning a large spatial area (from 67˚N to 49˚S) in the Atlantic. Those authors found that primary productivity did not impact the energy transfer between phytoplankton and mesozooplankton in either coastal or open ocean systems. However, seasonality and stability were found to be important in determining slope gradients due to the coupling between phytoplankton and zooplankton. During phytoplankton blooms periods, stronger coupling led to increased numbers of mesozooplankton and energy transfer through the zooplankton community. Conversely, during low productive winter months, mesozooplankton numbers were low and corresponded with less energy retention. San Martin et al., (2006) did not sample polar communities which may have important structural differences to lower latitude communities. In order to survive in polar environments, organisms are required to exhibit specific adaptations or life cycles. In copepods, these often include multi-year life cycles and/or large body sizes in order to store energy throughout the winter. This may mean that coupling with phytoplankton blooms is less pronounced within these areas with energy being retained within copepods for longer periods than found in more temperate regions. This extension of energy storage time would lead to an increased rate of energy retention within the community as copepods have a longer life span and greater storage capacity, potentially explaining the relatively shallow slopes reported within this thesis. Nevertheless, this is the first study in which the energy retention specifically within the copepod community of the Southern

Ocean has been studied. It is evident that this community has a high energy retention rate, irrespective of relative levels of primary production. While there may be several drivers behind the shallow slopes found within these communities, this study provides further support for the importance of copepods within the wider Southern Ocean ecosystem.

5.3 High Latitudes and Larger Copepods: implications for environmental change

Another aspect of high latitudes is the size of organisms. The low temperatures and short productive seasons often lead to extended multi-year lifecycles and high internal energy storage (Murphy et al., 2016). During the productive season, organisms can have a rapid growth rate but this ceases during the extended winter when productivity is low, leading to a low overall growth rate (Atkinson, 1998). In order to survive the winter, energy must be accrued during the comparatively short productive season. In copepods, this is usually in the form of lipids such as wax ester compounds (Lee et al., 2006). Multi-year lifecycles, and the need to accrue lipids, results in polar organisms having larger body sizes than their temperate counterparts. In this thesis, it was found that larger copepods made great contributions to the biomass and were responsible for the shallowing of the normalised biomass spectral slope. This finding is in line with that of Tarling et al., (2012), who also report that the zooplankton community within the Southern Ocean had shallower spectral slopes when the proportional abundance of large organisms was higher. This link between high energy retention and greater organism size is likely to mean that high latitude areas have a greater potential to store energy than temperate areas. Comparisons across latitudes are difficult due to the majority of studies focussing on specific areas, often relying on different methodologies and net sizes, meaning that each study samples a slightly different section of the community. However, when examining the zooplankton community in the Barents Sea, Basedow et al., (2010), reported shallower biomass spectral slopes for Arctic waters than for Atlantic water, lending further support to Polar Regions having greater levels of energy retention.

Higher energy retention due to larger sized organisms is of importance when considering the future of the Polar Regions. Global warming is occurring at a faster rate in these areas than other areas of the planet, meaning that changes in zooplankton community structures and dynamics are likely to take place. As the oceans warm, species distributions are likely to change, with true polar species contracting in geographic range and temperate species moving polewards (Hop et al., 2019). This incursion of temperate species has already been reported in the Arctic. Over the last 20 years Arctic copepods such *as C. glacialis* and *C. hyperboreus* have declined in numbers and biomass, while the Atlantic *C. finmarchicus* has undergone a northwards shift due to the increased water temperatures (Møller & Nielsen, 2020). While these calanoid copepods have similar life cycle traits they differ in size, lipid content and phenology (Falk-Petersen et al., 2007). *C. finmarchicus* is the smallest of these species and therefore an increase in abundance of this species will lead to a decrease in the average copepod size within the area, particularly if combined with a reduction in the larger copepods. Currently, there are very few studies assessing the community changes that may occur as temperatures increase in our polar regions, however, it is likely that incursions of smaller temperate species towards higher latitudes will be common resulting in a shift to smaller organisms. Within the present study, taxonomic analysis found that more northerly, warmer water stations at the Polar Front had greater proportional abundances of smaller species than the cooler locations within the Southern Ocean. This suggests that, as water temperatures rise, these smaller species become more prevalent in southerly latitudes of the Southern Ocean, altering the size spectral slopes and the energy retention potential of the region. A shift towards a community dominated by smaller copepods may result in less energy and carbon flowing through the community, decreasing the contribution that copepods within this area make to the BCP.

The contribution to the BCP from copepods in Polar Regions may be reduced further as a result of warming due to the differences in lipid storage of polar and temperate copepods. During periods of high productivity, high latitude copepod growth can be rapid (Clarke & Peck, 1991), with energy being stored in the form of lipids, such as wax ester compounds (Lee et al., 2006). The biosynthesis of these compounds is very efficient with lipids exceeding 60 % of the dry weight of some polar calanoids (Cavallo & Peck, 2020; Sargent et al., 1988). Whilst in diapause at depth, stored lipids are metabolised, releasing carbon at depth and contributing to the BCP. This is thought to be a sizeable but often overlooked contribution to the BCP with estimates suggesting that *C. finmarchicus* across the North Atlantic may transport 2–6 g C m^{-2} y^{-1} to depth in the form of lipids each year. *C. finmarchicus* is the smallest of the biomass dominant calanoids found within the Arctic, therefore it is likely that the larger lipid rich species such as *C. glacialis* and *C. hyperboreus* may have a greater contribution to the BCP that has yet to be quantified. However, the borealisation of Polar Regions may decrease the volume of lipids transported to depth. Jónasdóttir et al., (2015) speculated that, in the Arctic, an increase in smaller *C.*

finmarchicus and decreases in *C. hyperboreus* and *C. glacialis* would lead to an overall reduction in lipids within the *Calanus* community along with metabolism of these lipids taking place and different times of year. This reduction and phenology change will mean that lipid flux within the high latitudes will reduce, decreasing the amount of carbon sequestered to depth. While these studies were constrained to a small number of copepod species, more generally, it is likely that, as smaller temperate species increase in abundance at high latitudes, similar patterns of lipid reductions within copepod communities will be seen, with the potential to significantly reduce the lipid flux. However, not all copepods currently inhabiting Polar Regions undergo diapause, with the work of Berge et al., (2009) showing that DVM takes place throughout the polar night. This thesis found that the relatively small and non-diapausing *Oithona spp.* undertook vertical migrations. While this is one of very few studies reporting migrations in these abundant copepods, it is of great importance as winter DVM by smaller species such as *Oithona spp*. may provide an alternative mechanism by which carbon is transported to ocean depths. DVM by abundant smaller species may have the potential to counter any deficit lost through decreased abundance of large lipid rich polar species.

5.4 The Complexity of Vertical Migration: further evidence of non-traditional DVM at high latitudes

The undertaking of conventional diel vertical migration by the zooplankton community is a longstanding view of behavioural cycles in this taxonomically diverse group. However, throughout this thesis I found that behaviour and physiology of copepods can be more complex. In the Scotia Sea, evidence of traditional DVM was not always apparent, with copepods being found throughout the water column at all sample times. However, depth was found to play a role in copepod distribution. The majority of the copepod biomass was located within the upper 500 m of the water during both day and night samples. However, there was a redistribution of this biomass between day and night, indicating that copepods were not stationary within the water column but undertook vertical movements. The absence of a day time deepening of the biomass suggests that traditional diel vertical migration (up in the night and down in the day) was not the only source of this redistribution, but indicates that foray behaviour and reverse migration were equally as prevalent. Chapter 3 went on to consider this issue further using the novel MUDL net. This net showed, for the first time in the open ocean, that a range of copepod species undertook vertical movements at both dawn and dusk. Copepod assemblages did not differ between the upward and downward net at either dawn or dusk, indicating that asynchronous migrations were undertaken by a range of species.

This finding of asynchronous vertical migration adds to a growing body of evidence suggesting that DVM behaviour is more complex than previously thought (e.g. Blachowiak-Samolyk et al., 2006; Cottier et al., 2006; Pearre, 2003; Zadereev et al., 2012). A number of reasons have been proposed for asynchronous zooplankton migrations, particularly in Polar Regions. The Polar Regions have particularly extreme seasonal light regimes, making them an interesting place for the study of DVM. During summer months, high latitudes experience constant light conditions with very short nights, with the converse being the case in winter. This short or absent night time period during the summer means that zooplankton feeding only under the cover of darkness would not have sufficient time to consume an adequate amount of resource. A number of authors have investigated this with many reporting a cessation in synchronous DVM and a shift to asynchronous migrations (e.g. Cisewski & Strass, 2016; Cisewski et al., 2010; Cottier et al., 2006; Picco et al., 2017). The small size and relatively short digestion times of copepods may also lead them to making a number of migrations over a 24-hour time period. This is addressed in the hunger satiation hypothesis, which states that zooplankton will feed in surface waters until they are satiated after which they sink to depth to digest and return to shallow depths when digestion has taken place. It is thought that this process takes two to three hours and would therefore lead to a number of vertical migrations by each zooplankton over a 24-hour period. Due to individual zooplankton taking differing times to feed and digest, this would lead to asynchrony in the timings of migration at the population level. Another reason for non-traditional DVM may be the presence of non-visual predators. DVM is thought to convey an advantage by feeding in the dark and therefore avoiding the detection of visual predators. However, in the regions studied within this thesis, the primary predators of copepods within the zooplankton community include chaetognaths (Kruse et al., 2010) and ctenophores (Purcell et al., 2010). These predators use mechanoreceptors to detect prey movement (Feigenbaum & Maris, 1984; Waggett & Buskey, 2006), meaning that light levels do not impact upon their capture rates. A number of studies have found that some chaetognath populations do not undertake DVM but remain at mid water depths throughout the diel cycle (e.g. Conroy et al., 2020; Froneman et al., 1998). A lack of migration within predators is likely to have a cascading effect on their prey such as copepods. The continuous threat from predators over the diel cycle means that feeding at night no longer conveys an advantage and it becomes more important to avoid the layers where predators reside. So long as the copepods minimise the time they spend in these risky layers, they can feed throughout the diel cycle, migrating up and down according to their physiological needs. This behaviour would exhibit the same migratory patterns as expected by the hunger satiation hypothesis, resulting in asynchronous migrations taking place over comparatively short timescales.

The finding of both up and down vertical migrations at dawn and dusk in Chapter 3, combined with the varied DVM patterns reported in Chapter 2 may have implications for estimations of carbon flux within the region. Models estimating carbon flux are generally poorly parameterised when accounting for zooplankton behaviour and do not consider the complexity of vertical migrations. In order to produce more accurate estimates, models assessing carbon flux generated by the zooplankton community must include greater complexity than a standard pattern of DVM. For instance, a simplistic model incorporating traditional DVM found that the presence of DVM within the model increased the global export flux out of the euphotic zone by 14 % (Archibald et al., 2019). However, in a more complex model, carbon export through faecal pellet release at depth increased when foray behaviour was present (Wallace et al., 2013), showing that behaviours such as those seen in this thesis need to be incorporated into model estimates of carbon flux, particularly in Polar Regions where vertical migrations may vary through an annual cycle.

5.5 New insight into the importance of *Oithona* behaviour in carbon flux

The global copepod community is composed of thousands of species ranging in size from less than 1 mm to tens of millimetres. As seen in Chapter 2, the composition of different sized copepods within a community influences its energy storage and carbon transport potential. However, despite smaller copepods being numerically dominant in many oceans, they are often understudied compared to the larger species when assessing migration and carbon transport. In Chapter 3, *Oithona* spp., a small but ubiquitous copepod, dominated the MUDL catches, showing that their movements may have profound consequences for the transport of material within the water column. To date, few studies have focussed on *Oithona* spp. migration patterns. As they are often found within upper layers at all times of day and night, it has been assumed that these species remain stationary in the water column. In this thesis, the use of a MUDL net allowed the vertical migration behaviour within this genus to be discriminated for the first time at an appropriate vertical sampling resolution. *Oithona* spp. were found in both upward and downward looking MUDL nets across all times, depths and locations, suggesting that they undertake foray behaviour. The reasons for these vertical forays require further investigation, and could be many fold. One potential reason could be food distribution. *Oithona* spp. are able to feed on a variety of food items, with some authors reporting herbivory (Gauld, 1966), coprophagy (Gonzalez & Smetacek, 1994) and carnivory (Lampitt, 1978; Nakamura & Turner, 1997). Although *Oithona* spp. has a wide dietary breadth, it does exhibit certain preferences such as ciliates over diatoms (Atkinson, 1996; Castellani et al., 2005a) and mobile prey over non-motile prey (Uchima & Hirano, 1986). Using video analysis of female *O. similis*, it was found that hydromechanical detection of prey movement allowed them to ambush and successfully capture prey (Svensen & Kiørboe, 2000). This may relate to both motile prey and sinking detritus such as faecal pellets. This prey detection method may account for the vertical movement seen within this study. As an ambush predator, *Oithona* spp. hang in the water column until they detect movement, at which point they jump to the point at which the prey was detected (Svensen & Kiørboe, 2000). As they stay motionless, they sink at a rate of 0.009 cm s^{-1} (Svensen & Kiørboe, 2000). Possibly accounting for the downward movements detected within this thesis. Once *Oithona* spp. have sunk to depths below food rich layers they will need to re ascend in order to increase their chances of prey capture resulting in upward vertical migrations being detected. Further to this, the ability to utilise a number of food sources may allow *Oithona* spp. to vary its diet depending on its location within the water column. It may be that *Oithona* spp. undertake vertical migrations to reach water depths where an alternative food source is either abundant or where competition for the food source is reduced.

Another reason for the vertical movements observed in this species is predator avoidance, such that *Oithona* spp. avoid surface layers during daylight in order to minimise the risk of visual detection. Studies investigating predation rates on *Oithona* spp. are rare, however due to their small size they are likely to be prey for a number of species including ctenophores (Purcell et al., 2010), fish larvae (Lankov et al., 2010), chaetognaths and many other planktivores. Hirst and Ward (2007) proposed that the mortality of male *O. simillis* is 12 times higher than that of females, which cannot be accounted for by physiological differences alone, therefore predation must be occurring at relatively high levels. Further, this sex dependent mortality rate was thought to be as a result of behavioural differences, with females remaining stationary within the water column and only moving comparatively short distances to capture prey, while males are far more mobile in searching for mates.

This more active behaviour makes males more likely to be detected through both visual and hydro mechanical sensors, increasing their predator risk. It is possible therefore that predator avoidance plays a role in the vertical movements of *Oithona* spp. with males likely to avoid areas of high predator concentrations. *Oithona* spp. observed moving vertically within the present work may only remain in the surface layers for short periods throughout both day and night, to minimise exposure to both visual and chemosensory predators. This pattern of behaviour contributes to asynchronous movements observed at both dawn and dusk.

The finding that *Oithona* spp. move vertically within the water column may have important implications for global carbon flux, both in terms of the faecal pellet flux and respiration flux. Wallace et al., (2013) found that over 90 % of faecal pellets were released below 30m when foray behaviour was simulated compared to 50 % when no migration is present. While very little information on faecal pellet production in *Oithona* spp. is available, their very high abundance (up to 7000 individuals m^{-3} (Morales et al., 1993)) combined with a release of pellets just tens of metres deeper than the main feeding depth will amount to a very large downward transport of carbon with enhanced potential to be exported to the ocean interior. Furthermore, the same level of downward movement may contribute to the respiration flux if the copepods cross the mixed layer boundary when migrating. Future deployments of the MUDL towards the bottom of the mixed layer would be instructive in this regard.

5.6 Respiration flux and the impact of physiological responses to temperature

Carbon loss through respiration, known as respiration flux, from copepods residing in deep water is another way in which copepods can contribute to the BCP. The volume of carbon transported via this route is, as yet, poorly quantified. Longhurst and Williams (1992) argue that the contribution that respiration flux plays in the global oceanic carbon sink is very small and makes up less than 1 % of global contributions from sinking particles, and decreases further when considering copepods in cooler climates. However, when calculating the global contribution of 0.012-0.018 Pg C year^{-1} from vertical migrants, Longhurst and Williams (1992) made a number of assumptions. These assumptions include copepods undertaking seasonal migrations, spending the spring and summer months in shallow waters but residing in deep waters during autumn and winter. Importantly, vertical migrations on shorter timescales were not taken into account. However, it is becoming increasingly apparent that vertical migrations take place over short and long time scales and that many migration patterns are evident within the copepod population.

Currently, very little is known of the respiration flux, particularly in Polar Regions, making it an important area to investigate further, hence this was one of the main research themes of the present thesis. In Polar Regions, the biomass dominating copepods are often large calanoids (Hirche et al., 1991). In the Arctic this includes species such as *Calanus hyperboreus*, *C. finmarchicus*, *C. glacialis* and *Metridia spp*. (Kosobokova & Hirche, 2009), while the Southern Ocean has high abundances of species such as *C. acutus*, *Rhincalanus* spp. and *Metridia* spp*.* (Atkinson, 1998; Atkinson & Sinclair, 2000). When investigating the contribution copepods make to the BCP through respiration, it is important to consider life-history and behaviour. Many calanoid species inhabiting high latitudes undergo diapause, a behaviour in which they enter a near dormant state through the winter and often descend to great depths. This behaviour may have a profound effect upon the BCP with seasonal vertical migrations contributing to carbon flux. Jónasdóttir et al., (2015) found that the carbon released from the respiration of *C. finmarchicus* in the North Atlantic during diapause was equivalent to that from sinking particulates, doubling previous estimates of carbon sequestration in the region. This contribution to carbon sequestration highlights the need to resolve this process across a greater number of species and over larger spatial scales. However, not all calanoids enter diapause. The biomass dominant calanoid copepod *Metridia* spp., for instance, does not enter diapause but displays daily vertical migrations throughout the annual cycle, making them a potential vector for carbon to reach deeper layers over the entire year, further increasing the active carbon flux. Kobari et al., (2008) found that, when comparing *M. pacifica* with *Neaocalanus* spp*.* in the subarctic Pacific Ocean, the active carbon flux from *M. pacifica* diel migration was equivalent to up to 44 % of the sedimentary POC flux, while *N. flemingeri* had an active carbon flux of 9 % of the sedimentary POC as a result of ontogenetic migration. This estimate shows that respiration and migratory behaviours of copepods are a crucial component within the BCP. Due to the pronounced vertical migratory behaviour in *Metridia* spp., *M. longa* was chosen in the present study to further explore the impacts migration has upon physiology and the contribution this species could make to the transport of CO_2 to depth through respiration flux.

A further assumption made by Longhurst and Williams (1992) when considering the contribution respiratory flux makes to the BCP was that respiration rates did not vary according to environmental gradients, meaning that respiratory carbon flux of each copepod was assumed not to change throughout the water column. However, physiological rates are closely linked to environmental conditions and would therefore be expected to reflect how these conditions change over the course of their vertical migrations. Ikeda et al., (2001) synthesised a large amount of zooplankton data, covering 43 species, to relate how respiration rates increase with temperature, and the strong relationships that were derived underline how sensitive these organisms are to temperature change. This may be the case for the copepods studied in this thesis. Metabolic rates of *O. similis* have been found to be strongly coupled with temperature with exponential increases in respiration rates occurring with increased water temperature (Castellani et al., 2005b). This strong temperature dependency means that residing in cooler waters to digest could be beneficial and be a driver of the vertical movement reported in Chapter 3 of this thesis. The metabolic advantage theory of diel vertical migration was first detailed by McLaren (1963), where he proposed that by digesting in cooler waters, plankton may gain a “metabolic advantage” over non-migrating animals with the possibility of a sufficient increase in fecundity to compensate for slower growth rates (Enright, 1977; McLaren, 1974) as a consequence of reduced metabolism. In this thesis, *Metridia longa* were used to further investigate the effects that depth and temperature play on respiration rates. Contrary to the assumption made by Longhurst and Williams (1992), this study found that the respiration rates of *M. longa* did vary with depth. However, this was only the case for males not for females, suggesting that differing physiologies and life histories may cause behavioural differences within a copepod species. In line with the metabolic advantage theory, males caught in deeper layers had lower weight specific rates than their shallower counterparts. Nevertheless, at the time of sampling, temperature did not always decrease with increasing depth even to say that, for the most part, surface layers were cooler than the deeper layers. This would suggest that temperature alone was not driving male *M. longa* to reduce their respiration rates.

When considering the metabolic advantage hypothesis, Enright (1977) produced three conditions that must be met for the theory to hold true. These were: (1) high food abundances; (2) populations are near equilibrium and controlled by predation; and (3) populations experience extreme conditions either as a result of seasonality or high juvenile mortality. Meeting all three conditions is often difficult in practise. Nevertheless, conditions found during the present study on *M. longa* appear to meet them. Firstly, the food availability at the time of sampling was likely to be high due to the seasonal spring blooms.

Secondly, the presence of predators within the region would have an impact upon the *M. longa* populations and finally the high latitudes are extremely seasonal with a large thermal range across an annual cycle, therefore *M. longa* inhabiting this area experience a strongly seasonal environment. The decrease in respiration rates of deep residing males would appear then to support the metabolic advantage theory. However, the apparent uncoupling of water temperature and respiration indicates that the observed reduction in metabolic rate is not a result of residing in cooler waters. An alternative explanation is that the males caught at these depths are exhibiting different behaviours to those caught in the shallow waters, and are potentially in a near dormant state with reduced activity, feeding and respiration.

This difference in respiration rates in males but not females found within this thesis indicates that the different sectors of the population are exhibiting different behaviours. This is in line with Osgood and Frost (1994b), who found that male *M. lucens* did not undertake the vertical migrations that were observed in females. While the present study did not have the capacity to determine migration behaviours and movements, the similarities found between females in both shallow and deep catches indicates that these copepods were undertaking vertical movements. The differences seen between the males caught in the near surface layers and those caught deeper suggest that these two groups were not mixing, indicating that vertical movements were less prevalent in males than in females. Further to this, the presence of *M. lucens* at both near surface and mid water column depths simultaneously, shows that DVM in *M. lucens* may be asynchronous, suggesting the presence of foray behaviour in females.

The differing migration behaviours are likely to influence the role *M. lucens* plays within the BCP. The migrations carried out by females will increase the respiratory carbon flux, whilst shallow residing males will increase the cycling of carbon only within the upper layers due to their elevated respiration rates. To explore this further, I carried out a sensitivity model where I assumed different percentages of the male population migrated between the near surface and deeper layers each day to determine its impact on the respiration flux (Table 5.1). In the model, I assumed that all females were undertaking migrations and non-migrating males always resided in deeper layers, leaving a varying percentage of males undertaking regular vertical migrations. For simplicity, migration was set to a 12 hour day and normal DVM assumed, i.e. migrating animals spent 12 hours in shallow water and 12 hours in deep water. In order to obtain a value of carbon per m^3 it was assumed that *M. lucens* population was 20 individuals m^{-3}, as this is the lower range of the density found by

Kane (2003). The sex ratio was assumed to be equal. In the model, it was found that by increasing the percentage of males migrating, the greater the total respiratory carbon produced, due to the elevated respiratory rates of males in shallow waters. However, the amount of carbon released in the deeper layers decreases since, although migrating males have a higher respiration rate, half of this takes place in the near surface layers and hence is not sequestered. Deep males have a comparatively lower respiration rate compared to near surface males and all females. Nevertheless, if their body mass was accumulated during an earlier life-cycle phase where they fed at the surface and assuming that they now no longer feed at depth, the body mass they lose through respiration at depth could add a further 25 % to the total respiratory C flux generated by the migratory part of the population.

While this calculation makes a number of assumptions, it is a useful indicator showing that respiratory carbon flux is altered depending on what parts of the population are actively migrating. Specifically, the sex dependent behaviour revealed by my work emphasises the importance of looking at individual zooplankton migrations within populations. My findings emphasise that respiratory flux calculations must take into account the gender composition of a population as well as the environmental parameters. It also suggests that the respiratory flux of *M. longa* and other zooplankton exhibiting similar migratory patterns may make a greater contribution to the global carbon flux than previously assumed.

Percentage of Males migrating	Respiratory Carbon Produced (mg C m^{-3} day^{-1})		
	Near surface layers	Deeper layers	Total
100 %	0.266513	0.144034	0.410547
75 %	0.233518	0.157898	0.391415
50 %	0.200522	0.171762	0.372284
25 %	0.167527	0.185625	0.353153
10 %	0.14773	0.193943	0.341674
0 %	0.134532	0.199489	0.334021

Table 5. 1: Respiratory Carbon produced by *Metridia longa* per m^3 per day assuming different percentages of the male population migrates vertically between the near-surface and deeper layers each day. Values converted to carbon volume using the following equation: C= (R* RQ* (12/22.4))*W, where R is the respiration rate as reported in this thesis (Figure 4.9) converted to mg O_2 l^{-1} h^{-1} mg C^{-1}. A respiratory quotient (RQ) of 0.97 was used for assuming a protein based

metabolism (Gnaiger, 1983), (12/22.4) represents the volume of C produced for every mole of CO_2, and W represents the average carbon weight as found within this thesis (Figure 4.8).

5.7 Conclusions

The overall aim of this thesis was to investigate the role copepod foray behaviour plays in carbon sequestration within high latitude areas. This is an area of study that is gaining traction but so far has been understudied due to the difficulties in studying plankton movements at the individual level. I have shown that:

- The copepod community in the Scotia Sea showed a comparatively shallow normalised biomass size spectra indicating high levels of energy retention within larger size classes compared to other open ocean areas.
- Primary production had some influence on the copepod size structure, but a comparatively shallow spectra was evident in both highly productive and low productivity environments, indicating that other factors such as seasonality and life-cycle strategy are also influential in determining community size structure.
- The successful development and deployment of the MUDL net allowed the vertical movements of zooplankton to be directly recorded in the open ocean for the first time, enabling us to further resolve migration patterns of zooplankton species.
- Using a mixture of nets, I found that copepods undertake a range of migrations, suggesting that foray behaviour and reverse migration may be more prevalent than previously thought.
- The MUDL net found that *Oithona spp*. carry out vertical movements within the upper water column, moving in both directions at dawn and dusk. The contribution these species make to the global carbon cycle has been previously overlooked since *Oithona spp*. are not considered to be strong vertical migrants. This finding shows that *Oithona spp*. must be considered when modelling zooplankton contributions to the BCP as, by undertaking migrations, *Oithona spp*. will be transporting carbon within the water column.
- Residence depth appeared to influence respiration rates in male *M. longa* but this was not found to be the case in females, suggesting that differing physiologies and behavioural strategies may be present within the *M. longa* population of the Fram Strait. In order to gain a better understanding of how respiration rates vary across

copepod populations, and the subsequent impact on the BCP, copepod community composition and dynamics must be resolved further.

- Overall, this thesis has found that migration behaviour within copepods is complex and variable. When looking at the contribution migrations make to the BCP, copepod community structure along with environmental parameters must be considered. Based on the findings within this thesis, the volume of carbon transported as a result of zooplankton migrations is likely to be significantly higher than current estimates suggest.

5.8 Future Work

The global ocean carbon cycle is currently an area of high importance and relevance and is likely to become more so as our climate changes. This is highlighted by the United Nations Sustainable Goals, the thirteenth being: take urgent action to combat climate change and its impacts. Many governments have decided to tackle this goal by striving for a carbon neutral future; however, in order to achieve this, carbon cycles and carbon export processes must be better understood. Therefore, greater emphasis must be placed on the oceanic carbon cycle, which thus far is often overlooked when investigating how to reduce net carbon emissions. This thesis makes a contribution to our understanding of the oceanic carbon cycle by addressing the role copepods play in the BCP. As I explain in Chapter 1, the oceanic carbon cycle is comprised of a larger number of processes. If we are to understand this cycle better, we must explore these processes and how each one interacts with every other. One way of doing this is to carry out large scale projects in which a number of teams, each with different specialities, come together to provide insights into the system as a whole. An example of this is the NASA funded Export Processes in the Ocean from Remote Sensing (EXPORTS). This project brings together a wide range of groups, from chemists and biologists through to oceanographers specialising in remote sensing in order to fulfil the project aim: to develop a way in which export and fate of oceanic primary productivity can be predicted as well as its implications. The findings contained within this thesis can be fed into such programs and can influence the direction in which future similar projects may take. Within the context of the EXPORTS project the results presented in this thesis provide links and insights into potential mechanisms in which the primary productivity, as observed by satellites, reaches the carbon flux observed within sediment traps. In support of this, a recent analysis by Boyd et al., (2019) concluded that, in order to understand the contributions different processes are making to carbon sequestration, we must explore all mechanisms further, starting with the mesopelagic migrant pump as this was found to be the most important mechanism. Building on this, my findings show that zooplankton migration is complex and can contribute to ocean carbon cycles in ways that are presently poorly parameterised.

This thesis has shown that, in order to understand zooplankton migration and its contribution to the BCP, we need to move beyond only looking at bulk movements of populations and resolve individual migrations within the populations. While this thesis has begun the process of looking at polar copepods in this way, more research is required to establish migration patterns across greater temporal and spatial scales. This could be done in a number of ways; the first would be to repeat much of the sampling carried out within this study across a greater number of time points. In order to build up a whole picture of zooplankton behaviour, samples need to be collected throughout the year to highlight any seasonal changes. This was not possible in the present study due to the difficulty in accessing high latitude regions during the winter months. However, it would be possible to carry out a similar study across an annual cycle within more accessible regions, such as the ice edge and sub-polar regions. Further to this, the recent completion of the Multidisciplinary Drifting Observatory for the Study of Arctic Climate (MOSAiC) Expedition demonstrates that we are now capable of sampling previously unreachable areas. The deployment of plankton nets and subsequent physiological analysis throughout this expedition provide valuable insights into the behaviours of copepods in ice covered areas throughout the winter, which could help resolve the role migration plays in the BCP in high latitudes.

Temporal sampling could also be improved with a greater number of net deployments over a 24 hour cycle. The MOCNESS samples in the present study show a redistribution of biomass, highlighting that copepods are not stationary within the water column over a 24 hour period. A higher temporal resolution would allow the tracking of this biomass throughout a daily cycle. If combined with a greater number of MUDL samples, it would be possible to gain a greater understanding of species specific patterns of migration that could be used to further constrain the contribution of zooplankton behaviour to rates of vertical carbon flux. While MOCNESS nets require ships to be travelling, MUDL nets require stationary vessels and have shorter deployment times, making them easier nets to deploy multiple times during a 24 hour period. Samples from a greater number of time points throughout a 24 hour period would allow us to observe whether vertical movements of zooplankton are limited to certain times of the day or continuously throughout the 24 hours. We would also be able to build up a picture of which zooplankton species are carrying out DVM, reverse DVM and asynchronous migrations. Increasing the number of MUDL deployments would also give flexibility in terms of deployment depths. Within this thesis, the MUDL net was deployed to depths of 100m and just below the chlorophyll maximum. However, zooplankton migration takes place over much larger distances; therefore, to truly understand when migrations are taking place and whether foray behaviour is present within the population, a greater range of depths must be sampled. This will not only allow us to build up a picture of where and when zooplankton are undertaking vertical movements but will also aid in assessing the implications these movements have on the BCP. Zooplankton species that are caught within both upward and downward looking nets of the MUDL at all times at all depths are likely to be undertaking large asynchronous vertical migration, having a larger contribution to the active flux of the BCP than those species found to be constrained to smaller depth ranges. Such finding would be able to help identify which species should be considered in more detail, with respect to their contribution to the BCP.

The respiration rates of *M. longa* reported here show that migration behaviour plays an important role in the transport of respiratory carbon, with females likely to be transporting more than males. However, this is only one species of copepod out of thousands and each one may have different migration and physiology patterns. In Chapter 3, I found that *Oithona spp*. were migrating upwards and downwards at both dawn and dusk, suggesting that these species possibly exhibit foray behaviour. In contrast to *M. longa*, *Oithona spp*. are not thought to migrate over large distances. However, their ubiquitous nature makes gaining an understanding of how their physiology changes during their ascents and descents vital to unravelling their contribution to the BCP. This could be done in a number of ways, firstly respiration rates of *Oithona spp*. could be measured in the same way as reported for *M. longa* in this thesis. Beyond this, elemental composition analysis and gut fluorometry of migrating *Oithona spp*. across a number of time points throughout a 24 hour cycle would be informative for assessing the role these species play in carbon transport. *Oithona spp.* are abundant throughout all the global oceans therefore, this work could be carried out, initially, in easily accessible locations, such as off-shore mid-latitudes areas. The spatial area sampled would need to increase to include all regions in order to build a global picture of *Oithona spp*. role in the BCP.

When looking at the respiration rates of *M. longa*, it was only possible to collect copepods during the day and oxygen consumption rates were taken for a short period of time after collection in order to avoid hypoxic conditions within the wells, altering copepod respiration rates. It is thought that one driver of migration is the preservation of energy through slowing metabolism when residing in deeper water (McLaren, 1963). If this theory is correct, a daily cycle in respiration should be present in species that undertake DVM, such as *M. longa*. Therefore, in order to build a more complete picture, copepods should be collected at other time points over the daily cycle and subjected to longer incubations in larger chambers. This would allow a truly representative daily respiration pattern to be resolved.

In addition to respiration rates, other physiological measurements may provide a useful insight into the activity of copepods. One such measure is gut fluorescence which would enable us to look for recent feeding activity and could be utilised to build on the work presented in all chapters of this thesis. In Chapter 2, gut fluorescence would show whether plankton were feeding during the day and night and whether satiated plankton were found throughout the water column or were restricted to the upper layers. This knowledge could be used to further infer movements of plankton in relation to feeding behaviour. In Chapter 3, gut fluorescence carried out on MUDL samples would allow for comparisons to be made between plankton travelling vertically upwards and those moving downwards. It would be expected that those travelling downwards out of the upper water layers would have much higher gut fluorescence, having recently fed, than those moving into these upper layers. Such a finding would provide evidence for satiation sinking, supporting the hunger satiation theory extensively reviewed in Pearre (2003). In Chapter 4, gut fluorescence would complement the respiration rates and provide an insight into whether the sample population had recently fed. Metabolism is often influenced by digestion, therefore understanding where copepods are within a digestive cycle may further help understand the reported respiration rates and the influence of specific dynamic action.

This thesis has also involved the use of novel equipment, both in the field and within the laboratory. As technology advances, it will be possible to undertake more detailed studies in this area. The ZooScan provided images of preserved copepods that could be used to provide biomass estimates and normalised biomass size spectra of net caught samples. However, with recent advances such as the development of the UVP5 (underwater vertical profiler 5), an imaging device that can be deployed from a ship, images of plankton can be taken within the water column in real time (Picheral et al., 2010). This advancement could provide more information than it is presently possible to glean from preserved samples. Each plankton image could be attributed to a specific depth rather than depth integral; the direction of movement may be determined from which trajectories could be extrapolated. The use of such technology would be able to build on the findings in this work and further resolve the role zooplankton play in the BCP (Christiansen et al., 2018; Giering et al., 2020), particularly if combined with nets in order to resolve the taxonomy of imaged plankton.

Another technological advancement that has been gaining traction recently is the development of autonomous underwater autonomous vehicles (AUVs). AUVs can be deployed from the shore or a vessel and are preprogramed to follow a path or to carry out a sequence of manoeuvres based upon the readings it takes whilst deployed. These vehicles have the advantage of being able to reach locations that would not be possible to reach via a vessel and have the potential to allow us to carry out science in previously unreachable regions such as under the sea ice, an area of great importance for understanding oceanic carbon flux. Another feature of AUVs is that they can be modified in a modular manner to carry different pieces of equipment. In order to investigate plankton movements in relation to daylight, such a vehicle could be fitted with an ADCP to detect movements of large volumes of zooplankton, a camera with similar technology of that found in the UVP5 enabling plankton images to be taken in situ, a light sensor to inform us of light levels to be able to match zooplankton movement to light levels, a fluorometer to assess the chlorophyll levels within the water, along with a CTD to provide measurements pertaining to depth, temperature and salinity. The deployment of such vehicles would allow us to gather large volumes of data regarding plankton movements in regions where net sampling may not be possible. Using this data it would be possible to build up a more detailed picture of where and when zooplankton are moving, allowing migration patterns to be further resolved. Additional information on light levels and chlorophyll will help inform us of whether these parameters influence migration behaviours, which may be an important step in recognising and predicting migrations across temporal and spatial zones.

A further way in which technological advances can play a role in resolving zooplankton migration behaviours and subsequent implications on the carbon cycle is through the development of machine learning and artificial intelligence. The optical instruments used and mentioned in this thesis use machine learning, where software is taught to recognise and classify images based on a small subset of verified images. There is currently a movement towards advancing the capabilities of machine learning and incorporating artificial intelligence into scientific processes. Applying these technologies to a project such as the present thesis could enable a greater volume of data to be processed in short time periods allowing changes such as seasonal migrations to be spotted sooner, which could inform us of how carbon flux may alter seasonally and annually. A combination of autonomous vehicles equipped with sensors using artificial intelligence would potentially be able to track zooplankton migration in real time. For instance, if an AUV was able to match the direction and speed of zooplankton as detected by its ADCP to track migration alongside zooplankton, it would be possible to use other data collected to understand the environmental conditions experienced by zooplankton throughout their migrations. Further to this, if photos were collected in situ, species could be identified, shedding light on which species are carrying out which behaviours, which is currently only possible by conducting net sampling. Gaining a knowledge of which species and locations are important for migrations will help inform us of where to focus future efforts. Once species are identified, it would then be possible to target these species for collection though net sampling campaigns in order to carry out similar respiration incubations as within this thesis. By using data regarding temperature gleaned from a vehicle, tracking migrations respiration experiments could be set up to reflect the natural temperature changes zooplankton experience throughout a migration, providing further information on the contribution zooplankton make to the carbon cycle through respiratory flux.

When assessing the global carbon flux an important but currently under researched area is the marginal ice zone. This region is difficult to access due to the dangers the ice poses to vessels. However, it is an important area for the flux of materials therefore a vital area to study in relation to the role zooplankton inhabiting these regions play in the carbon cycle. These regions are often areas of high seasonal productivity due to the melting of ice in spring releasing trapped nutrients, which fuel seasonal blooms. Gaining access to these regions during this time would provide valuable insights into the carbon flux of these areas and could be done using a combination of the methods described above. In order to resolve the role zooplankton play in carbon flux, understanding the timing of seasonal migrations as well as daily migratory patterns would be vital. This could be done using the methods within this thesis or a number of new techniques could be deployed. As this area is extremely difficult to reach during the winter months, it would be practical to deploy floats or moorings that could be collected in the following summer, further allowing data to be collected throughout an annual cycle. Within these instruments, sediment traps could be mounted in order to assess the vertical flux of material. This is a common approach to assessing the carbon sequestration (e.g. Belcher et al., 2017; Manno et al., 2015) and can be programmed so that material enters a particular trap over a set amount of time allowing us to discern when the particles were sinking. This approach could answer the question of how changes in ice cover and the seasonal melt impacts the carbon flux. However, sediment traps are not the only instrument that could help quantify the role zooplankton play in the carbon cycle. ADCPs would be able to detect mass migrations by plankton, informing us of when zooplankton are most active and the timing and amplitude of migration which has implications for the carbon flux within the area. Additionally, the incorporation of optical instruments that are able to determine species and direction of travel would provide a valuable insight into zooplankton migratory behaviour, potentially showing asynchronous migrations throughout the year. This would make a significant contribution towards our understanding of zooplankton mediated processes within the carbon cycle.

While this thesis has shown that detecting foray behaviour in copepods is possible, further work is required to build a more comprehensive overview of this behaviour and its implications. I recommend that, in order to do this, many aspects of the current study should be repeated over larger temporal and spatial scales as well an increased frequency of sampling over 24 hour periods to enable zooplankton behaviour and the environmental parameters they experience throughout migrations to be better restrained in biogeochemical and ecosystem models. The use of emerging technology is likely to enable us to resolve individual plankton movements within the water column, and combining this with physiological measurements will aid in assessing zooplankton contributions to carbon cycles. Using these techniques, the uncertainty surrounding the individual behaviours of zooplankton could be reduced, allowing these aspects of carbon cycling to be better constrained in carbon models.

Glossary

AFDW Ash Free Dry Weight

APF Antarctic Polar Front

AUV Autonomous Underwater Vehicle

BCP Biological Carbon Pump

C Carbon

chl Chlorophyll

CO_2 Carbon dioxide

CTD Conductivity, Temperature, Depth profiler

DIC Dissolved Inorganic Carbon

DVM Diel/ Diurnal Vertical Migration

DW Dry Weight

EGC East Greenland Current

EGPF East Greenland Polar Front

FP(s) Faecal Pellet(s)

HNLC High Nutrient Low Chlorophyll

MIZ Marginal Ice Zone

MUDL Motorised Upward Downward Looking Net

N Nitrogen

O_2 Oxygen

P2 Time-series/ Process station 2 in the Scotia Sea

P3 Time-series/ Process station 3 in the Scotia Sea

PF Polar Front

POC Particulate Organic Carbon

RAC Return Atlantic current

rDVM Reverse DVM

RQ Respiratory Quotient

SACCF Southern Antarctic Circumpolar Current Front

SAF Sub-Antarctic Front

SO Southern Ocean

VM Vertical Migration

WSC West Spitsbergen Current

WW Wet Weight

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Appendix 1

MOCNESS Net	P2 Day	P2 Night	P3 Day	P3 Night
2	50.00 %	100.00 %	100.00 %	50.00 %
3	100.00 %	100.00 %	100.00 %	100.00 %
4	50.00 %	50.00 %	100.00 %	25.00 %
5	50.00 %	25.00 %	50.00 %	50.00 %
6	25.00 %	25.00 %	25.00 %	6.25 %
7	25.00 %	25.00 %	12.50 %	25.00 %
8	25.00 %	12.50 %	1.56 %	6.25 %
9	12.50 %	12.50 %	6.25 %	6.25 %

Table 6. 1: Proportions of total sample scanned using the ZooScan to assess copepod abundance and biomass within the MOCNESS samples in Chapter 2.

Date	Start Time (GMT)	End Time (GMT)	Event No	Net No	Latitude	Longitude	Net depth	Location
04/01/2018	18:42:00		26		-52.8223	-40.1095	0	P3
04/01/2018	19:43:00	20:04:00	26	2	-52.7888	-40.1064	998.3	P3
04/01/2018	20:04:00	20:04:00	26	3	-52.7837	-40.1052	876.9	P3
04/01/2018	20:04:00	20:15:00	26	4	-52.7786	-40.1042	750.5	P3
04/01/2018	20:15:00	20:25:00	26	5	-52.7735	-40.1034	627.2	P3
04/01/2018	20:25:00	20:37:00	26	6	-52.7681	-40.1026	501	P3
04/01/2018	20:37:00	20:49:00	26	7	-52.7624	-40.1014	376.3	P3
04/01/2018	20:49:00	21:00:00	26	8	-52.7567	-40.0997	236.7	P3

04/01/2018	21:00:00	21:10:00	26	9	-52.7507	-40.098	125.5	P3
05/01/2018	01:31:00	02:40:00	30		-52.7952	-40.1225	0.6	P3
05/01/2018	02:40:00	02:52:00	30	2	-52.7769	-40.068	1000.5	P3
05/01/2018	02:52:00	03:02:00	30	3	-52.7721	-40.0597	875.5	P3
05/01/2018	03:02:00	03:15:00	30	4	-52.768	-40.053	750.7	P3
05/01/2018	03:15:00	03:24:00	30	5	-52.7633	-40.0453	625.4	P3
05/01/2018	03:24:00	03:38:00	30	6	-52.7593	-40.0389	500.5	P3
05/01/2018	03:38:00	03:48:00	30	7	-52.7535	-40.03	375.5	P3
05/01/2018	03:48:00	04:01:00	30	8	-52.7489	-40.0229	250.7	P3
05/01/2018	04:01:00	04:12:00	30	9	-52.7436	-40.0146	125.2	P3
16/01/2018	12:51:00	13:50:00	110		-55.2501	-41.2734	0.3	P2
16/01/2018	13:50:00	14:04:00	110	2	-55.251	-41.3287	1000.7	P2
16/01/2018	14:04:00	14:13:00	110	3	-55.2515	-41.3386	851.4	P2
16/01/2018	14:13:00	14:23:00	110	4	-55.2517	-41.3454	752.6	P2
16/01/2018	14:23:00	14:34:00	110	5	-55.2519	-41.3532	625.1	P2
16/01/2018	14:34:00	14:44:00	110	6	-55.2525	-41.3613	501.5	P2
16/01/2018	14:44:00	14:55:00	110	7	-55.2529	-41.3696	375.5	P2
16/01/2018	14:55:00	15:07:00	110	8	-55.2536	-41.378	250.1	P2

16/01/2018	15:07:00	15:15:00	110	9	-55.2545	-41.3869	124.2	P2
17/01/2018	01:17:00	02:24:00	117		-55.2452	-41.2292	0.3	P2
17/01/2018	02:24:00	02:33:00	117	2	-55.213	-41.2581	999.7	P2
17/01/2018	02:33:00	02:45:00	117	3	-55.2086	-41.2626	875.5	P2
17/01/2018	02:45:00	03:00:00	117	4	-55.2031	-41.2683	750.7	P2
17/01/2018	03:00:00	03:09:00	117	5	-55.1967	-41.2742	624.6	P2
17/01/2018	03:09:00	03:18:00	117	6	-55.1924	-41.2785	501.8	P2
17/01/2018	03:18:00	03:33:00	117	7	-55.1878	-41.2833	375.2	P2
17/01/2018	03:33:00	03:44:00	117	8	-55.181	-41.2901	246.4	P2
17/01/2018	03:44:00	03:54:00	117	9	-55.1758	-41.2956	126	P2

Table 6. 2: Details of all MOCNESS deployments at during 2017/18, JR17002 and analysed in Chapter 2.

Net	Open time (GMT)	Close time (GMT)	Time opened (min)	Net Angle	Angle in radians	Opening (m^2)	Speed (knots)	Speed (m/min)	Water flow (m^{-3})
2	19:43:00	19:54:00	00:11:00	-29.02	0.51	0.49	2.00	61.73	329.38
3	19:54:00	20:04:00	00:10:00	-33.24	0.58	0.55	2.00	61.73	338.42
4	20:04:00	20:15:00	00:11:00	-30.71	0.54	0.51	2.00	61.73	346.84
5	20:15:00	20:25:00	00:10:00	-29.92	0.52	0.50	2.00	61.73	307.92
6	20:25:00	20:37:00	00:12:00	-31.07	0.54	0.52	2.00	61.73	382.30
7	20:37:00	20:49:00	00:12:00	-33.22	0.58	0.55	2.00	61.73	405.84
8	20:49:00	21:00:00	00:11:00	-33.04	0.58	0.55	2.00	61.73	370.24
9	21:00:00	21:10:00	00:10:00	-33.21	0.58	0.55	2.00	61.73	338.10

Table 6. 3: Details of day time MOCNESS deployment at P3 (event number 26) during 2016/17, JR17002, showing opening times and tow speeds used to calculate water flow in order to calculate copepod abundance and biomass per m^{-3}.

Net	Open time (GMT)	Close time (GMT)	Time opened (min)	Net Angle	Angle in radians	opening (m^2)	Speed (knots)	Speed (m/min)	Water flow (m^{-3})
2	02:40:00	02:52:00	00:12:00	-31.94	0.56	0.53	2.00	61.73	391.93
3	02:52:00	03:02:00	00:10:00	-33.71	0.59	0.56	2.00	61.73	342.65
4	03:02:00	03:15:00	00:13:00	-32.25	0.56	0.53	2.00	61.73	428.22
5	03:15:00	03:24:00	00:09:00	-31.59	0.55	0.52	2.00	61.73	291.08
6	03:24:00	03:38:00	00:14:00	-33.30	0.58	0.55	2.00	61.73	474.46
7	03:38:00	03:48:00	00:10:00	-34.14	0.60	0.56	2.00	61.73	346.49
8	03:48:00	04:01:00	00:13:00	-33.93	0.59	0.56	2.00	61.73	447.93
9	04:01:00	04:12:00	00:11:00	-33.89	0.59	0.56	2.00	61.73	378.64

Table 6. 4: Details of night time MOCNESS deployment at P3 (event number 30) during 2016/17, JR17002, showing opening times and tow speeds used to calculate water flow in order to calculate copepod abundance and biomass per m^{-3}.

Net	Open time (GMT)	Close time (GMT)	Time opened (min)	Net Angle	Angle in radians	opening (m^2)	Speed (knots)	Speed (m/min)	Water flow (m^{-3})
2	13:50:00	14:04:00	00:14:00	-28.32	0.49	0.47	2.00	61.73	410.03
3	14:04:00	14:13:00	00:09:00	-31.30	0.55	0.52	2.00	61.73	288.61

4	14:13:00	14:23:00	00:10:00	-29.83	0.52	0.50	2.00	61.73	307.12
5	14:23:00	14:34:00	00:11:00	-29.71	0.52	0.50	2.00	61.73	336.56
6	14:34:00	14:44:00	00:10:00	-29.67	0.52	0.50	2.00	61.73	305.60
7	14:44:00	14:55:00	00:11:00	-30.09	0.53	0.50	2.00	61.73	340.44
8	14:55:00	15:07:00	00:12:00	-28.83	0.50	0.48	2.00	61.73	357.17
9	15:07:00	15:15:00	00:08:00	-27.35	0.48	0.46	2.00	61.73	226.87

Table 6. 5: Details of day time MOCNESS deployment at P2 (event number 110) during 2016/17, JR17002, showing opening times and tow speeds used to calculate water flow in order to calculate copepod abundance and biomass per m^{-3}.

Net	Open time (GMT)	Close time	Time opened (min)	Net Angle	Angle in radians	opening (m^{2})	Speed (knots)	Speed (m/min)	Water flow (m^{-3})
2	02:24:10	02:33:35	00:09:25	-31.04	0.54	0.52	2.00	61.73	299.86
3	02:33:35	02:45:50	00:12:15	-33.43	0.58	0.55	2.00	61.73	416.61
4	02:45:50	03:00:28	00:14:38	-31.91	0.56	0.53	2.00	61.73	444.75
5	03:00:28	03:09:35	00:09:07	-30.20	0.53	0.50	2.00	61.73	283.19
6	03:09:35	03:18:29	00:08:54	-32.91	0.57	0.54	2.00	61.73	298.55
7	03:18:29	03:33:17	00:14:48	-34.22	0.60	0.56	2.00	61.73	513.84
8	03:33:17	03:44:35	00:11:18	-32.29	0.56	0.53	2.00	61.73	372.67

9	03:44:35	03:54:54	00:10:19	-31.72	0.55	0.53	2.00	61.73	334.93

Table 6. 6: Details of night time MOCNESS deployment at P2 (event number 117) during 2016/17, JR17002, showing opening times and tow speeds used to calculate water flow in order to calculate copepod abundance and biomass per m^{-3}.