

ACTIVE CARBON TRANSPORT AND FEEDING ECOLOGY OF PELAGIC DECAPODS IN
THE NORTH PACIFIC SUBTROPICAL GYRE

by

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Abstract

Pelagic decapods were collected during two cruises in the central North Pacific Subtropical Gyre (NPSG): in 2011 depth stratified samples with a MOCNESS-10 (10 m² Multiple Opening/Closing Net and Environmental Sensing System) were carried out at two stations to the west and north of the Hawaiian island of Oahu (21°20.6'N, 158°16.4'W and 22°45'N, 158°00'W), and in 2004 samples were collected using three different micronekton sampling gears in the shallow backscattering layer (SSL) and deep backscattering layer (DSL) off the southwest coast of Hawaii. A total of 40 decapod taxa were identified. Amongst the 22 species with sufficient representation, three migration classes were identified: full migrators (6 species); partial migrators (13 species); and non-migrators (3 species). Using measured local temperature profiles along with published models of respiration, excretion and mortality, the individual and total active downward carbon flux was calculated. From the 2004 samples, diets of nine pelagic decapod species were established through stomach content analysis. It was found that decapod diet varied not only with size, but also with taxonomy. All decapods fed more in the SSL at night than in the DSL during the day or night. However, decapods did not feed entirely at night in the SSL, a common assumption made in previous estimates of active flux for a wide variety of organisms. Instead, feeding in the DSL was equal to 9.67 – 44.69% of feeding in the SSL by weight. Using these feeding estimates, and assuming a micronekton sampling efficiency of 33.33% for the MOCNESS-10, the active flux due to decapod migrations was calculated to be 382.7 - 625.0 $\mu\text{gC}/\text{m}^2/\text{day}$. Compared to the local passive flux, this active flux was equal to 4.8 - 7.8% of passive flux at the mean night time residence depth (710.7 m), 2.1 - 3.4% of passive flux at the mean daytime residence depth (261.8 m), and 1.5 - 2.4% of passive flux at the base of the euphotic zone (173 m).

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List of abbreviations

NPSG North Pacific Subtropical Gyre

MICE Micronekton Inter-calibration Experiment

MOCNESS Multiple Opening/Closing Net and Environmental Sensing System

WMD Weighted mean depth

SSL Shallow backscattering layer (centered at ~120 m)

DSL Deep backscattering layer (centered at ~550 m)

POM Particulate organic matter

DOM Dissolved organic matter

POC Particulate organic carbon

DW Dry weight

WW Wet weight

CL Carapace length

SFI Stomach fullness index

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1 General Introduction

Micronekton are actively swimming marine organisms, generally larger than drifting mesozooplankton (often < 2 cm), but smaller than larger nekton (often > 10 cm) (Brodeur et al., 2005). While they can be defined precisely based on Reynolds numbers, they are often defined operationally as taxa too small to be caught by most large meshed pelagic trawls, but too mobile to be caught efficiently by conventional plankton gears (Brodeur et al., 2005). Their patchy distribution and high mobility makes them very difficult to sample without bias (Pakhomov and Yamamura, 2010). For these reasons, micronekton tend to be poorly sampled and poorly understood (Brodeur and Yamamura, 2005). Micronekton are of particular ecological importance in the mesopelagic zone, where they are one of the most conspicuous members of the community (Brodeur et al., 2005), and are also significant components of the epipelagic as many taxa migrate into the epipelagic zone at night to feed (Brodeur and Yamamura, 2005). Studies have shown that micronekton are a primary food source for a wide variety of nektonic species that are commercially harvested, and as vertical migrators they are consumed both by large epipelagic predators (such as tuna, swordfish and sharks) as well as abyssal/bathypelagic predators that migrate up into the mesopelagic (Brodeur et al., 2005). Thus micronekton function not only as a key link in the food chain between mesozooplankton and the higher trophic levels, but also as a link between surface and deep waters (Brodeur and Yamamura, 2005).

Pelagic decapods are an abundant and important component of the micronekton community throughout many regions of the world's oceans (Maynard et al., 1975; Hopkins et al., 1989; Flock and Hopkins, 1992). In the waters near Hawaii, the central North Pacific

Subtropical Gyre (NPSG), previous studies have shown penaeid and caridean shrimp to be the 2nd and 5th most abundant micronekton groups respectively in deep net tows (from 0 - 1200 m), and the 1st and 5th most abundant micronekton groups in shallow night time tows (0 - 400 m) (Maynard et al., 1975). Despite the high local abundance and functional importance of micronekton, very little is known about the diet or trophic role of pelagic decapods in the central NPSG. While numerous extensive feeding ecology studies have been carried out for pelagic decapod assemblages in the Atlantic and Gulf of Mexico (Foxton, 1970a, 1970b; Foxton and Roe, 1974; Donaldson, 1975; Fasham and Foxton, 1979; Flock and Hopkins, 1992; Hopkins et al., 1994; Hopkins and Sutton, 1998), to date only one community scale study addressing the feeding ecology of pelagic decapods in the NPSG has been performed, and it covered only sergestid shrimps (Walters, 1975). Furthermore, this study only reported presence/absence of prey items, with little numerical analysis. As the NPSG is the largest ecosystem on the planet, and a region heavily studied by the HOT program in terms of physical and biogeochemical processes (Karl, 1999), it is important to gain further insight into the feeding ecology of local pelagic decapods.

Not only is the diet of pelagic decapods in the central NPSG poorly understood, but the effects of their feeding coupled with diel migratory behavior has not yet been studied. Diel migrants feed primarily in the epipelagic, yet reside in both the epipelagic and mesopelagic layers. Consequently, they transfer carbon to their mesopelagic resident depths through a process known as the active flux (Longhurst et al., 1990). Active flux attributed to migrant mesozooplankton in various areas of the world's oceans has been estimated to be significant compared to local gravitational fluxes (Longhurst et al., 1990; Longhurst and Williams, 1992;

Dam et al., 1995; Le Borgne and Rodier, 1997; Zhang and Dam, 1997; Steinberg et al., 2000, 2002; Al-Mutairi and Landry, 2001). Similarly, two studies in the western North Pacific have found active fluxes related to the migrations of micronekton, including decapods, to be highly significant compared to local gravitational fluxes (Hidaka et al., 2001; Kitamura et al., in review). However, up until now no studies have quantified the active flux due to migrant decapods in the central NPSG.

The main objectives of this work were twofold. First, to investigate the diel vertical migrations of pelagic decapods in the central NPSG, and quantify the contribution of this taxonomic group to the local vertical carbon flux, assuming 100% feeding at the shallow night time depths. Second, to investigate decapod feeding ecology, testing the shallow feeding assumption, and estimating the extent to which decapod diets are specialized based on both organism size and taxonomy.

2 Pelagic decapod vertical migrations and active carbon transport in the North Pacific Subtropical gyre

2.1 Introduction

The oceans are estimated to have absorbed approximately 48% of total anthropogenic fossil fuel and cement manufacturing emissions since the beginning of the industrial revolution (Sabine et al., 2004). The ocean's carbon reservoirs dwarf those of the atmosphere; for example, as of the year 1990 the atmosphere held ~750 Gt C, compared to ~1,020 Gt C in the surface ocean, and 38,100 Gt C in intermediate and deep waters (Siegenthaler and Sarmiento, 1993). The physical and biological processes that mediate the transfer of carbon from the surface ocean to the ocean's interior are therefore a key component of the global carbon cycle. A detailed understanding of these processes is critical to accurate modelling of current and future carbon fluxes in the oceans.

The biological pump is one of the most important pathways through which carbon is transported vertically in the ocean. The biological pump refers to the processes through which inorganic carbon is fixed into organic carbon by photosynthesis, and then transported downwards through the passive sinking of POM (particulate organic matter), diffusion and advection of DOM (dissolved organic matter), and active transport by the vertical migration of animals (Hidaka et al., 2001). In the past the passive sinking of POM (also known as the "gravitational flux" or "passive flux") and diffusion and advection of DOM were considered to be the most important processes mediating vertical transport, however, since the mid-1990s, the importance of active transport of carbon by vertical migrators has been increasingly recognized (Dam et al., 1995).

Many species of marine zooplankton and nekton reside below the euphotic zone during the day and migrate to the surface at night in order to feed (Lampert, 1989). A significant

biomass of zooplankton and nekton perform these diel vertical migrations, which results in the transfer much of the organic matter consumed at the surface to their daytime residence depths through a combination of respiration, excretion, defecation and mortality (Longhurst, 1991). The latter processes also occur at the surface, but since food is primarily consumed at the surface, this represents a net transport of carbon from the night time feeding depths to the daytime residence depths (Longhurst, 1991).

Longhurst et al. (1990) were the first attempting to quantify the active flux due to the migratory zooplankton. Using data from tropical and subtropical stations in the northwestern Atlantic and eastern Pacific, they showed that respiratory carbon flux due to zooplankton migrations across the pycnocline was equal to 13-58% of gravitation fluxes at the same stations. A significant component of downward carbon flux had thus been completely missed in previous carbon models (Longhurst et al., 1990). That study also indicated that active flux was widely variable between locations, and depended strongly upon zooplankton community composition (Longhurst et al., 1990). Details of Longhurst et al.'s (1990) study, as well as subsequent studies that have attempted to quantify active carbon flux are summarized in Table **2.1**.

Table 2.1 Studies to date comparing the relative contributions of active and passive carbon flux. Active fluxes shown are values corrected for under sampling due to netavoidance, when applicable

Gear	Location	Type(s) of active flux estimated	Active flux (mg C m ⁻² day ⁻¹)	Active flux vs. POC flux	Reference
BIONESS (1m ² mouth opening, 200-243 µm mesh size)	5 stations in the subtropical northwest Atlantic, 2 stations in the eastern tropical Pacific	Respiratory flux	3 – 107	13 – 53% of POC flux across the pycnocline	Longhurst et al., 1990
MOCNESS (0.25 m ² mouth opening, 64 µm mesh size)	BATS	Respiratory flux	6 – 41	18 – 70% of POC flux at 150 m	Dam et al., 1995
MOCNESS (0.25 m ² mouth opening, 64 µm mesh size)	Central equatorial Pacific	Respiratory and mortality flux	0.59 – 1.06	31 – 44% of POC flux at the base of the euphotic zone	Zhang and Dam, 1997
UNESCO WP-2 (0.25 m ² mouth opening, 200 µm mesh size)	Equatorial Pacific	Respiratory and gut flux	3.8 – 7.9	4 – 8% of POC flux at the base of the euphotic zone	Le Borgne and Rodier, 1997; Rodier and Le Borgne, 1997
Variety of mesozooplankton gears	North Atlantic	Respiratory and gut flux	n/a	19 – 40% of POC flux at 150 m	Morales, 1999
Unnamed gear (3.14 m ² mouth opening, 500 µm mesh size)	BATS	Respiratory and excretory flux	0 – 9.9	0 – 38.6% of POC flux at 150 m	Steinberg et al., 2000
Unnamed gear (1 m ² mouth opening, 200 µm mesh size)	Station ALOHA	Respiratory flux	1.0 – 9.2	5.6 – 25% of POC flux at 150 m	Al-Mutairi and Landry, 2001
ORI net for mesozooplankton (1 m ² mouth, 200 µm mesh); TANSYU otter trawl for micronekton (400 m ² mouth, 8 mm – 100 cm mesh)	Western equatorial Pacific	Respiratory, mortality and gut flux	9.97 – 23.53 for mesozooplankton; 15.2 – 29.9 for micronekton	18.2 – 42.9% of POC flux at 150 m for mesozooplankton; 27.7 – 54.6% of POC flux at 150 m for micronekton	Hidaka et al., 2001
IONESS (1.5 m ² , 330 µm mesh size)	Northwest North Pacific	Respiratory flux	6.85	3.4 – 16.7% of POC flux at 150 m	Kitamura et al., in review

Most previous estimates of active flux were made using sampling gears well suited to sampling mesozooplankton, but ill-suited to sampling macrozooplankton and micronekton such as decapods, euphausiids, stomatopods, and fish (**Table 2.1**). Steinberg et al. (2000) were the first to target macrozooplankton, finding that the active flux due to macrozooplankton was of a similar order of magnitude to previous studies on mesozooplankton (Steinberg et al., 2000). That study was also the first to make a distinction between fluxes at different depths, as opposed to treating all carbon fluxes to below the mixed layer as equal (Steinberg et al., 2000). While macrozooplankton active flux to below 150 m peaked at 38.6% of POC flux at that depth, most macrozooplankton were migrating significantly deeper than 150 m (Steinberg et al., 2000). Gravitational fluxes tend to decline with increasing depth as the POC is remineralized (Karl et al., 1996), thus as carbon is transported deeper, the active flux becomes relatively more important. When comparing active and gravitational flux to the 300-600 m layer, active flux reached up to 71.4% of gravitational flux (Steinberg et al., 2000).

To date only two studies, both conducted in the western North Pacific, have estimated active flux by the larger micronekton (Hidaka et al., 2001; Kitamura et al., in review). Active flux by micronekton is thus an understudied element of the biological pump, and little is known about how this flux varies throughout the world's oceans. It is possible that micronekton have been largely ignored in active flux studies due to their relatively small biomass compared to zooplankton. However, they also tend to migrate to deeper depths (Brodeur and Yamamura, 2005), and even relatively small active fluxes to deep depths can be important, as the passive gravitational flux declines exponentially with depth (Steinberg et al., 2000).

Up until now, only two studies have assessed the contribution of micronekton to vertical carbon flux. Both have been performed in the western North Pacific, in ecosystems where decapods were reasonably minor components of micronekton biomass and abundance. Hidaka et al. (2001) estimated vertical fluxes at two stations in the western equatorial North Pacific. Their micronekton catch was dominated by myctophids, with only minor catches of squid, euphausiids and decapods (Hidaka et al., 2001). The active carbon flux due to micronekton was found to be 57.4% and 29.5% of the sinking particle flux at the two stations (Hidaka et al., 2001), comparable to the upper range of estimates of mesozooplankton fluxes from around the world. As indicated above, this flux was almost entirely due to myctophids. The active flux due to shrimp was only 1.52% of the total attributed to micronekton, or 0.66% of the sinking particle flux (Hidaka et al., 2001). It is worth noting that this study focused on flux into and out of the euphotic zone, and did not compare active flux to passive flux at the depths the micronekton were migrating to. If the micronekton were migrating well below the base of the euphotic zone, the active flux of carbon to their daytime depths may have been significantly more important relative to passive gravitational flux at these depths.

Hidaka et al. (2001) showed that micronekton can be prominent contributors to the biological pump. However, additional studies across different regions are needed to estimate their importance on a global scale, especially since micronekton communities tend to be highly variable spatially (Brodeur and Yamamura, 2005). One other study has been performed on active flux by micronekton, in the western subarctic Pacific (Kitamura et al., in review). These authors measured the active flux via the crustacean micronekton relative to total POC flux across 5 different depths, reporting a flux of 3.4 – 16.7% of the POC flux at 150 m; 5.5 – 16.6%

at 200 m; 3.5 – 6.9% at 300 m; 1.3 – 2.7% at 400 m; and 0% at 500 m. Active flux was relatively small in comparison to Hidaka et al. (2001), most likely due to a small number of diel migratory species (Kitamura et al., in review). This study was also using a relatively small mouth net, and may thus have underestimated micronekton density. Fourteen micronekton crustacean species were identified, belonging to 4 orders (Euphausiacea, Decapoda, Mysida and Lophogastrida), but only four of the species showed diel vertical migratory patterns (three euphausiid species, *Euphausia pacifica*, *Thysanoessa inermis* and *Thysanoessa longipes*, as well as a single decapod species, *Sergestes similis*). The decapod species (*S. similis*) was a significant contributor to the overall crustacean active fluxes, making up 20.0% of the total active flux (0.7 – 3.3% of POC flux) past 150 m, 22.5% (1.2 – 3.7% of POC flux) past 200 m, 74.5% (2.6 – 5.1% of POC flux) past 300 m, and 100% (1.3 – 2.7% of POC flux) past 400 m (Kitamura et al., in review).

Both of the above micronekton studies were performed in ecosystems where decapods were relatively minor components of total micronekton biomass and abundance. During the 2004 *Oscar Elton Sette* cruise (second chapter of the thesis), both pelagic decapod diversity and contribution to the micronektonic community was high. Frame trawl catches contained roughly similar biomass of decapods, euphausiids, myctophids, and other fish. Stations ALOHA and Kahe, where this study took place, are widely studied oceanographic locations, established by the Hawaii Ocean Time-series (HOT) program. Monitoring of the biology, chemistry and hydrography at these stations has been ongoing since October 1988, with one of the key focuses of the study being to understand the local carbon cycle and biological pump (Karl and Lukas, 1996). Station ALOHA was chosen as a site that is representative of the North Pacific Subtropical Gyre (Karl and Lukas, 1996). The North Pacific Subtropical Gyre is the earth's

largest contiguous biome (Karl, 1999), but up until now the flux of micronekton has not been measured anywhere near it's center, with previous micronekton active flux studies being conducted only in very different ecosystems along its western edge. The goals of this research chapter are to:

- a) Describe the community structure, vertical distribution and diel vertical migrations of pelagic decapods in the central NPSG
- b) Estimate the contribution of these organisms to local vertical carbon flux

2.2 Materials and methods

2.2.1 Field sampling

Samples were collected between August 19th and 25th, 2011, aboard the *R/V Kilo Moana*. Midwater trawls were conducted at two stations near the Hawaiian Island of Oahu, Station Kahe and Station ALOHA (**Figure 2.1**).

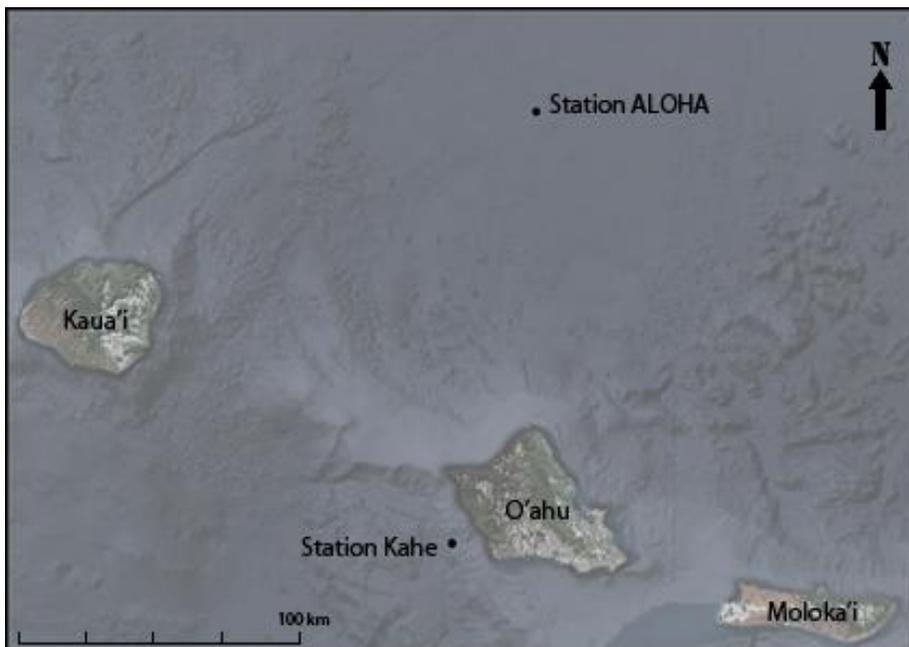


Figure 2.1 Map showing sampling stations for the August 2011. Imagery ©2012 TerraMetrics, Map data ©2012 Google.

Station Kahe is considered a coastal station, located ~10 km from land (at 21°20.6'N, 158°16.4'W), with a bottom depth of ~1500 m, while station ALOHA is considered an open ocean station, located ~100 km from land (at 22°45'N, 158°00'W) with a bottom depth of roughly 4800 m (Karl and Lukas, 1996).

Micronekton samples were collected using a MOCNESS-10 gear (Multiple Opening/Closing Net and Environmental Sensing System); a frame trawl with a 10 m² mouth opening and 6 mm mesh that was towed at a speed of 2 kts, and equipped with a SeaBird CTD to measure the physical properties of the water column. The MOCNESS-10 was outfitted with six nets: five of these nets were used to sample five discrete depth intervals, while the sixth net performed an oblique tow on the way down over the entire depth range. The catch from the oblique tow was ignored, because for this study it was necessary to know where within the water column samples were collected. All natant decapods from the nets sampling discrete depths were identified to the species level when possible, and carapace lengths were measured using digital calipers with a resolution of 0.1 mm. Carapace lengths were measured from the posterior middorsal margin of the carapace to the posterior edge of the orbit.

A total of six depth stratified tows were conducted, four at Station ALOHA and two at Station Kahe. Tows were made to depths of up to 1500 m during the day, and up to 2500 m at night. The number of samples taken at each depth interval are shown in **Figure 2.2**.

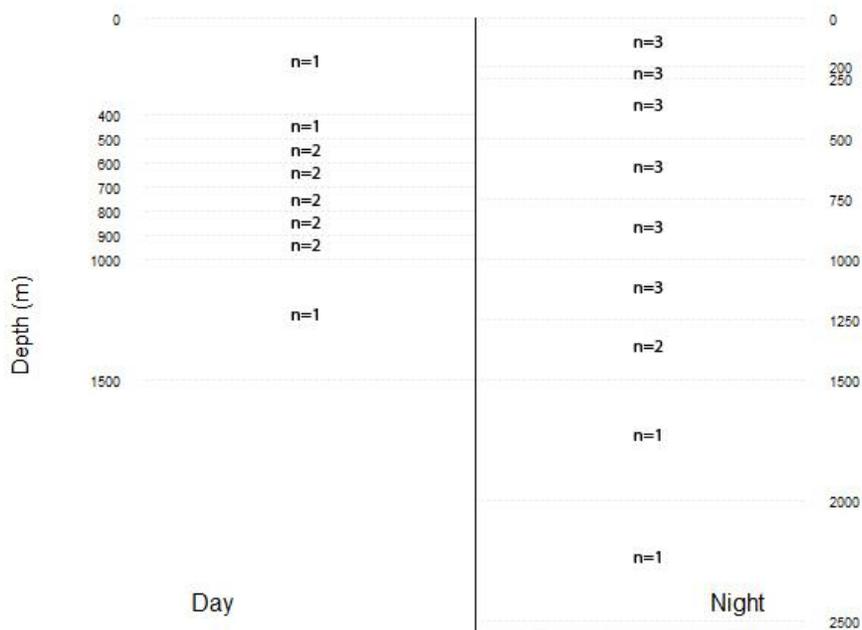


Figure 2.2 Sample size at each depth interval, for samples collected at Station Kahe and Station ALOHA combined

Samples from Station Kahe and Station ALOHA were analyzed together (**Figure 2.2**). While it would have been interesting to look at each station on its own, to compare a coastal site to an open ocean site, sample sizes would have been too small. Furthermore, as seen in the results, physical oceanography was similar between the two sites in terms of both temperature and salinity profiles (**Figures 2.3** and **2.4**). Species composition was also highly similar between the two sites, of the 22 decapod species analyzed in this study, 21 were present at both stations, with only one species, *Gennadas clavicarpus*, found exclusively at one station, Station ALOHA. Daytime and night time residence depths were also similar for all species.

Data from the 2004 *Oscar Elton Sette* cruise were also used in this chapter for length weight relationships, carbon weight to dry weight measurements, and estimation of active gut

fluxes. The specifics of the field sampling procedure for this cruise are described in Chapter 2 of this thesis.

2.2.2 Length weight relationships

Prior to the start of the 2011 *R/V Kilo Moana* cruise, carapace length to dry weight relationships were determined for each species using samples from the 2004 *Oscar Elton Sette* cruise. The samples had been preserved in 10% buffered formalin, and roughly 75 individuals per species were used to determine species specific carapace length to dry weight relationships. Individuals were rinsed thoroughly, their carapace lengths were measured as described in section 1b.1, and wet weights were measured to a resolution of 0.1 mg after blotting each individual with KimWipes to remove any excess water. The decapods were then dried in an oven at 50°C for 24-72 hours (24 hours for small individuals, 48 hours for moderate sized individuals, 72 hours for large individuals), then re-weighed on the same scale to determine their dry weights. Ten individuals from each size class were dried for the allotted time, weighed, then dried for an additional 48 hours and weighed again to ensure that they were fully dry the first time, and in no case was there a significant amount of weight lost after the extra 48 hours of drying.

It was necessary to determine a wet weight to dry weight relationship for natant decapods for two reasons. First, for species upon which a gut content analysis was performed, the above procedure, including the oven drying and measuring of dry weights, was performed in full. However, for species where no gut content analysis was performed, carapace lengths and wet weights were measured, but dry weights were not directly measured, so as to avoid

unnecessarily destroying the samples. Instead, a wet weight to dry weight relationship was determined, and these wet weights were converted to dry weights mathematically.

The second use for the wet weight to dry weight relationship relates to dry weight loss during formalin preservation. It has been well documented that zooplankton and micronekton that have been preserved in formalin lose a percentage of their dry weight relative to individuals that had their dry weights measured immediately after being caught, with no preservation (Gigugre et al., 1989; Pakhomov, 2003; Wetzel et al., 2005). **Equation 2.1**, derived by Pakhomov (2003), allows dry mass loss to be estimated based on body water content through a parabolic equation.

$$\text{Equation 2.1 } \textit{Dry mass loss} = 0.045 * (\textit{body water content})^2 - 6.898 * (\textit{body water content}) + 289.4$$

Dry mass loss is taken as a percentage of the mass of the unpreserved individual, while body water content is equal to the percentage of mass lost when an individual is dried completely in an oven.

Relationships between carapace length and corrected dry weight were then derived for each species. “Corrected dry weights” refers to dry weights that have been corrected for dry mass loss using **Equation 2.1**, as well as to wet weights that have been converted to dry weights, and then corrected for dry mass loss. The carapace length to dry weight relationships were determined by the expression:

$$\text{Equation 2.2 } DW = a * CL^b$$

Where a and b are constants estimated by the linear regression method, DW is corrected dry weight (mg), and CL is carapace length (mm). Equations of this form are standard for length-weight relationships for decapods (Özcan and Katağan, 2011).

2.2.3 Abundance and biomass

To estimate the abundance of each natant decapod species at each depth interval, the catch was divided by the volume of water filtered through the net. However, the purpose of this cruise was not solely to collect samples for this study, but also to collect samples for a number of other unrelated studies being conducted by other researchers. Because of this somewhat different depth intervals were sampled during different tows. For example, on one net tow during the day there was one net for the 600-700 m depth interval, and another net for the 700-800 m depth interval, but on the next daytime tow there was only one net for the entire 600-800 m depth interval. It was thus necessary to either interpolate or extrapolate when estimating abundance for each depth interval, and interpolation was deemed more appropriate. For example, data from the 600-700 m, 700-800 m, and 600-800 m intervals were analyzed using the following equations:

Equation 2.3 *Estimated 600-700 m abund.* = $\frac{2}{3} * (600-700 \text{ m abund.}) + \frac{1}{3} * (600-800 \text{ m abund.})$

Equation 2.4 *Estimated 700-800 m abund.* = $\frac{2}{3} * (700-800 \text{ m abund.}) + \frac{1}{3} * (600-800 \text{ m abund.})$

In estimating the abundance at each interval it was also necessary to take into account net avoidance. It has been well established that nets underestimate the densities of zooplankton, micronekton and nekton. The catch efficiency of a net should therefore be taken into account when deriving abundance from net data (Aron and Collard, 1969; Misund et al.,

1999; Itaya et al., 2001, 2007; Wiebe et al., 2004). A micronekton catch efficiency of 33.33% was assumed for this study (see section 1d.3).

Finally, it was necessary to take into account reduced catches during the day. Due to increased visibility of the net during the day, avoidance is expected to be greater. It has been suggested that when night time estimated abundances exceed daytime by ≥ 1 order of magnitude, it should be assumed that this is due to visual net avoidance, and thus daytime abundances are actually equal to night time abundances (Kitamura et al., in review). However, as shown in the results section, this was only the case for 1 of the 19 migratory decapod species in this study (*Sergia bigemmeus*), so this was a fairly minor adjustment.

2.2.4 Diel vertical migrations

In order to determine whether a population is performing diel vertical migrations, the weighted mean depth (WMD) of each species must be calculated during both the day and the night. Weighted mean depth was calculated as:

$$\text{Equation 2.5 } WMD = \frac{\sum(n_i * z_i * d_i)}{\sum(n_i * z_i)}$$

Where d_i is the depth of a sample i (the depth at the center of the depth interval, in m), z_i the thickness of the interval (in m), and n_i is the abundance of individuals at that depth (individuals/1000 m³) (Andersen et al., 2001).

A t-test was performed to determine if there was a statistically significant difference between day and night WMDs of individual species. The t-tests were performed on abundances corrected for volumes of water filtered, as opposed to the raw number of

individuals caught in each depth interval. For example, if 30 individuals were captured in total, all in the 100-200 m and 200-300 m depth intervals, with a calculated abundance per unit volume twice as high in the 100-200 m interval than the 200-300 m interval, corrected abundances would be 20 individuals in the 100-200 m interval, and 10 individuals in the 200-300 m interval, regardless of the unadjusted catch in each interval. In general this represented only minor corrections to the unadjusted data, as the volumes of water filtered tended to coincide closely with the size of the depth interval being sampled.

The t-test used to compare daytime mean depth to night time mean depth was Welch's 2-sample t-test, which is an adaptation of Student's t-test that can be used for samples with unequal variances (Sawilowsky, 2002). Furthermore, t-tests in general are highly robust in terms of both Type I and Type II errors to departures from the assumption of normality, so non-normal distributions for some species should not be a significant issue (Sawilowsky, 2002). A p-value of 0.05 or less was required to reject the null hypothesis that means were equal. When a species' WMDs were significantly different between day and night, it was concluded that diel vertical migrations were being performed by that species.

In the case of some species there was no significant migration towards the surface at night, in other species the entire population migrated towards the surface at night (see results). A third category of partial migration was observed for some species, where part of the population migrated to the surface, while part of the population remained at the daytime depth. These partially migratory species were identified based on a bimodal distribution at night, with one peak at the daytime depth and another peak closer to the surface. For such partially migratory species, the percentage of the total night time population that was

migrating upwards was calculated, and the WMD for this migratory portion was calculated. For example, if there were 100 individuals/m² in the water column at night, but only 60 individuals/m² migrated to the surface, while the other 40 individuals/m² stayed at depth, it was determined that 60% of the population was migrating, and the night time WMD was calculated based only on these 60 individuals. Furthermore, estimates of active flux (which will be addressed in the next section) were calculated based only upon the migratory portion of the population, since by definition it is only migratory individuals that contribute to active flux.

2.2.5 Active flux

As described in the introduction, active flux of carbon by migrating micronekton can be separated into four components: respiration, excretion, mortality, and gut flux.

Respiratory flux was calculated using an empirical allometric relationship derived by Ikeda (1985), which predicts the respiration rate of a zooplankton or micronekton organism based on ambient temperature and the organism's biomass.

$$\text{Equation 2.6 } \ln RO = -0.2512 + 0.7886 * \ln DW_{mg} + 0.0490 * T$$

RO is the rate of respiratory oxygen uptake ($\mu\text{L O}_2 \text{ organism}^{-1} \text{ hr}^{-1}$), DW_{mg} is the dry weight of the organism (mg), and T is the environmental temperature ($^{\circ}\text{C}$). This hourly respiration rate was then converted to a daily respiration rate by the number of hours of daylight, which at Station ALOHA over the study period was 12.6 hours of daylight per day.

Once rates of oxygen uptake were determined, it was necessary to convert these rates into respiratory equivalents. The following equation from Al-Mutairi and Landry (2001) was used:

$$\text{Equation 2.7 } RC = RO * RQ * 12/22.4$$

RC is the respiratory carbon equivalent ($\mu\text{g C organism}^{-1} \text{ hr}^{-1}$), RQ is the respiratory quotient, which is the molar ratio of carbon produced to oxygen utilized, 12 is the molecular weight of carbon, and 22.4 is the molar volume of an ideal gas at standard pressure and temperature. The respiratory quotient was assumed to be 0.97 (Gnaiger, 1983).

Active excretory flux was calculated based on the findings of Steinberg et al. (2000). The authors measured CO_2 respiration and DOC excretion of a wide variety of diel migratory crustacean species at the US JGOFS Bermuda Atlantic Time-series Study. Respiration and excretion rates were found to vary similarly, with both rates depending on environmental temperature and the dry weight of the organism (Steinberg et al., 2000). In the case of diel migratory decapods, DOC excretion averaged 32% of CO_2 respiration in terms of $\mu\text{g C}$ respired or excreted per mg dry weight (Steinberg et al., 2000). Thus, for this study, excretory DOC was assumed to be equal to 32% of respiratory CO_2 .

Active mortality flux was calculated by estimating the hourly weight-specific mortality rate using the organism's dry weight, based on the model of Peterson and Wroblewski (1984).

$$\text{Equation 2.8 } HM = 2.196 * 10^{-4} * DW_g^{-0.25}$$

HM is the hourly weight-specific mortality rate (hr^{-1}), and DW_g is the dry weight of the animal (g). This was converted into a mortality flux using the following equation:

Equation 2.9 $M_{flux} = HM * DW_{\mu g} * CR * TD$

M_{flux} is the daily mortality flux, $DW_{\mu g}$ is the dry weight of the animal (μg), CR is the carbon weight to dry weight ratio, and TD is the number of hours per day the organism spends at depth, assumed to be 12.6 hours per day as described above. During the 2004 *Oscar Elton Sette* cruise, the carbon weight to dry weight ratio for pelagic decapods captured off the coast of Hawaii was measured to be 0.42, so this value was used for the CR.

Gut flux was estimated primarily using **Equation 3.8** from the second chapter of this thesis. This equation was derived from pelagic decapods captured during the 2004 *Oscar Elton Sette* cruise, and predicts stomach content dry weight based on organism dry weight and stomach fullness.

Equation 3.8 $FB_{DW} = 0.020 * Org_{DW} * Fullness$

FB_{DW} is the food ball dry weight (mg), Org_{DW} is the organism's dry weight (mg), and $Fullness$ is the visually estimated stomach fullness, expressed as a proportion. The food ball dry weight for all migratory individuals was determined using this equation and species specific values for peak night time stomach fullness. For those species where no stomach content data was obtained, the mean peak night time stomach fullness of 0.52 across all species was used. During the 2004 *Oscar Elton Sette* cruise, the carbon weight to dry weight ratio averaged across all potential prey species captured (fish, squid, euphausiids and copepods) was measured to be 0.46, so this value was used to convert food ball dry weights to food ball carbon weights. It was assumed that the entire peak night time stomach content of migrant shrimp was carried from the euphotic to the mesopelagic zone, then ingested and evacuated at depth (Clarke, 1980). An

ingestion ratio of 88% for the stomach contents was assumed, so the estimate of peak food ball weight (in mg C) was multiplied by 0.12 to estimate the carbon weight of the egested material (Hopkins and Baird, 1977).

The above equations allow for respiratory, excretory, mortality and gut fluxes to be calculated for individual migratory organisms, but in order to calculate the carbon respired at depth for each species as a whole, it is necessary to define the migratory community for each species. In most studies the migratory community is measured as either the community moving out of the epipelagic during the day, or as the community moving up from the mesopelagic during the night, with the most common measurement being the night time epipelagic community minus the daytime epipelagic community, since defining the migratory community in this manner makes for the simplest sampling procedure, as only the epipelagic needs to be sampled. In this study, however, the full distribution of all species during both the day and night was sampled, so the active respiratory flux was calculated based on both the community moving out of the surface and the community moving up from depth. These two calculated values of the active respiratory flux were then averaged. The portion of the community migrating (and thus contributing to all active fluxes) was defined as the abundance migrating to the surface at night divided by the total night time abundance at surface and depth.

2.2.6 Comparison to passive flux

Once active fluxes were determined for each species, it was necessary to combine these fluxes into one value for comparison with the passive flux. Active fluxes for each species were

summed, and a weighted average taken to determine the mean depth that carbon was transported to. Weighting was based on the size of the active flux, for example, if “Species A” migrated to a daytime WMD of 800 m, with a total active flux of 90 $\mu\text{gC}/\text{m}^2/\text{day}$, while “Species B” migrated to a daytime WMD of 700 m, with a total active flux of 10 $\mu\text{gC}/\text{m}^2/\text{day}$, there would be a total of 100 $\mu\text{gC}/\text{m}^2/\text{day}$ transported to a weighted mean depth of 790 m.

Once this overall daytime WMD was calculated for all species, the active flux to this depth was compared to the passive flux at the same depth. A 5-year time-series study performed at Station ALOHA found that, below the base of the euphotic zone, long-term passive carbon flux could be accurately modelled based on depth using the following equation (Karl et al., 1996):

$$\text{Equation 2.10 } PC\text{-FLUX}(Z) = 28.7 * (Z/150)^{-0.818}$$

Where PC-FLUX(Z) is the particulate carbon flux to a depth of Z meters, in $\text{mgC}/\text{m}^2/\text{day}$. The same study also found the base of the euphotic zone to be located at 173 ± 7 m, so **Equation 2.10** should only be used to predict passive carbon flux at Station ALOHA for depths greater than or equal to 173 m.

2.3 Results

2.3.1 Temperature and salinity

Temperatures at Station ALOHA remained steady at ~ 25.5 °C in the mixed layer (~ 0 -60 m), before rapidly declining in the thermocline, with temperatures declining to ~ 6.3 °C at the base of the thermocline (~ 530 m) (**Figure 2.3 a**). Temperatures continued to decline below the

thermocline, reaching ~ 2.9 °C at 1500 m (**Figure 2.3 a**). Salinity remained constant at ~ 35.1 PSU in the mixed layer, rising to ~ 35.3 PSU at ~ 100 m, before falling rapidly to ~ 34.0 PSU at the base of the halocline (~ 500 m) (**Figure 2.3 b**).

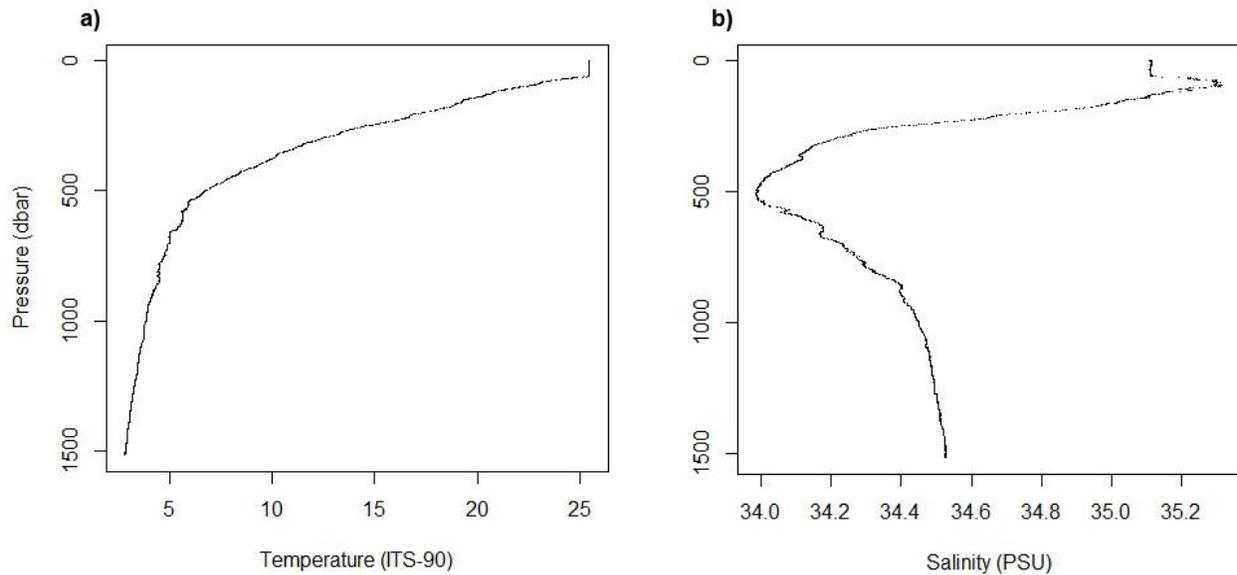


Figure 2.3 Typical daytime **a)** temperature and **b)** salinity profiles at Station ALOHA during the 2011 *R/V Kilo Moana* cruise

Temperature and salinity profiles at Station Kahe were highly similar to those found at Station ALOHA. The main differences were lower salinity in the mixed layer at Station Kahe (34.5 PSU at Station Kahe compared to 35.1 PSU at Station ALOHA), and a shallower base of the thermocline (490 m at Station Kahe compared to 530 m at Station ALOHA) (**Figure 2.4**).

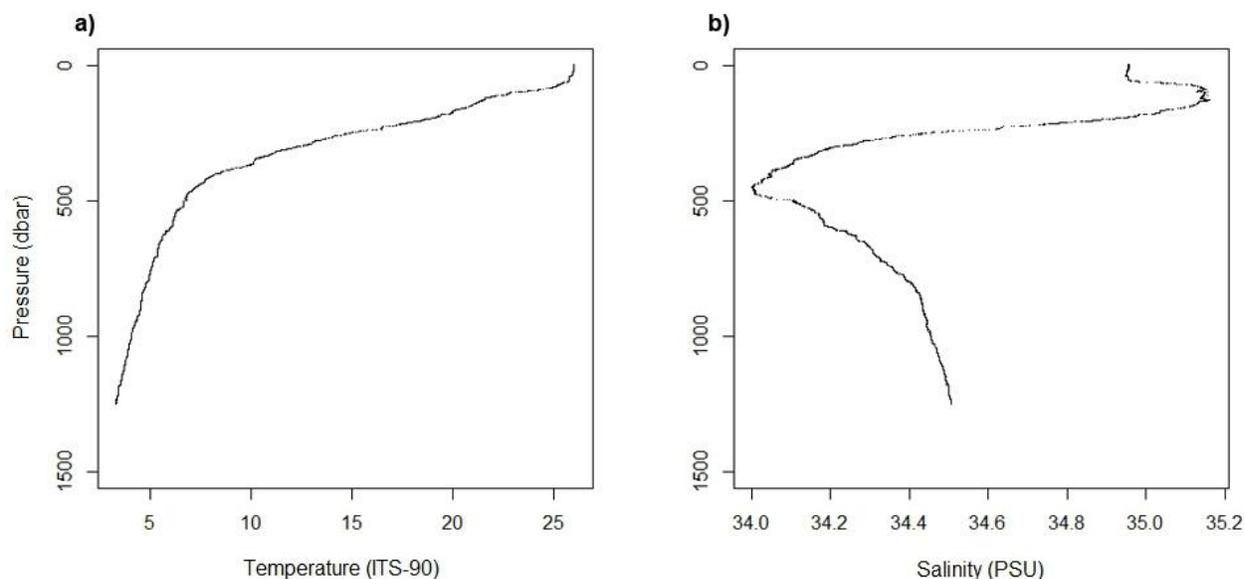


Figure 2.4 Typical daytime **a)** temperature and **b)** salinity profiles at Station ALOHA during the 2011 *R/V Kilo Moana* cruise

2.3.2 Pelagic decapod diversity

Diversity of pelagic decapods was extremely high at the sites sampled, with a total of 40 taxonomic groups identified. Most specimens were identified to the species level, and all were identified to at least the genus level. A full list of all 40 pelagic decapod species/genera collected on this cruise can be found in **Table 2.3**. In total 21 genera and 5 families were represented (Oplophoridae, Pasiphaeidae, Penaeidae, Sergestidae and Sicyoniidae). All species for which fewer than 10 individuals were caught were excluded from the analysis of fluxes, as any estimates of abundance and biomass at different depths would have been unreliable due to the small sample sizes. *Sergia spp.* larvae were also excluded from the analysis, as they were relatively rare (**Table 2.3**), and all were caught at the same depth. In total 22 species/groups were included in the analysis.

2.3.3 Biomass and abundance

A highly significant linear relationship (2×10^{-16} ($t = 140.9$, $df = 479$), and an R^2 of 0.9764) was determined between wet weight and dry weight, based on samples from the 2004 *Oscar Elton Sette* cruise, for all shrimp and prawn species that were found to perform significant diel vertical migrations (**Figure 2.5**).

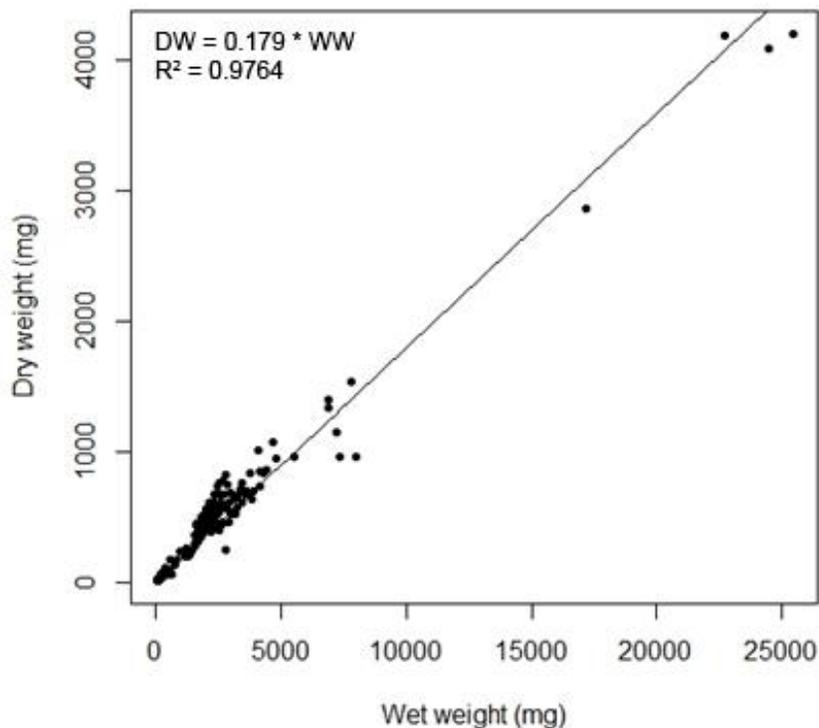


Figure 2.5 Wet weight (mg) vs. dry weight (mg) for all pelagic decapods found to perform significant diel vertical migrations

This relationship was described by the following equation:

Equation 2.11 $DW = 0.179 * WW$

Where DW is the dry weight (mg), and WW is the wet weight (mg).

Equation 2.11 implies a water content of 82.1%, and using this water content in **Equation 2.1** gave a dry mass loss of 26.4%. Thus before preservation in formalin, the decapods

would have had a dry weight 35.9% higher than measured after preservation, as $1/(1 - 0.264) = 1.359$. After all dry weights were corrected for dry mass loss, **Equation 2.2** ($DW = a*CL^b$) was used to describe the relationship between carapace lengths and corrected dry weights for each of the 22 pelagic decapod species analysed in this study. For all species the relationship was significant ($p < 0.0001$) (**Table 2.2**).

Table 2.2 Relationship between carapace length and corrected dry weights for all pelagic decapod species found to perform diel vertical migrations. “a” and “b” are constants derived by regression analysis for the equation $DW = a*CL^b$, where DW is corrected dry weight in mg, and CL is carapace length in mm.

Species	Relationship based on	a	b	p-value	r ²
<i>Acantheephyra smithi</i> *	DW	0.2862	2.7956	<0.0001	0.968
<i>Allosergestes pectinatus</i>	WW	0.1415	2.7634	<0.0001	0.849
<i>Allosergestes sargassi</i>	WW	0.4947	2.0937	<0.0001	0.950
<i>Deosergestes erectus</i>	WW	0.0575	2.8279	<0.0001	0.997
<i>Gennadas spp.</i> **	DW	0.7724	2.2225	<0.0001	0.949
<i>Janicella spinicauda</i>	DW	0.3375	2.6935	<0.0001	0.708
<i>Neosergestes consobrinus</i>	WW	0.0450	3.2939	<0.0001	0.955
<i>Neosergestes orientalis</i>	DW	0.2956	2.3369	<0.0001	0.792
<i>Notostomus elegans</i> ***	DW	0.0121	3.4175	<0.0001	0.987
<i>Parasergestes armatus</i>	DW	0.0743	2.8101	<0.0001	0.893
<i>Sergestes atlanticus</i>	WW	0.0421	3.2794	<0.0001	0.993
<i>Sergia bigemmeus</i>	WW	0.1345	2.8011	<0.0001	0.993
<i>Sergia gardineri</i>	DW	0.6103	2.1930	<0.0001	0.820
<i>Sergia scintillans</i>	DW	0.2389	2.5427	<0.0001	0.778
<i>Stylopandalus richardi</i>	DW	0.1108	3.1685	<0.0001	0.907
<i>Systellaspis debilis</i>	WW	0.0985	3.1415	<0.0001	0.990

* Also used for *Acantheephyra curtirostris*

** Used for all *Gennadas* species (*bouvieri*, *clavicularpus*, *capensis*, *incertus* and *tinayrei*)

*** Used for *Notostomus gibbosus*

Individuals captured in the 2004 cruise were used to derive these length-weight relationships, and in a few cases the species caught in 2004 were not represented in 2011 and vice versa. *Acantheephyra curtirostris* was not caught in 2011, but was caught in 2004, so the length-weight relationship for *Acantheephyra smithi* was used for *Acantheephyra curtirostris*, as the two species are very similar in terms of their external morphology. Likewise, the length-weight relationship for *Notostomus elegans* was used as a proxy for *Notostomus gibbosus*,

which was not caught in 2004. Finally, one length-weight relationship was used for all *Gennadas* species, as the external morphology of all species are virtually identical, differing significantly only in the structure of their reproductive organs, so length-weight relationships can be expected to be very similar for all species. Also indicated in **Table 2.2** is whether this relationship was derived from direct measurements of dry weight, or from measurements of wet weight that were then converted to dry weights using **Equation 2.11**.

It was deemed unnecessary to explicitly show all the data from which the length-weight relationships in **Table 2.1** were derived. Instead the data for just one typical species (*Stylopandalus richardi*) is shown, to give an idea of the shape of the data, and the applicability of the $DW = a * CL^b$ model (**Figure 2.6**).

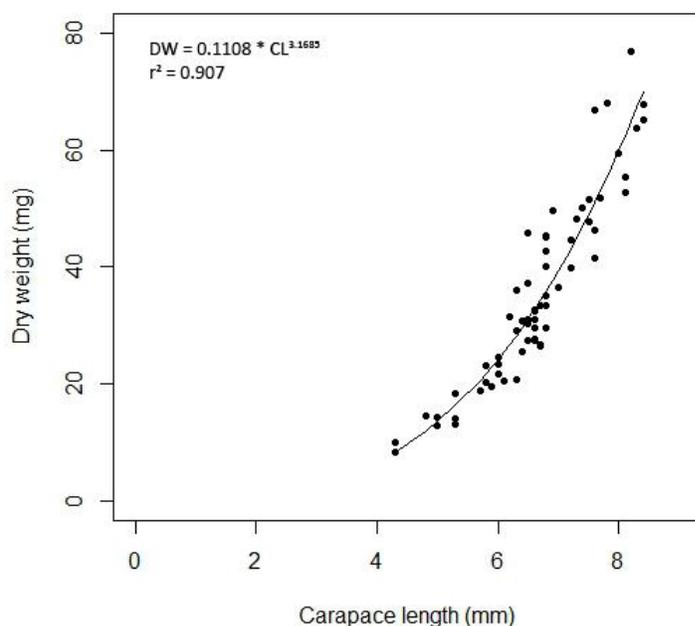


Figure 2.6: Carapace length vs. corrected dry weight for *Stylopandalus richardi*

The carapace length to dry weight relationships for each species shown in **Table 2.2** were used to calculate the total biomass and the mean dry weight per individual for each species included in the analysis (**Table 2.3**). *Notostomus gibbosus* was the largest decapod, and made up the most biomass, while *Gennadas bouvieri* was the most abundant.

Table 2.3 All pelagic decapod species caught on the 2011 *R/V Kilo Moana* cruise. Abundance and biomass values listed for each species are the mean of daytime and night time estimates.

Species	Number of individuals caught	Included in analysis?	Mean dry weight per individual (mg)	Abundance (organism/m ²)	Biomass (mg/m ²)
<i>AcanthePHYra curtirostris</i>	41	Yes	209.16	0.256	56.438
<i>AcanthePHYra smithi</i>	17	Yes	626.34	0.0934	59.287
<i>Allosergestes pectinatus</i>	38	Yes	12.10	0.152	1.771
<i>Allosergestes sargassi</i>	10	Yes	31.32	0.049	1.571
<i>Deosergestes erectus</i>	26	Yes	154.26	0.146	25.253
<i>Gennadas bouvieri</i>	95	Yes	84.96	0.481	41.773
<i>Gennadas capensis</i>	48	Yes	94.27	0.331	35.780
<i>Gennadas clavicarpus</i>	33	Yes	67.76	0.121	8.265
<i>Gennadas incertus</i>	13	Yes	50.70	0.071	3.694
<i>Gennadas spp.</i>	80	Yes	58.98	0.372	22.496
<i>Gennadas tinayrei</i>	10	Yes	51.45	0.048	2.753
<i>Janicella spinicauda</i>	18	Yes	40.15	0.105	4.3779
<i>Neosergestes consobrinus</i>	26	Yes	10.56	0.132	1.426
<i>Neosergestes orientalis</i>	29	Yes	29.76	0.146	4.202
<i>Notostomus gibbosus</i>	23	Yes	1746.01	0.166	275.861
<i>Parasergestes armatus</i>	44	Yes	67.76	0.278	19.117
<i>Sergestes atlanticus</i>	19	Yes	25.55	0.073	1.719
<i>Sergia bigemmeus</i>	17	Yes	77.72	0.118	10.544
<i>Sergia gardineri</i>	117	Yes	35.62	0.560	20.376
<i>Sergia scintillans</i>	24	Yes	45.60	0.092	4.120
<i>Stylopandalus richardi</i>	28	Yes	65.76	0.167	12.171
<i>Systellaspis debilis</i>	28	Yes	362.29	0.151	54.920
<i>AcanthePHYra prionota</i>	4	No	212.83	n/a	n/a
<i>AcanthePHYra sp. larvae</i>	7	No	53.22	n/a	n/a
<i>Bentheogennema sp.</i>	4	No	164.97	n/a	n/a
<i>Funchalia taaningi</i>	3	No	401.31	n/a	n/a
<i>Glyphus sp.</i>	2	No	35.35	n/a	n/a
<i>Heterocarpus ensifer parvispina</i>	1	No	113.15	n/a	n/a
<i>Meningodora marptocheles</i>	1	No	283.94	n/a	n/a
<i>Oplophoridae sp. larvae</i>	3	No	15.48	n/a	n/a
<i>Oplophorus gracilirostris</i>	4	No	824.93	n/a	n/a
<i>Parapasiphae sulcatifrons</i>	1	No	476.44	n/a	n/a
<i>Parasergestes vigilax</i>	4	No	16.40	n/a	n/a
<i>Penaeidae sp.</i>	7	No	40.22	n/a	n/a
<i>Petalidium sp.</i>	3	No	31.08	n/a	n/a
<i>Sergia bisulcatus</i>	3	No	534.03	n/a	n/a
<i>Sergia inequalis</i>	4	No	272.13	n/a	n/a
<i>Sergia spp.larvae</i>	12	No	56.50	n/a	n/a
<i>Sergia tenuiremis</i>	4	No	475.53	n/a	n/a
<i>Sicyonia sp.</i>	1	No	148.50	n/a	n/a

2.3.4 Diel vertical migrations

Using Welch's 2-sample t-test, it was determined that there was no evidence of significant diel vertical migrations for 3 of the species (**Table 2.4**). For 6 species the entire population migrated upwards at night, and for the remaining 13 species there were partial migrations, with a portion of the population migrating up at night, but part of the population remaining at depth (**Table 2.4**).

Table 2.4 Diel migratory data for all pelagic decapod species in this study. For all species, daytime and night time Weighted Mean Depth (WMD) for the entire population (ppln) are provided. For the partially migratory species, the night time WMD for only the portion that migrates is also provided. Results of Welch's 2-sample t-tests are provided for each species (t, df, p), with the test comparing daytime WMDs to night time WMDs for the whole populations.

Species	Day WMD (whole ppln, m)	Night WMD (whole ppln, m)	t	df	p	Percent of population migrating	Night WMD (migratory portion, m)
Species for which the entire population migrates							
<i>AcanthePHYra smithi</i>	677.98	370.01	3.53	15.45	0.003	100	n/a
<i>Allosergestes sargassi</i>	475.00	234.64	5.02	7.89	0.001	100	n/a
<i>Gennadas bouvieri</i>	803.25	459.17	11.00	81.33	<0.001	100	n/a
<i>Gennadas incertus</i>	898.08	247.79	12.61	8.55	<0.001	100	n/a
<i>Neosergestes orientalis</i>	507.52	113.15	18.26	7.89	<0.001	100	n/a
<i>Parasergestes armatus</i>	561.64	281.15	3.86	17.31	0.001	100	n/a
Species for which part of the population migrates							
<i>Allosergestes pectinatus</i>	542.71	313.84	3.17	15.23	0.006	69.35	110.04
<i>Deosergestes erectus</i>	671.21	254.56	4.86	14.57	<0.001	92.24	167.28
<i>Gennadas capensis</i>	1102.69	540.71	6.69	39.68	<0.001	71.01	323.75
<i>Gennadas clavicarpus</i>	700.00	233.70	9.18	27.7	<0.001	78.67	114.26
<i>Gennadas spp.</i>	725.77	419.54	5.73	50.82	<0.001	49.64	107.16
<i>Gennadas tinayrei</i>	758.68	248.93	13.92	6.88	<0.001	80.41	120.77
<i>Janicella spinicauda</i>	482.64	185.68	24.88	9.00	<0.001	87.82	103.94
<i>Neosergestes consobrinus</i>	563.82	394.31	2.18	23.71	0.040	55.44	107.84
<i>Sergestes atlanticus</i>	591.96	193.85	3.95	3.99	0.017	88.22	116.28
<i>Sergia bigemmeus</i>	900.00	224.03	7.90	6.22	<0.001	89.67	149.05
<i>Sergia gardineri</i>	748.39	274.96	10.19	100.74	<0.001	76.43	113.36
<i>Sergia scintillans</i>	660.40	261.13	6.55	19.00	<0.001	76.72	105.17
<i>Stylopandalus richardi</i>	571.59	194.81	5.84	14.96	<0.001	88.05	116.09
Non-migratory species							
<i>AcanthePHYra curtirostris</i>	973.77	922.9	0.50	13.13	0.627	0	n/a
<i>Notostomus gibbosus</i>	904.15	955.31	0.52	18.61	0.606	0	n/a
<i>Systellaspis debilis</i>	684.83	680.59	0.06	6.25	0.953	0	n/a

All 3 non-migratory species resided in the mesopelagic, none occurring in the epipelagic. Of the 6 fully migratory species, 5 had a night time WMD that was below the base of the euphotic zone, with only *Neosergestes consobrinus* migrating to within the euphotic zone (as stated in **Section 2.2.6**, the base of the euphotic zone at Station ALOHA is at ~173 m). In contrast, for the partially migratory species, 12 of the 13 species migrated to a WMD within the epipelagic, with only *Gennadas capensis* migrating to a WMD below the base of the euphotic zone.

Acanthephyra curtirostris, *Notostomus gibbosus* and *Systellaspis debilis* were all found to be non-migratory species according to t-tests (**Table 2.4**). *Acanthephyra curtirostris* and *N. gibbosus* resided at similar depths, with WMDs ranging from 904.15 – 973.77 m during both the day and night (**Figures 2.7 and 2.8**). *Systellaspis debilis* resided at shallower depths, with WMDs of 684.83 m during the day and 680.59 m during the night (**Figure 2.9**).

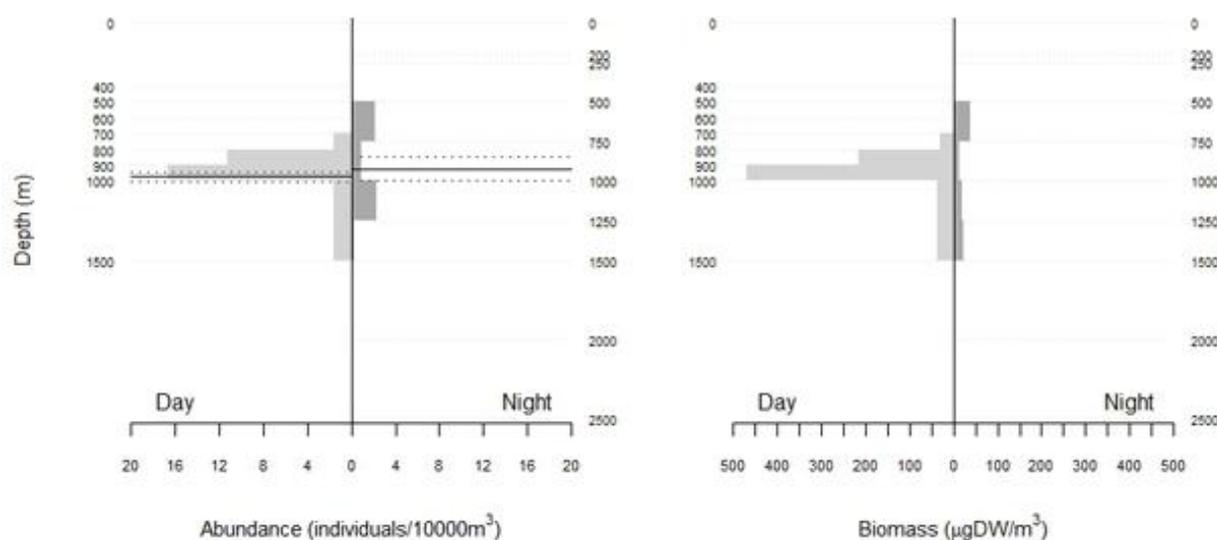


Figure 2.7 Abundance and biomass depth profiles for *Acanthephyra curtirostris*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

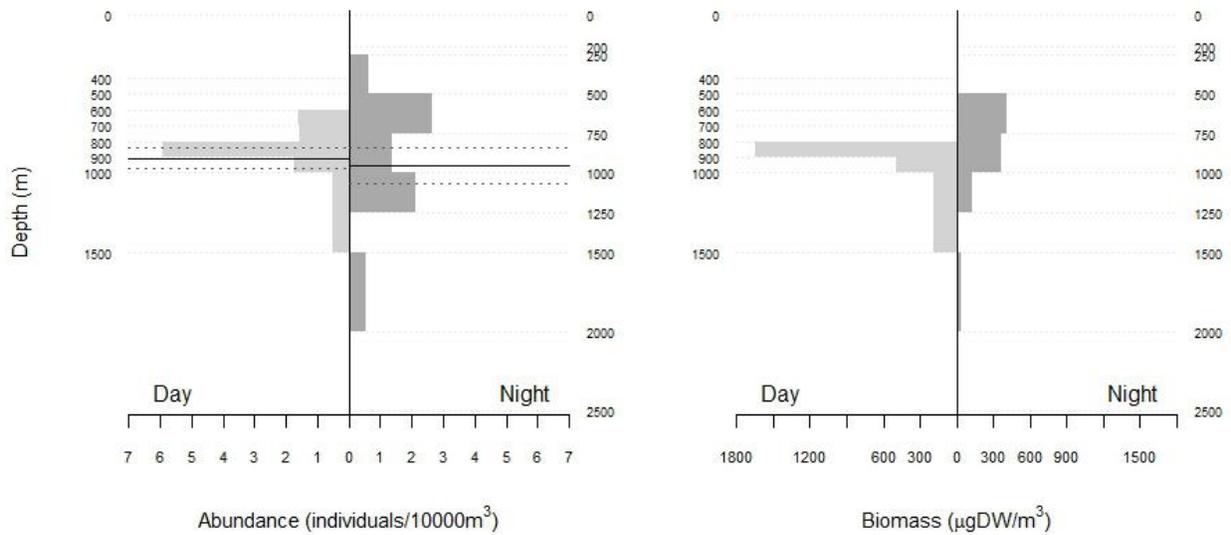


Figure 2.8 Abundance and biomass depth profiles for *Notostomus gibbosus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

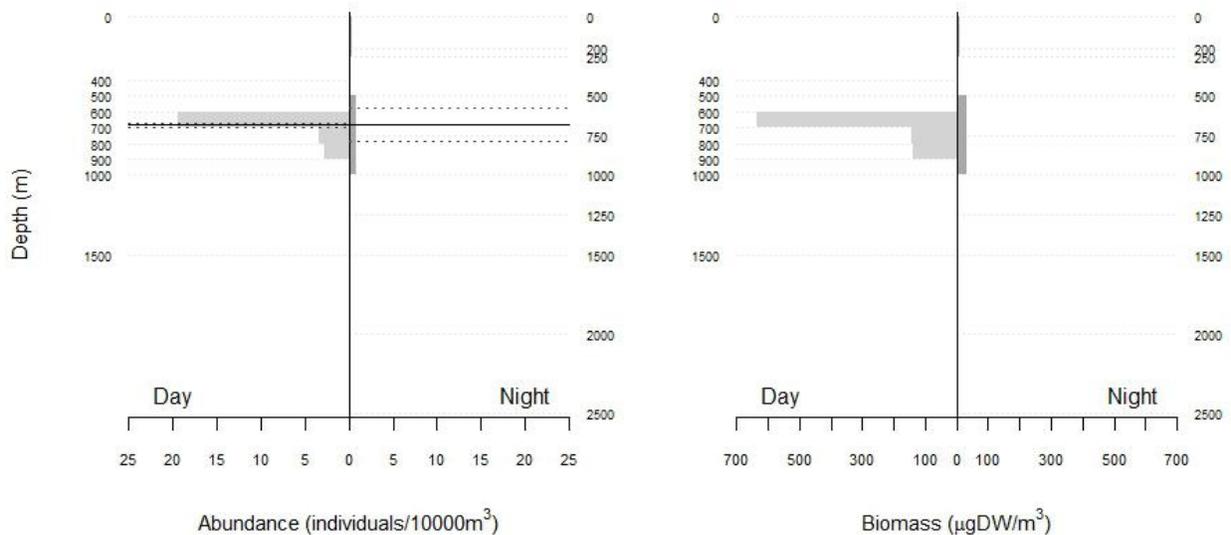


Figure 2.9 Abundance and biomass depth profiles for *Systellaspis debilis*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

Of the non-migratory decapods, *A. curtisostris* was the most abundant (a mean abundance of $0.256 \text{ individuals/m}^2$ between day and night estimates throughout the water column), but *N. gibbosus* made up the most biomass, with a mean biomass of 275.86 mgDW/m^2 between day and night estimates throughout the water column (**Table 2.3**). All non-

migratory species were relatively large (*A. curtirostris* being the smallest with an average mass of 220.43 mgDW/individual), and all belonged to the family Oplophoridae (**Table 2.3**).

Acanthephyra smithi, *Allosergestes sargassi*, *Gennadas bouvieri*, *Gennadas incertus*, *Neosergestes orientalis* and *Parasergestes armatus* were all found to be migratory species according to t-tests (**Table 2.3**). For all six species, the entire population migrated towards the surface at night. Of these, *G. bouvieri* and *G. incertus* resided at the deepest depths during the day, at 803.25 m and 898.08 m respectively (**Figures 2.10** and **2.11**).

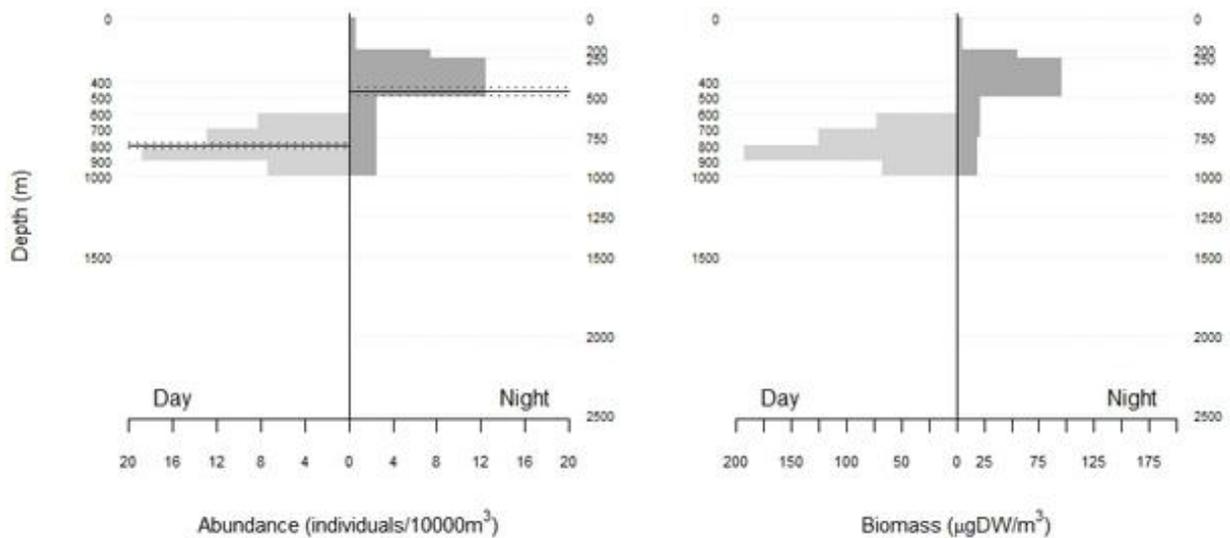


Figure 2.10 Abundance and biomass depth profiles for *Gennadas bouvieri*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

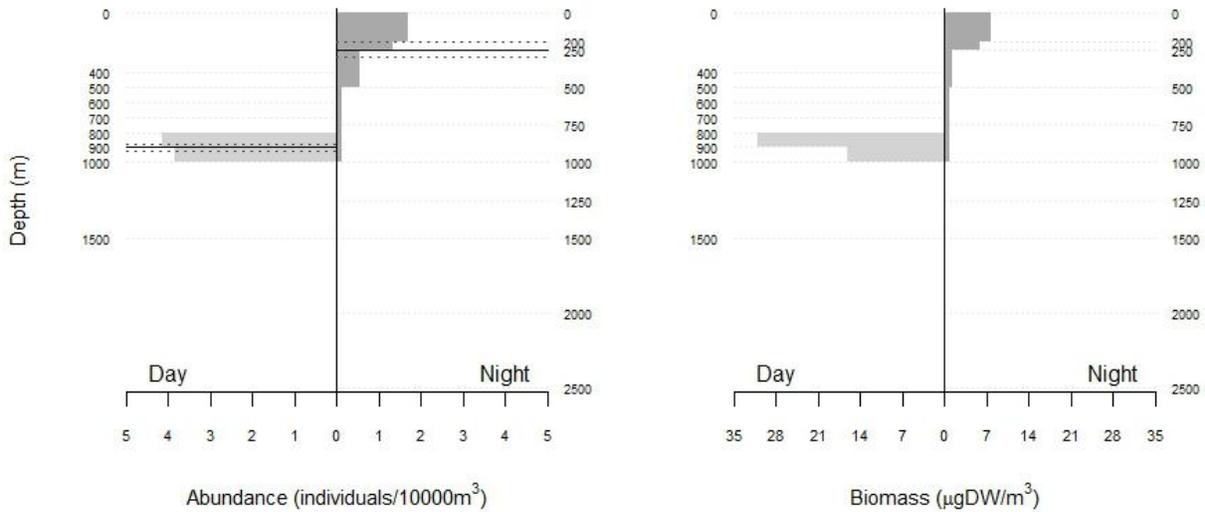


Figure 2.11 Abundance and biomass depth profiles for *Gennadas incertus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

Acanthephyra smithi resided at a shallower daytime depth of 677.98 m (**Figure 2.12**), while *A. sargassi*, *N. orientalis* and *P. armatus* resided at the shallowest daytime depths, at 475.00 m, 507.52 m and 561.64 m respectively (**Figures 2.13, 2.14 and 2.15**). Of all six fully migratory species, only *N. orientalis* migrated into the euphotic zone during the night, with a night time WMD of 113.15 m (**Figure 2.14**). *Gennadas incertus*, *A. sargassi* and *P. armatus* migrated to just below the base of the euphotic zone, with day time WMDs of 234.64 m, 247.79 m, and 281.15 m (**Figures 2.11, 2.13 and 2.14**).

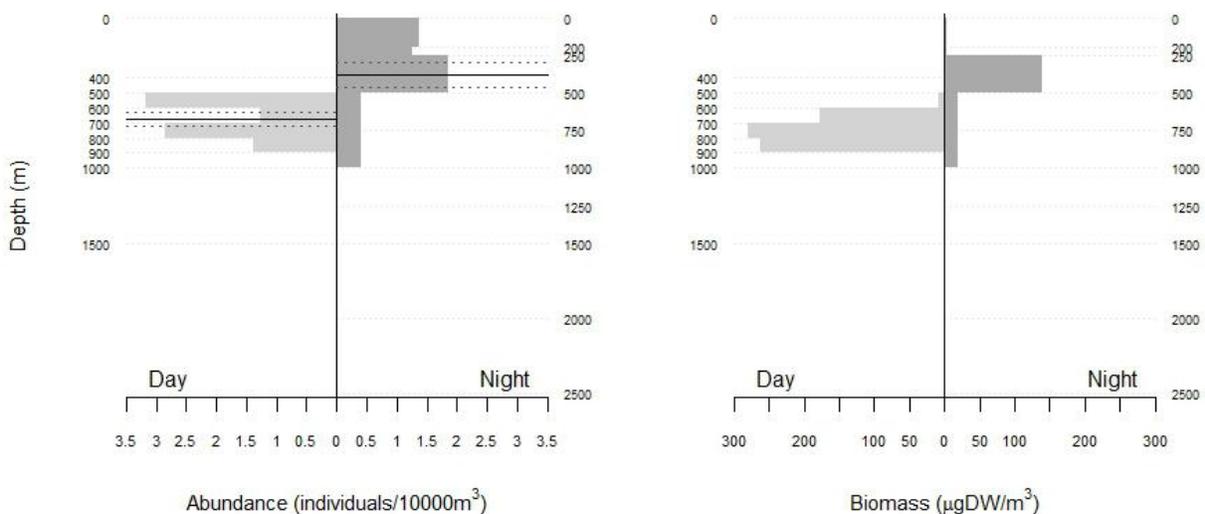


Figure 2.12 Abundance and biomass depth profiles for *Acanthephyra smithi*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

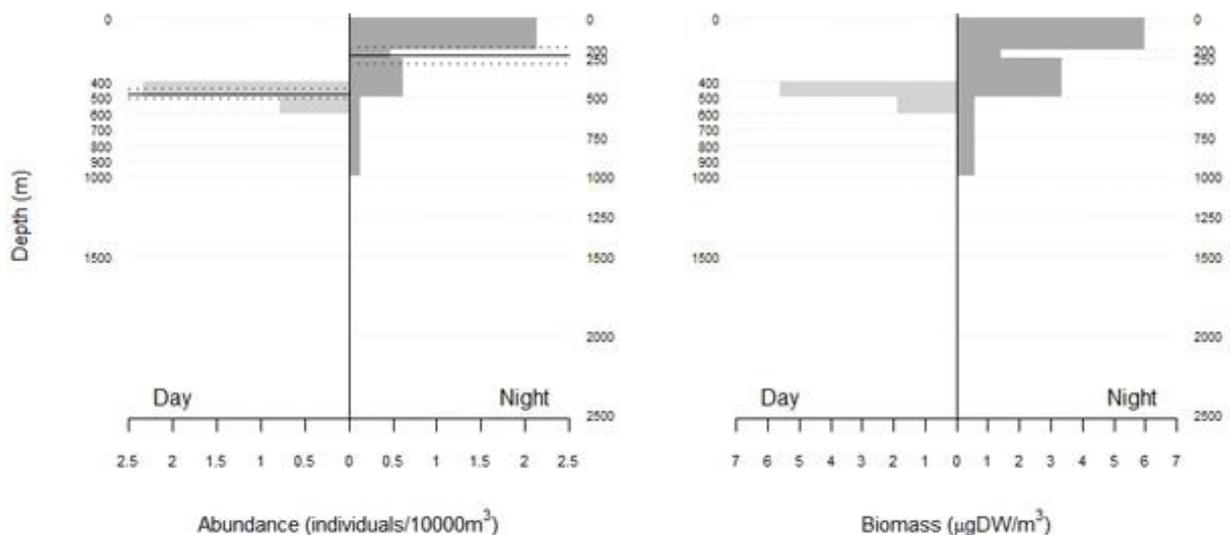


Figure 2.13 Abundance and biomass depth profiles for *Allosergestes sargassi*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

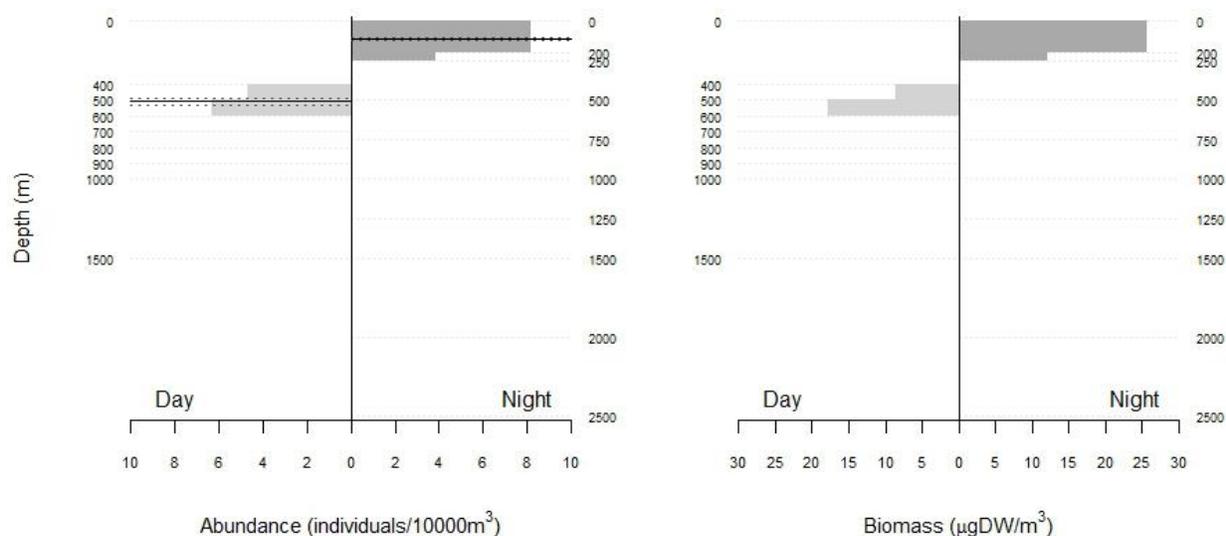


Figure 2.14 Abundance and biomass depth profiles for *Neosergestes orientalis*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

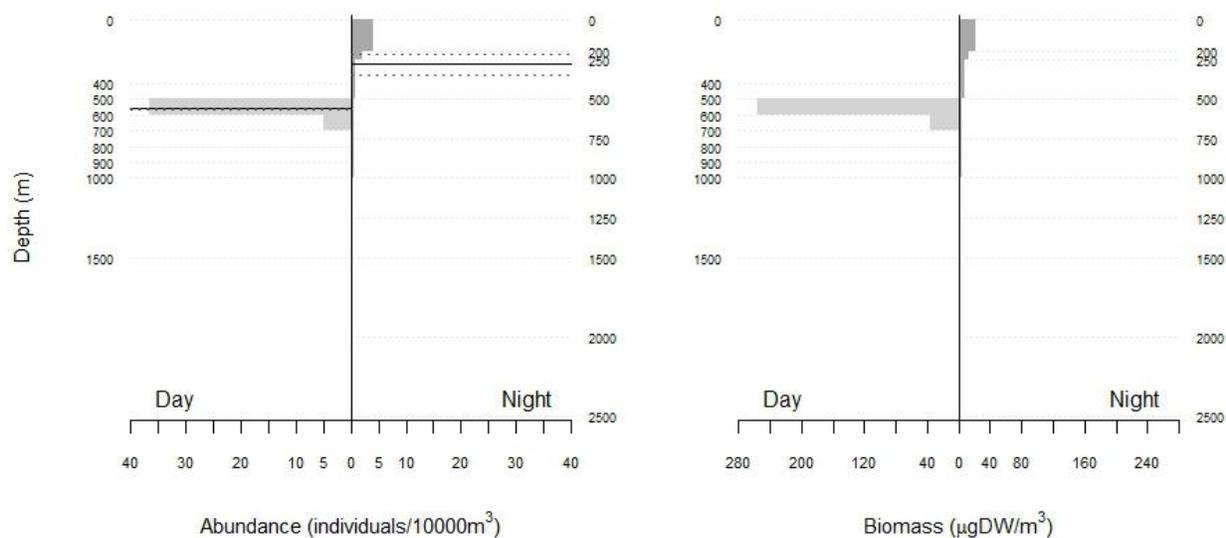


Figure 2.15 Abundance and biomass depth profiles for *Parasergestes armatus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors.

Of the fully migratory species, *G. bouvieri* was the most abundant (0.481 individuals/m²), while *A. smithi* had the highest biomass, at 59.29 µgDW/m², as well as the highest biomass per individual (634.54 µgDW/individual) (**Table 2.3**). Unlike the non-migratory species, which all belonged to the family Opolophoridae, the fully migratory species were

taxonomically diverse, with 1 species from the family Opolophoridae (*A. smithi*), 2 species from the family Benthescycmidae (*G. bouvieri* and *G. incertus*), and 3 species from the family Sergestidae (*A. sargassi*, *N. orientalis*, and *P. armatus*). Other than *A. smithi*, all were of a small to moderate size, ranging from 28.74 mgDW/individual for *N. orientalis*, to 86.78 mgDW/individual for *G. bouvieri* (**Table 2.3**).

Allosergestes pectinatus, *Deosergestes erectus*, *Gennadas capensis*, *Gennadas clavicornis*, *Gennadas spp.*, *Gennadas tinayrei*, *Janicella spinicauda*, *Neosergestes consobrinus*, *Sergestes atlanticus*, *Sergia bigemmus*, *Sergia gardineri*, *Sergia scintillans*, and *Stylopandalus richardi* were all found to be migratory species, according to t-tests (**Table 2.4**). All were partially migratory species, showing bimodal night time distributions, with a portion of the population migrating towards the surface at night, and a portion remaining at the day time depth. Of these, only *G. capensis* migrated to a night time depth below the base of the euphotic zone (WMD 323.75 m) (**Figure 2.16**).

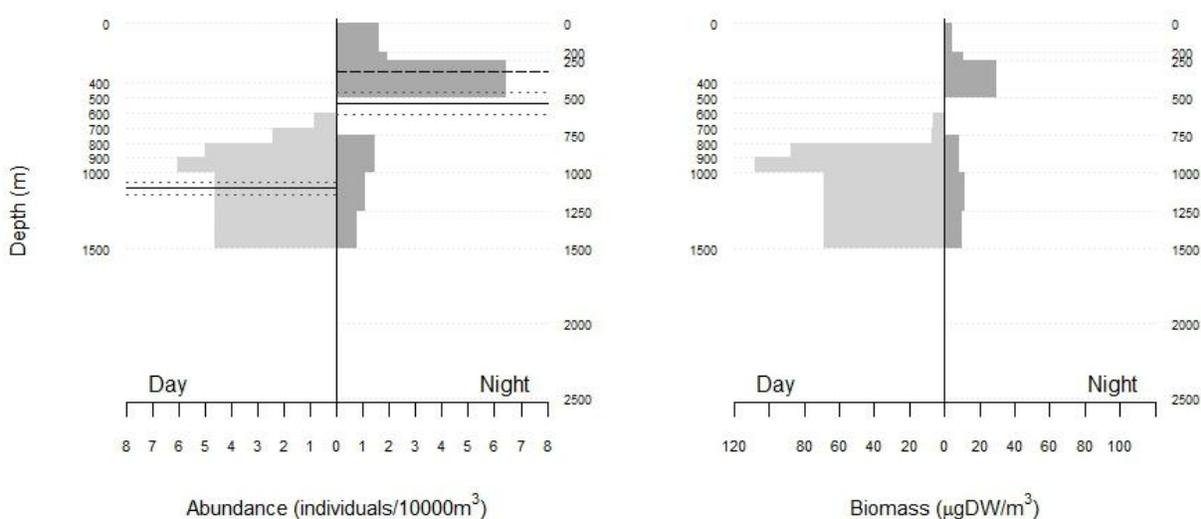


Figure 2.16 Abundance and biomass depth profiles for *Gennadas capensis*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

The other three members of the genus *Gennadas*, *G. clavicarpus*, *G. tinayrei*, and *G. spp.* (damaged individuals that could not be identified to the species level) all showed similar migratory patterns, migrating from daytime depths of 700.00 – 758.68 m to night time depths of 107.16 – 120.77 m (Figures 2.17, 2.18 and 2.19).

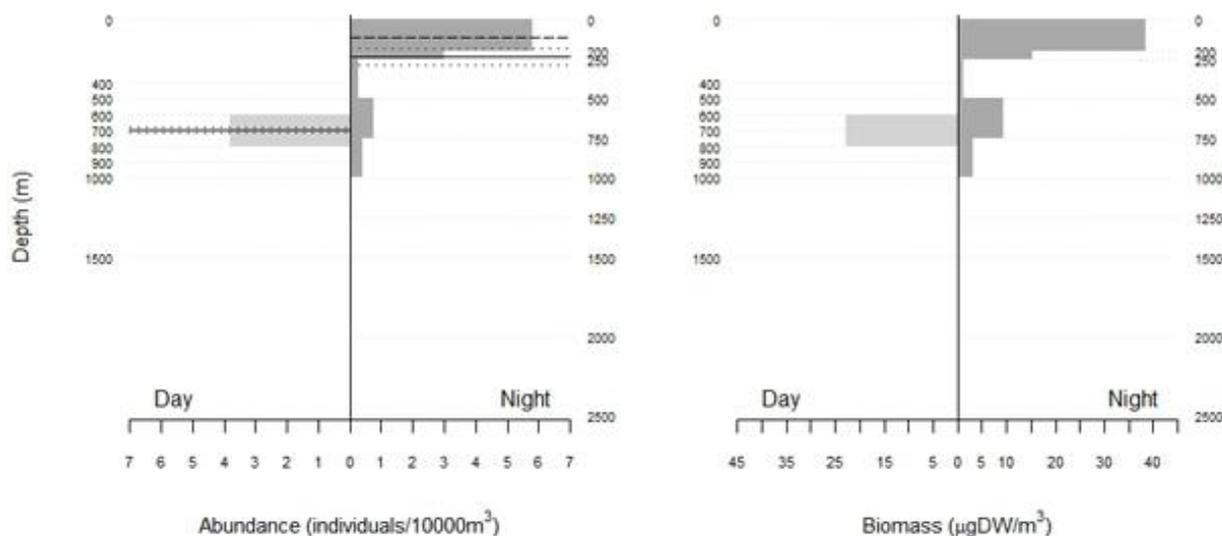


Figure 2.17 Abundance and biomass depth profiles for *Gennadas clavicarpus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

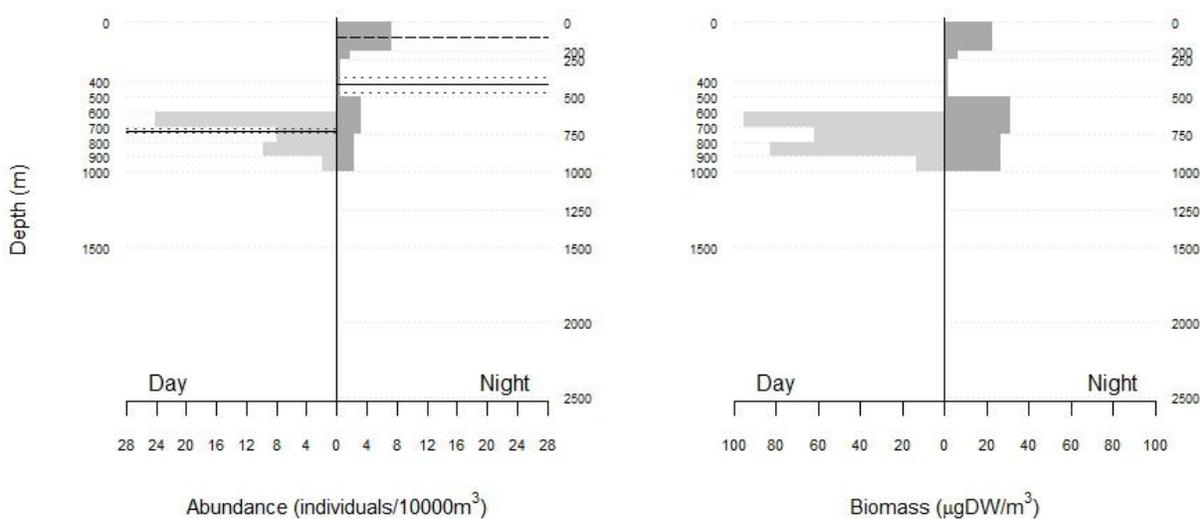


Figure 2.18 Abundance and biomass depth profiles for *Gennadas spp.* For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

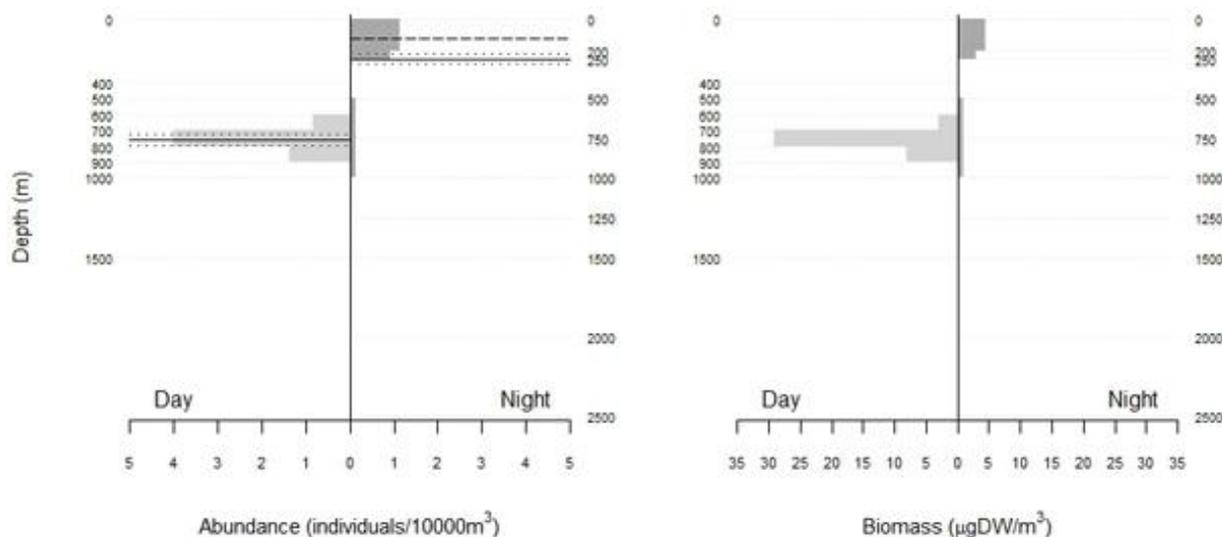


Figure 2.19 Abundance and biomass depth profiles for *Gennadas tinayrei*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

The three members of the genus *Sergia* displayed differing migratory distributions.

While all three were partial migrators migrating to similar depths within the euphotic zone at night, *S. bigemmeus* resided at 900.00 m during the day, while *S. gardineri* resided at 748.39 m, and *S. scintillans* resided at 660.4 m (**Figures 2.20, 2.21 and 2.22**).

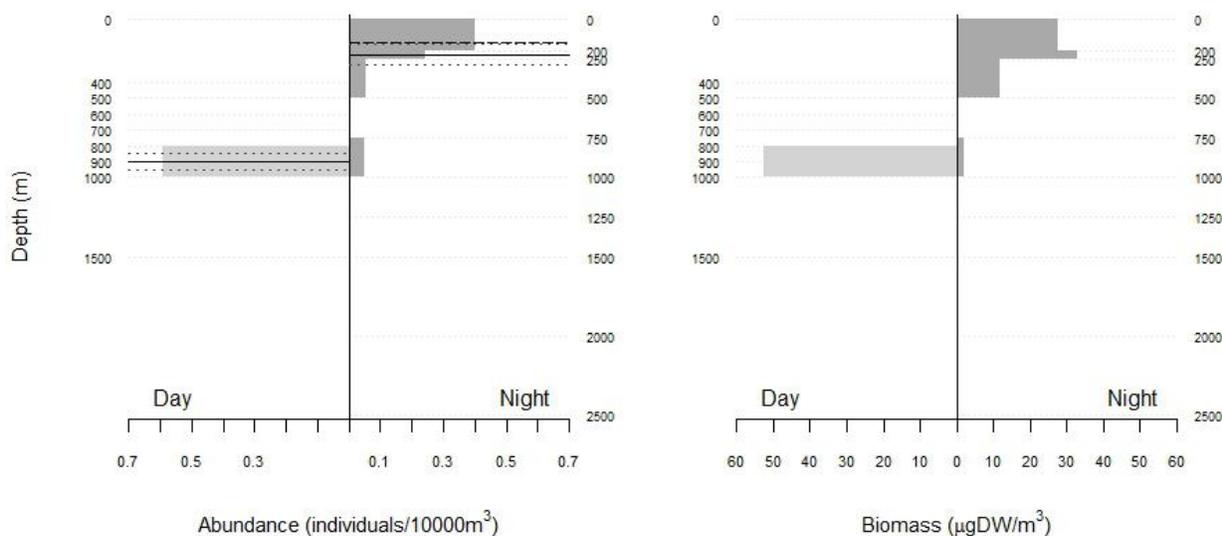


Figure 2.20 Abundance and biomass depth profiles for *Sergia bigemmeus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

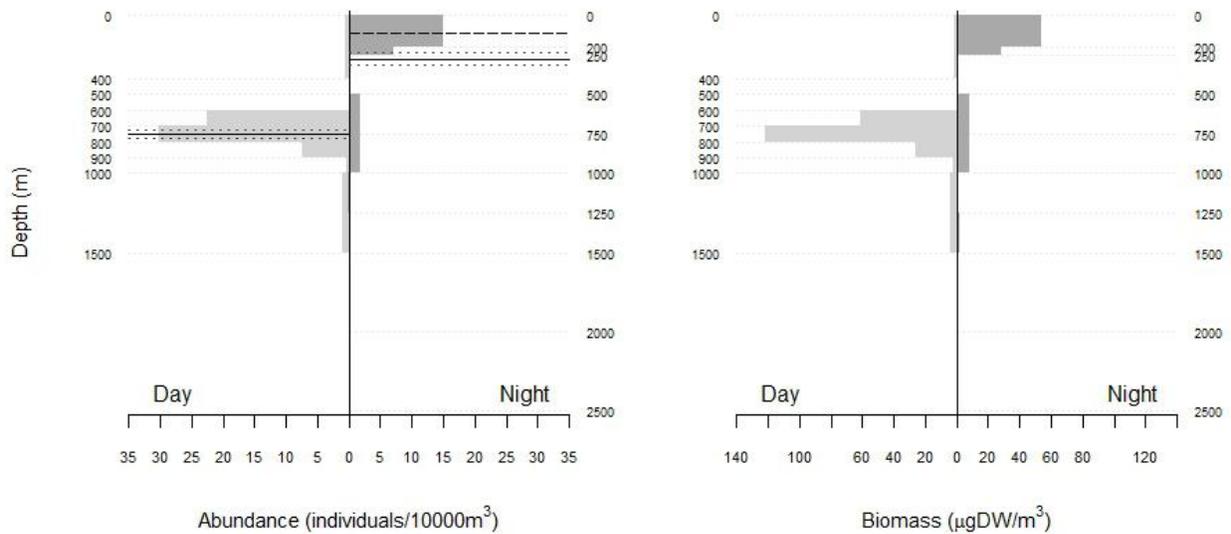


Figure 2.21 Abundance and biomass depth profiles for *Sergia gardineri*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

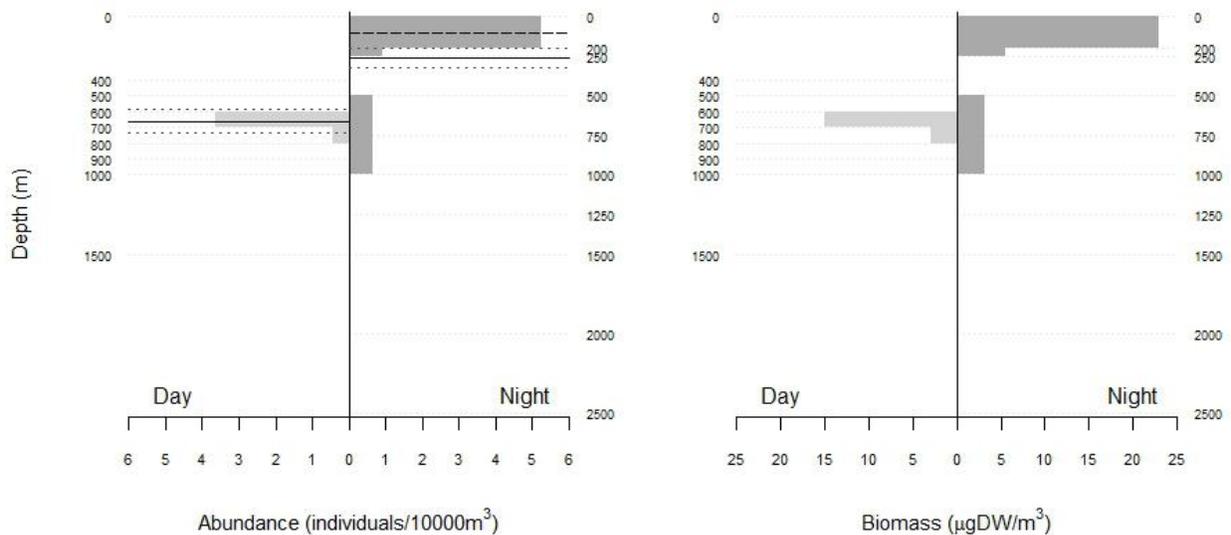


Figure 2.22 Abundance and biomass depth profiles for *Sergia scintillans*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

In contrast to decapods of the genus *Sergia*, decapods of the now defunct genus *Sergestes* displayed similar migratory distributions. While the genus *Sergestes* has been recently re-classified into six separate genera (*Allosergestes*, *Deosergestes*, *Eusergestes*,

Neosergestes and *Parasergestes*) (Judkins and Kensley, 2008), the genera remain closely linked in terms of external anatomy, and this appears to be reflected in their migratory distributions. *Allosergestes pectinatus*, *N. consobrinus* and *S. atlanticus* are all particularly similar in their distributions, all migrate to 107.84 – 116.28 m during the night, and to depths of 542.71 – 591.96 m during the day (Figures 2.23, 2.24 and 2.25).

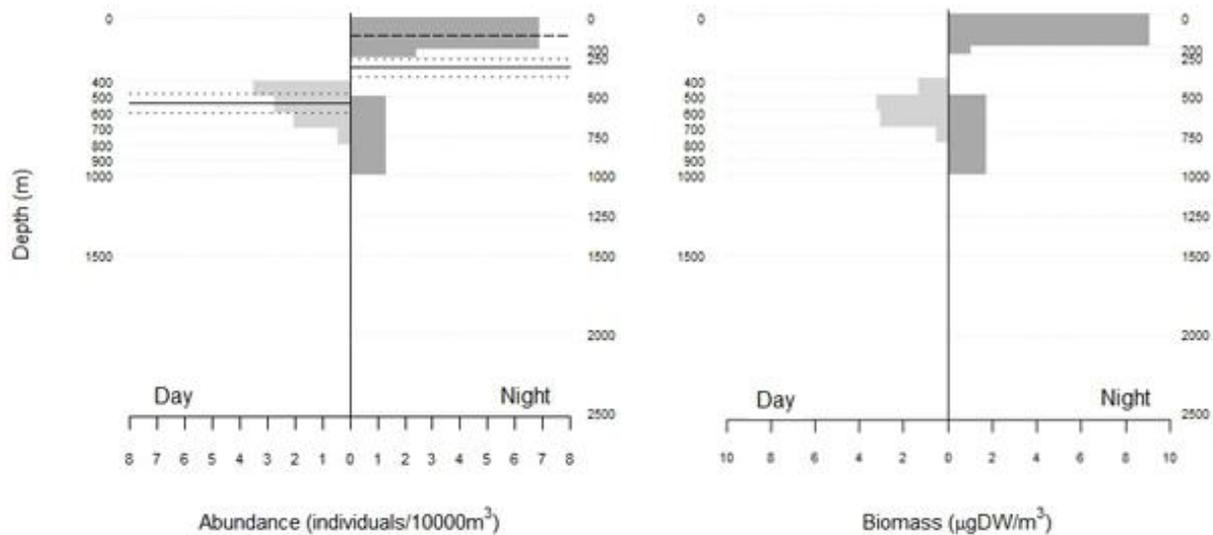


Figure 2.23 Abundance and biomass depth profiles for *Allosergestes pectinatus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

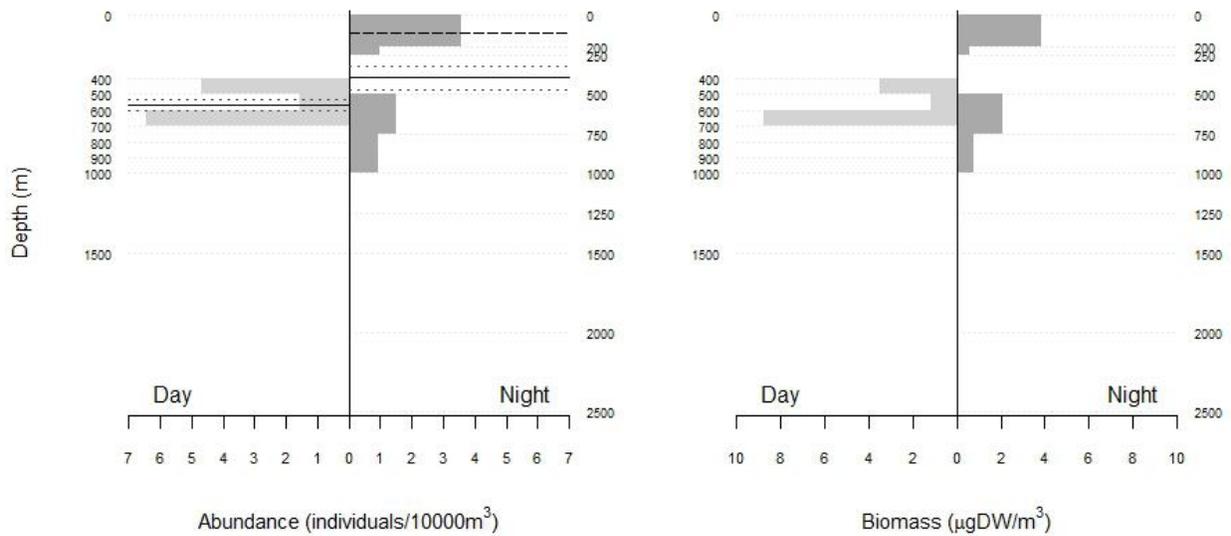


Figure 2.24 Abundance and biomass depth profiles for *Neoseргestες consobrinus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

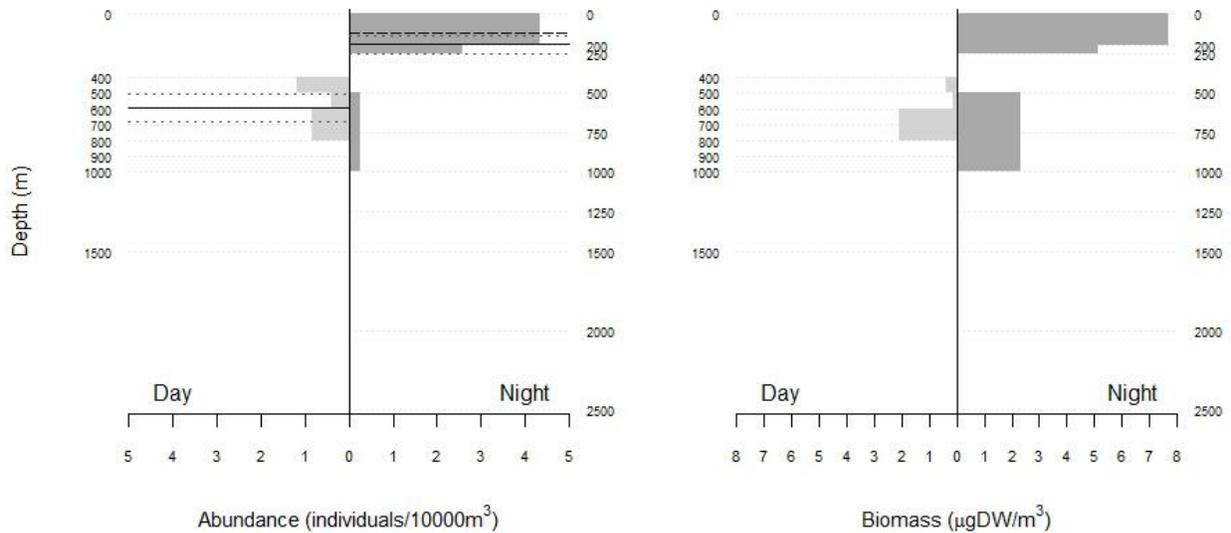


Figure 2.25 Abundance and biomass depth profiles for *Sergestες atlanticus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

In contrast to the virtually identical distributions for *A. pectinatus*, *N. consobrinus* and *S. atlanticus*, *D. erectus* was found at deeper depths during both the day and night (671.21 m during the day, 167.28 m at night) (**Figure 2.26**). It should be noted that *D. erectus* is a much

larger species, while *A. pectinatus*, *N. consobrinus* and *S. atlanticus* had mean dry weights of 10.56 – 25.55 mg/individual, *D. erectus* had a mean dry weight of 154.26 mg/individual.

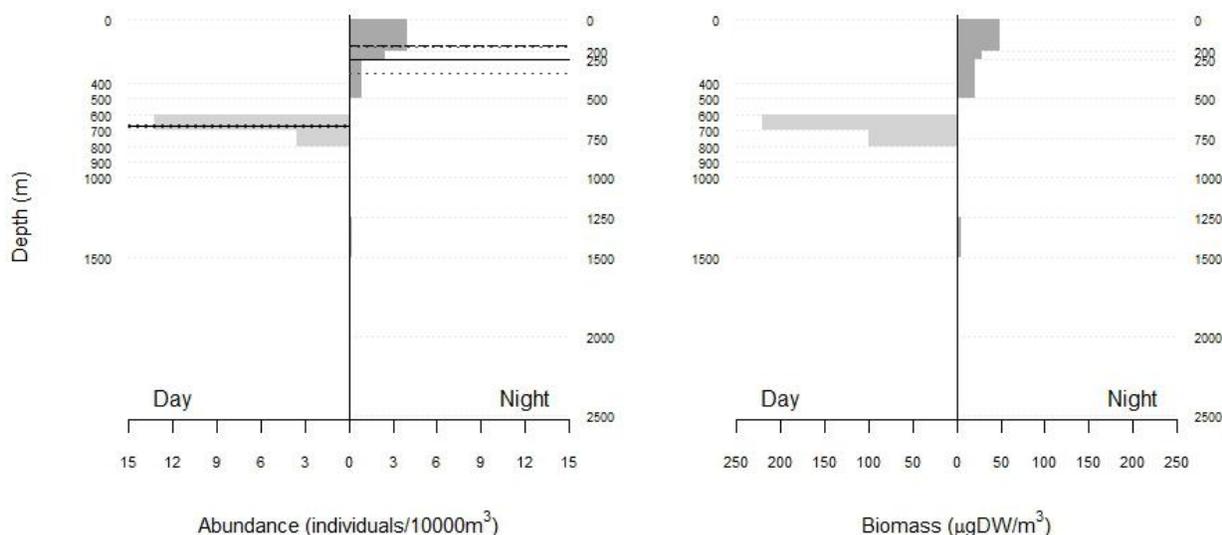


Figure 2.26 Abundance and biomass depth profiles for *Deosergestes erectus*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

The final two partially migratory species were *J. spinicauda*, of the family Ophlophoridae, and *S. richardi*, of the family Pandalidae. The two species displayed similar migratory distributions, with *J. spinicauda* having daytime and night time WMDs of 482.64 m and 103.94 m respectively, and *S. richardi* having daytime and night time WMDs of 571.59 m and 116.09 m respectively (**Figures 2.27** and **2.28**). Both were of similar size, *J. spinicauda* averaging 40.15 mg DW/individual, and *S. richardi* averaging 65.76 mg DW/individual. *S. richardi* was significantly more abundant, and made up significantly more biomass (**Figures 2.27** and **2.28**).

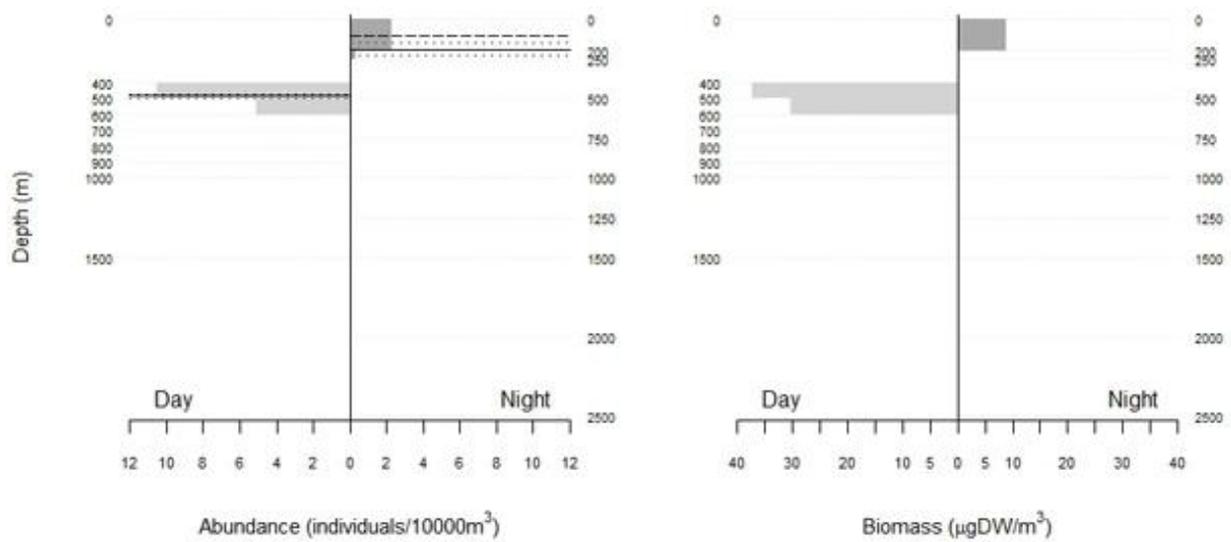


Figure 2.27 Abundance and biomass depth profiles for *Janicella spinicauda*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

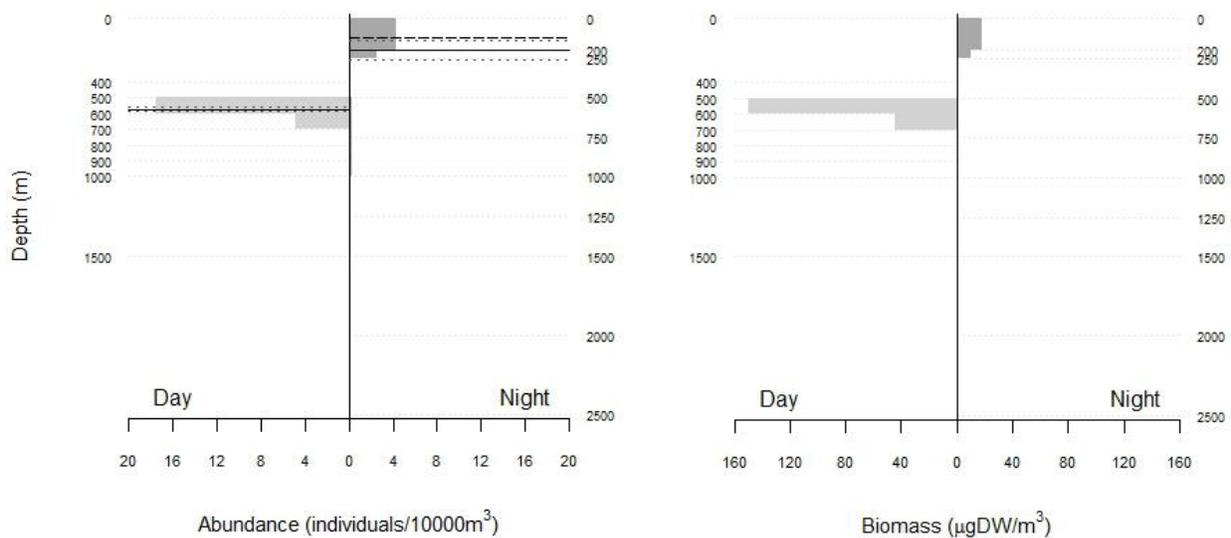


Figure 2.28 Abundance and biomass depth profiles for *Stylopandalus richardi*. For the abundance profile, daytime and night time WMDs are shown as solid lines, with dotted lines indicating standard errors, while the dashed line indicates the night time WMD for only the portion of the population that migrates to the surface.

A relationship between decapod dry weight and the depth to which they migrate to during the day was recognized. For all migratory decapod species with a mean dry weight below 100 mg per individual, there was a positive correlation between decapod dry weight and

daytime WMD ($p = 0.002$) (**Figure 2.29 b**). However, when species with a mean dry weight greater than 100 mg per individual were included (*Deosergestes erectus* and *Acanthephyra smithi*), the correlation was no longer significant ($p = 0.654$) (**Figure 2.29 a**).

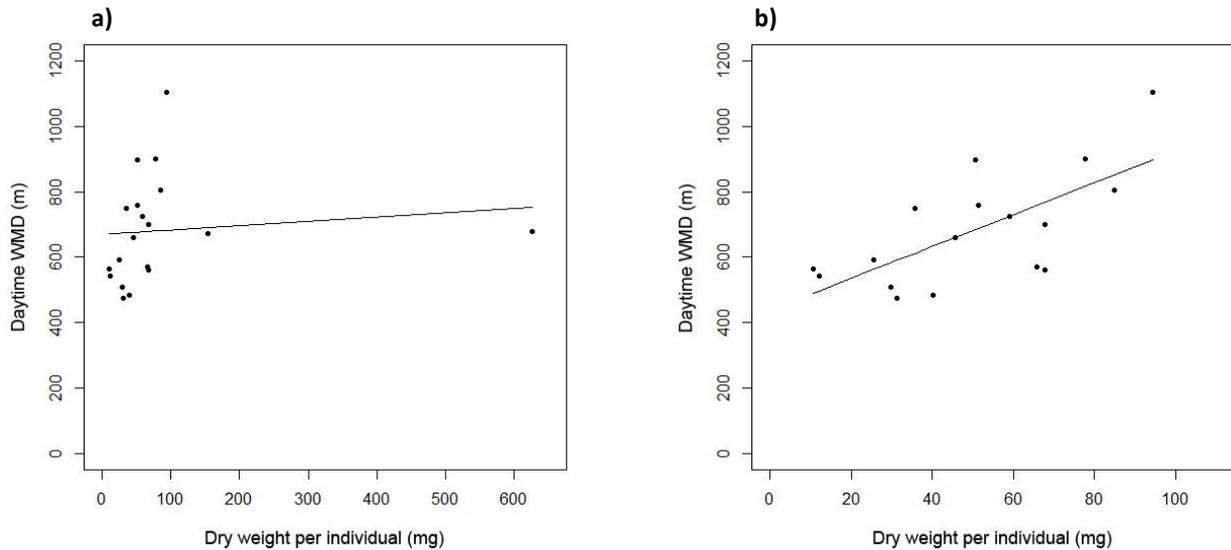


Figure 2.29: Dry weight vs. daytime WMD. Each point represents the mean dry weight and mean daytime WMD for one species. The relationship for all migratory species is show in **a**) ($R^2 = 0.0121$, $p = 0.654$, $F = 0.209$, $df = 1$ and 17), while **b**) shows the same relationship with all species with a mean dry weight larger than 100 mg/individual excluded ($R^2 = 0.473$, $p = 0.00228$, $F = 13.46$, $df = 1$ and 15)

2.3.5 Active flux

G. bouvieri and *A. smithi* were the greatest contributors to all four classes of active flux, while *D. erectus*, *G. capensis*, *Gennadas spp.*, *P. armatus*, *S. gardineri* and *S. richardi* also contributed significantly (**Table 2.5**).

Table 2.5: Active downward carbon fluxes for all diel migratory decapod species.

Species	Respiratory flux ($\mu\text{g C/m}^2/\text{day}$)	Excretory flux ($\mu\text{g C/m}^2/\text{day}$)	Mortality flux ($\mu\text{g C/m}^2/\text{day}$)	Gut flux ($\mu\text{g C/m}^2/\text{day}$)
<i>Acanthephyra smithi</i>	3.11	1.01	76.44	30.91
<i>Allosergestes pectinatus</i>	1.38	0.45	4.30	0.64
<i>Allosergestes sargassi</i>	0.92	0.30	4.28	0.82
<i>Deosergestes erectus</i>	3.58	1.16	41.55	12.14
<i>Gennadas bouvieri</i>	11.0	3.57	88.57	21.78
<i>Gennadas capensis</i>	5.57	1.81	51.01	13.25
<i>Gennadas clavicornis</i>	2.08	0.67	14.65	3.39
<i>Gennadas incertus</i>	1.42	0.46	8.80	1.93
<i>Gennadas spp.</i>	3.90	1.27	25.92	5.83
<i>Gennadas tinayrei</i>	0.80	0.26	5.21	1.15
<i>Janicella spinicauda</i>	1.84	0.60	9.80	1.53
<i>Neosergestes consobrinus</i>	0.92	0.30	2.82	0.41
<i>Neosergestes orientalis</i>	2.61	0.85	11.75	1.89
<i>Parasergestes armatus</i>	6.13	1.99	42.93	9.97
<i>Sergestes atlanticus</i>	1.06	0.34	4.45	0.79
<i>Sergia bigemmeus</i>	2.43	0.79	19.92	4.93
<i>Sergia gardineri</i>	7.89	2.6	41.03	5.84
<i>Sergia scintillans</i>	1.38	0.45	7.90	1.97
<i>Stylopandalus richardi</i>	3.30	1.07	23.75	6.40
Total flux for all species	61.31	19.90	485.16	125.56

For all species combined, carbon was transported from a mean depth of 261.80 m at night to a mean depth of 710.74 m during the day (these are mean depths weighted by active flux, as described in section 1c.6). The total active flux to this mean daytime depth was 691.93 $\mu\text{gC/m}^2/\text{day}$.

2.3.6 Comparison to passive flux

Using **Equation 2.10**, the passive particulate carbon flux at the mean daytime depth of 710.74 m was calculated to be 8039.45 $\mu\text{gC/m}^2/\text{day}$. The passive flux at the mean night time depth, 261.80 m, was calculated to be 18198.07 $\mu\text{gC/m}^2/\text{day}$. The passive flux at the base of the euphotic zone, 173 m, was calculated to be 25538.94 $\mu\text{gC/m}^2/\text{day}$. Thus all four active

fluxes were equal to 8.61% of the passive flux to the mean daytime depth, 3.80% of the passive flux to the mean night time depth, and 2.70% of passive flux at the base of the euphotic zone.

2.4 Discussion

2.4.1 Comparison to previous active flux estimates

The active flux estimated in this study is on the low end compared to active fluxes estimated in previous studies. As shown in **Table 2.1**, previous estimates of active flux due to mesozooplankton migrations in various regions of the world have shown this flux to range from 0-70% of the local gravitational flux at the base of the euphotic, with most estimates falling in the range of 18-40%. The active flux due to migrant shrimp and prawns in the central NPSG is thus near the bottom of this range, at only 2.70% of passive flux at the base of the euphotic. This is to be expected, as mesozooplankton communities tend to be larger than micronekton communities in terms of both total abundance and biomass, and thus able to transport more carbon (Hidaka et al., 2001), and this study focused on just one taxonomic group within the micronekton community. However, it should be noted that comparing the active flux only to export production ignores how deep the carbon has been transported. This is significant because, as described earlier, passive flux declines with depth below the base of the euphotic zone (Karl et al., 1996). The only previous study to take the depth of carbon transport into account was Steinberg et al.'s 2000 study, conducted at the Bermuda Atlantic Time-series Study (BATS) station, which found that while macrozooplankton active flux peaked at 38.6% of export production, the macrozooplankton were migrating to well below the base of the euphotic zone, and at a mean depth of 450 m the active flux may account for up to 71.4% of passive flux (Steinberg et al., 2000). In our study the micronekton migrated even deeper than the

macrozooplankton in Steinberg et al.'s study, to a weighted mean depth of 710.74 m, and active flux rose from 2.70% of passive flux at the base of the euphotic to 8.61% of passive flux at 710.74 m. This shows that, when calculating active flux for deeper migrating organisms, it is important to sample throughout the depth range of the organisms' migrations, to be able to calculate the depth to which carbon is transported.

While the active flux due to micronektonic decapods in our study was on the low end compared to previous studies focusing on zooplankton, it was quite significant compared to the two previous estimates of micronekton active flux. Compared to Kitamura et al. (in review), the active flux due to migrant decapod micronekton measured in this study was high. While Kitamura et al. estimated the overall flux due to crustacean micronekton to be equal to 3.4-16.7% of local carbon flux at the base of the euphotic, this was for all crustacean micronekton, not just decapods. In their study area the only diel migratory decapod species was the prawn *Sergestes similis* (now known as *Eusergestes similis*), a species that is very abundant between 42° - 50° N in the Pacific (Percy and Forss, 1969), but which was not found in the area of this study. The estimated active flux due to migrations by *Eusergestes similis* was equal to a mean of 2% of export production (0.7 - 3.3%), reaching 3.85% (2.6 - 5.1%) of passive flux past 300 m (Kitamura et al., in review). In our study there were 19 migratory decapod micronekton species which accounted for a greater active flux in comparison to Kitamura et al.'s study. Furthermore, the migratory decapod micronekton in our study migrated to a weighted mean depth of 710.43 m, while they only reached 385 m in Kitamura et al.'s study. Thus the contribution of migratory decapod micronekton to carbon flux at daytime migratory depths was even more significant, 8.61% of passive flux in this study compared to 3.85% in Kitamura et al. (in review). This emphasizes the importance of understanding the migratory patterns of local

micronekton if we are to draw the budget of the downward carbon flux in any given area. The highly variable micronekton communities can lead to highly variable active fluxes, in comparison to gravitational flux to the base of the euphotic, and especially in comparison to gravitational flux to daytime migratory depths.

The variability in local active flux is further emphasized with a comparison of this study to Hidaka et al. (2001), that estimated the active flux of all micronekton in the western equatorial North Pacific. In Hidaka et al.'s study, the micronekton catch was strongly dominated by myctophids, with minimal catches of euphausiids, squid and shrimp. While the total active flux due to micronekton was high, a mean of 43.45% of gravitational flux at the base of the euphotic (29.5 - 57.4%), the active flux due to migrant shrimp was very low, ~0.66% of gravitational flux (Hidaka et al., 2001). The contribution of active flux to local export production attributed to migrant decapods was nearly an order of magnitude higher in this study than in Hidaka et al.'s study. While the active flux due to other migrant micronekton such as myctophids, euphausiids, and squid was not calculated in this study, qualitative observations indicated that the catch of decapods, myctophids, and euphausiids were similar in terms of both abundance and biovolume, quite different from the strongly myctophid dominated community found by Hidaka et al. in the western equatorial North Pacific. This qualitative observation was reinforced by the Micronekton Inter-calibration Experiment (MICE) off the coast of Hawaii in 2004, which found that night time abundance of micronekton as measured by a frame trawl was composed of 22% myctophids, 14% decapods, 12% euphausiids, 44% other fish, and 8% other micronekton species (Pakhomov et al., 2005). It should be noted, however, that the dramatic differences in micronekton community structure, and thus active flux due to different micronekton groups, between this study and Hidaka et al.'s 2001 study

could be due not only to differences in the communities themselves, but to differences in the sampling procedure. During the MICE, night time samples taken with a 4 m² frame trawl, similar to the gear used in the present study, comprised 22% myctophid and 14% decapod by abundance (Pakhomov et al., 2005). By contrast, when sampling with a Cobb trawl, similar to the gear used in Hidaka et al. (2001), the night time catch was roughly 56% myctophid and 6% decapod by abundance. During the MICE it was noted that the Cobb trawl tended to catch larger organisms than the HUFT (Pakhomov et al., 2005). Thus, biased sampling by different gears could explain some of the difference in community structure between this study and Hidaka et al. (2001). This highlights the importance of understanding catch bias for different micronekton gears for any study attempting to quantify the micronekton community using net catches. While the MICE provided good insight into calibrating catches between different gears (Pakhomov et al., 2005), how these catches relate to the actual abundances of the various micronekton species in the water column is still not well understood.

Finally, it is worth noting that this study is the first active flux study to show evidence for Vinogradov's ladder of vertical migrations (Vinogradov, 1962). This contentious theory proposed that vertical migrations could be an important source of energy and materials to the bathypelagic and abyssopelagic zones of the ocean (Allison et al., 1996). While migrations from the bathypelagic to the surface are very rare, some deep living organisms will perform migrations to sub-surface depths. Vinogradov proposed that through predation an interconnected ladder of such migrations could be transporting significant energy and materials to great depths (Vinogradov, 1962; Allison et al., 1996). While the quantification of fluxes due to this ladder have proven difficult to calculate, as determining the migratory patterns of bathypelagic and abyssopelagic organisms is challenging due to their low abundance, and the

general time intensive nature of collecting net samples from great depths, there has been some supporting evidence for Vinogradov's ladder (Haedrich and Henderson, 1974; Yamamura et al., 1993; Allison et al., 1996). However, on a global scale it is believed to be a relatively minor food source for deep living fauna compared to sinking phytoplankton and other detritus originating from higher in the water column (Allison et al., 1996). In this study six of the migratory species migrated upwards to night time weighted mean depths that remained well below the base of the euphotic zone, and these six species included a number of the key contributors to the migrant decapod active flux (namely *A. smithi*, *G. bouvieri*, *P. armatus* and *G. capensis*). While this does not show a complete ladder of migrations from the surface to the abyssopelagic (the deepest migrator, *G. capensis*, migrated from a night time WMD of 323.75 m to a daytime WMD of 1102.69 m), it does show a "rung" of such a ladder. Furthermore, it emphasizes the importance of sampling deep within the water column when estimating active fluxes. Had this study estimated active flux purely based on the difference between daytime and night time abundance and biomass in the euphotic zone, all organisms which migrate upwards, but not all the way to the euphotic zone, would have been left unaccounted for.

2.4.2 Migration depth vs. migrant size

For all migrant decapod species with a mean dry weight of 100 mg or less per individual, there was a strong correlation between dry weight per individual and the depth to which they migrated during the day (**Figure 2.29 b**). This is not entirely unexpected, as larger decapods should be stronger swimmers, and thus are able to migrate deeper. Two of the main advantages to diel migratory behaviour are energy conservation due to lower metabolic rates in colder water, and predator avoidance in lower light conditions (Lampert, 1989), and both of

these advantages would grow with increasing daytime depths. However, the two largest migratory decapod species, *D. erectus* and *A. smithi*, did not follow this pattern of increasing daytime WMD with increasing size, as both species migrated to relatively shallow daytime WMDs of ~675 m (**Figure 2.29 a**). In many marine systems, especially coral reefs and intertidal systems, it has been recognized that if prey-species can attain a larger size, they may likely escape predation due to their lower vulnerability to predators (Paine, 1976). It is hypothesized here that a similar phenomenon could be responsible for the relatively shallow migrations of *D. erectus* and *A. smithi*; that there is a predator (or numerous predators) that forces smaller decapods to migrate as deep as possible, but that this predator does not prey on the largest shrimp. This hypothesis would need to be confirmed through a dietary study of the local higher predators.

2.4.3 *Relevance of the sampling locations*

As discussed in the methods section, samples were collected in the central NPSG, mostly at station ALOHA, but also at station Kahe, two oceanographic stations that have been regularly monitored by the Hawaii Ocean Time-Series (HOT) program since October 1988 (Karl and Lukas, 1996). One of the central goals of the HOT program is to understand local biological processes and particulate matter fluxes (Karl and Lukas, 1996). However, up until now the contribution of diel migratory micronekton active flux to downward carbon flux in the area has not been assessed, so this study contributes to a key knowledge gap relating to carbon flux in this highly studied region.

The central NPSG is a particularly relevant study site due to the very low passive gravitational flux in the region. In a global review of carbon flux, station PARFLUX-1 (located at

located at 15.5°N, 151.5°W, close to ALOHA) had the lowest estimated export production of 57 stations, along with a relatively low f-ratio, indicating a weak local biological pump (Francois et al., 2002). As the passive gravitational flux at the study site should be at the low end compared to the world's oceans as a whole, any active flux in this region would be a particularly significant contributor to overall local downward carbon flux. This point, and the high abundance of migrant shrimp and prawns in the study area, indicates that the estimate of active flux due to migrant decapods made in this study should represent the upper end of such fluxes on a global scale. The latter is reinforced by the high active flux for shrimp in this study compared to Hidaka et al. (2001) and Kitamura et al. (in review). A more thorough discussion on possible variations in active flux due to decapods worldwide is included in the conclusion of this thesis.

2.4.4 Potential sources of error – catch efficiency

A wide variety of models and assumptions were used in this study, so it is important to discuss the potential sources of error and uncertainty, and the possible magnitude of such errors. The largest potential source of error relates to estimating the catch efficiency of the net. Two variables affect the catch efficiency of a net: the mesh retention rate, which describes the extent to which animals can escape once they have entered the net, and the entering rate, which describes the extent to which animals can sense the net coming and avoid its path (Itaya et al., 2007). The mesh retention rate depends upon the size of mesh used, the speed at which the net is towed (if towed slower, the animals will be able to escape more easily), and the animal itself (stronger swimmers being more able to escape) (Barkley, 1964). The entering rate depends upon the size of the net's mouth opening (all else being equal, it's easier to swim out of the way of a smaller net), the speed at which the net is towed (if towed slower, animals will

have more time to swim out of the way), the swimming speed of the animal, and the distance from which the animal can sense the net coming (Barkley, 1964). While a larger net is harder to swim out of the way of, a larger net can also be recognized at a greater distance, and due to drag effects a larger net generally cannot be towed as fast, so it is not always the case that a larger net will yield higher catch efficiency.

For this study a net designed to catch micronekton was used, with a 10 m² mouth opening, significantly larger than nets designed to catch zooplankton, which tend to have mouth openings closer to 1 m². Due to its large size, and the design of the gear, it could only be towed at a relatively slow speed of ~2 kts. The assumed catch efficiency of 33.33% was based on the findings of Itaya et al. (2007), who towed frame trawls of a similar design to the one used in this study at a variety of speeds, using trawls with mouth openings with a variety of sizes. In their study a frame trawl with a 4 m² mouth opening was towed at speeds of 2, 3 and 4 kts, and the CPUE (catch per unit effort) was measured for different species (Itaya et al., 2007). Two micronekton species were identified to the species level; for one species (*Benthosema suborbitale*) the CPUE was ~3.3 times as large at a towing speed of either 3 kts or 4 kts versus 2 kts, while for the other species (*Diogenichthys atlanticus*) the CPUE was roughly 2.8 times as large at 3 kts versus 2 kts, and roughly 3.4 times as large at 4 kts versus 2 kts (Itaya et al., 2007). Since it is unlikely that a 4 m² frame trawl towed at 4 kts has 100% catch efficiency, the assumed catch efficiency of 33.33% was in all likelihood an overestimate.

While the above data would suggest that a catch efficiency lower than 30% should be used, Itaya et al.'s experiment was performed with a frame trawl with a 4 m² mouth opening (2 m by 2 m), while in the current study a frame trawl with a 10 m² mouth opening was used (3.33 m by 3.33 m). It is possible that with the wider net, the net avoidance would be less

pronounced even at the tow speed of 2 kts. While no equivalent studies have been performed for a frame trawl with a 10 m² mouth opening, species specific differences in CPUE have been found for a 4 m² and 12.3 m² trawl towed at 4 kts (Itaya et al., 2007). For *D. atlanticus*, the CPUE was similar between nets, while for *B. suborbital*, the CPUE for the 12.3 m² trawl was approximately double that of the 4 m² trawl. This would suggest that, for certain species, the 10 m² net used in this study would offset some of the net avoidance incurred by the lower tow speed. Thus, a catch efficiency of 33.33% was considered appropriate, as opposed to the catch efficiency below 30% indicated by tow speed alone.

A catch efficiency of 33.33% was also assumed by Kitamura et al. (in review) in their study on active flux by crustacean micronekton. In this case the correction factor was based on findings that a strobe light attached to the front of a MOCNESS net used to "stun" euphausiids, and thus prevent them from avoiding the net, increased catch by up to 3 times (Sameoto et al., 1993; Wiebe et al., 2004). Hidaka et al. (2001) assumed a catch efficiency of just 14% for an otter trawl (20 x 20 m mouth opening, with a mesh size starting at 100 x 100 cm at the mouth and decreasing to 8 x 8 mm at the cod end). However, these nets are known to have relatively low catch efficiency due to the fact that organisms can simply pass through the large mesh near the mouth opening. Overall, assuming a catch efficiency of 33.33% for micronekton for a 10 m² MOCNESS towed at 2 kts seems reasonable, but clearly there is much uncertainty here, and the actual catch efficiency could be significantly different. The catch efficiency assumption likely represents the largest source of uncertainty in this study.

2.4.5 *Potential sources of error – active flux models*

While catch efficiency represents the largest potential source of error, it is also worth taking into account uncertainty due to the models used to estimate respiratory flux, excretory flux, mortality flux and gut flux. Respiratory rates were estimated as a function of body mass and temperature, based on data from a wide variety of zooplankton and micronekton, including many animals that are taxonomically and anatomically similar to shrimp, such as decapods, euphausiids, stomatopods, amphipods and mysids, as well as less similar animals like fish, copepods and chaetognaths (Ikeda, 1985). Despite the wide variety of animals used, the organism's dry weight and habitat temperature explained 93.9% of the variability in the oxygen uptake data (Ikeda, 1985). This high coefficient of determination gives a high confidence in oxygen uptake estimates provided by the model. The fact that it was derived using decapods and other taxonomically and anatomically similar crustaceans gives added confidence that the model can be applied to decapods. Overall the uncertainty introduced by the use of this model should be relatively low, especially compared to the uncertainty introduced by the catch efficiency assumptions.

Mortality flux estimates were based on a size-dependent mortality rate model developed for particles in the size range of fish eggs (~0.1 mg dry weight) to adult fish (~1000 g dry weight) (Peterson and Wroblewski, 1984). Since it is a theoretical model, not an empirical model, there is no correlation coefficient. However the model was compared to data from various sources to test its accuracy. In **Figure 2.30**, the model predictions are compared to empirically measured mortality rates from a variety of different studies.

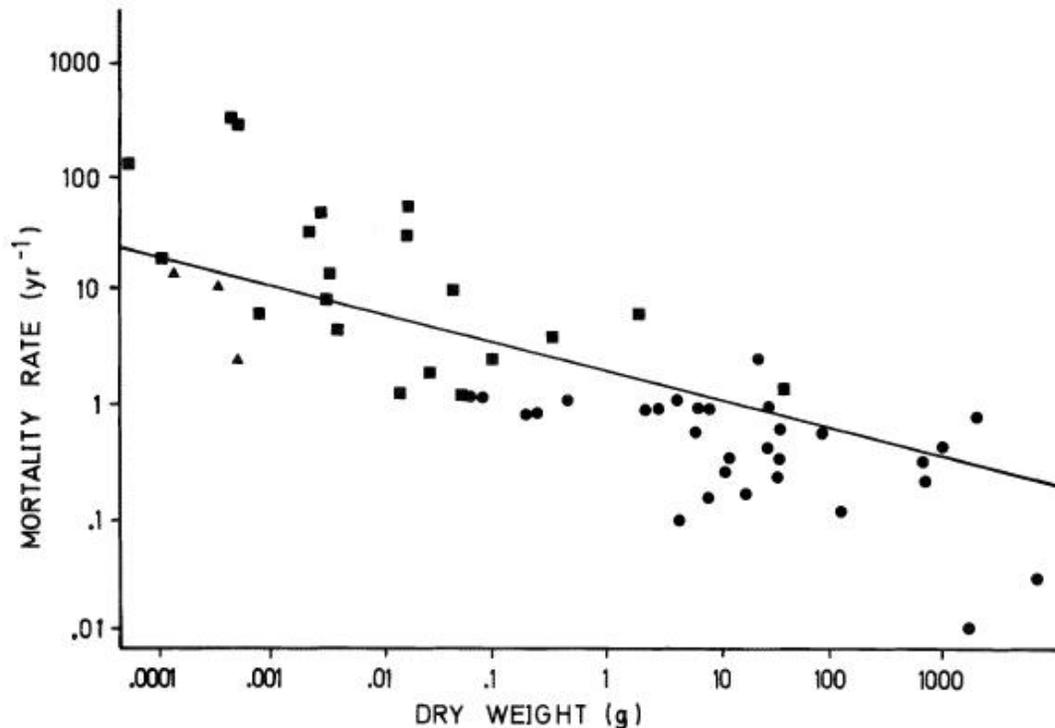


Figure 2.30: Natural mortality rate vs. dry weight, re-printed from Peterson and Wroblewski (1984). The straight line is described by **Equation 2.8**. ●, adult fish (Ursin, 1967); ■, larval and juvenile fish (Poulsen, 1931; Sette, 1943; Ahlstrom, 1954; Farris, 1961; Pearcy, 1962; Graham and Chenoweth, 1971, 1973; Cushing, 1974); ▲, chaetognaths (Sameoto, 1971).

There is considerable error associated with predictions made by this model, with empirically measured mortality rates up to an order of magnitude off predicted values. However, the greatest error occurs with the smallest and largest organisms; in the weight range of the individuals in this study (roughly 0.01 to 0.6 g dry weight per organism) the model tends to be closer to empirical values. Furthermore, each point in **Figure 2.30** represents a mortality rate for one species, and taking the mean mortality across many species should reduce error considerably given that errors are distributed fairly evenly above and below the predicted values. In this study the mortality flux was calculated for 19 different species, so while the predicted mortality flux for any individual species may be off significantly, the error should be much smaller for the estimate of overall mortality flux for all species.

Following Steinberg et al. (2000), excretory flux was assumed to be 32% of respiratory flux (in $\mu\text{g C per mg dry weight per hour}$). The standard error of the mean for this estimate was $\pm 4.7\%$, based on estimates for 11 different taxonomic groups (shrimp, euphausiid, copepod, amphipod and polychaete species). Respiration and excretion rates vary similarly, as both are influenced by the dry weight of the organism and seawater temperature, and excretion rates were consistently close to 32% of respiratory flux over a wide variety of zooplankton species. Therefore the error associated with the excretory flux estimate should be relatively minor, although it does intrinsically include the error associated with the respiratory flux, discussed above.

In terms of gut flux estimates, the main source of error would relate to **Equation 3.8** (derived in Chapter 2 of this thesis), which predicts food ball dry weight based on the dry weight of the organism and stomach fullness. 81.85% of the variance in the data was explained by the model, thus the error associated with the model's estimates was reasonably small. It should be noted that the gut flux estimate is likely to be an underestimate, since it was based on measurements of only the mass of material in the stomach, and ignored material in the intestines, which would also contribute to the gut flux.

Overall there are numerous sources of error associated with the active flux estimates in this study, as is the case with all studies that have attempted to estimate active fluxes, and to a certain extent all studies attempting to estimate micronekton biomass and abundance based on net catches. Nonetheless, the active flux estimate made by this show that migrant pelagic decapods may contribute significantly to downward carbon flux in the central NPSG, and that ignoring their contribution would lead to a significant underestimate of downward carbon flux.

2.4.6 *Concluding remarks*

The estimated active flux due to the diel vertical migrations of decapods was low compared to most previous estimates for zooplankton and micronekton communities as a whole, but high compared to two previous estimates of decapod specific active flux. The relatively high abundance of migratory decapods, combined with the low passive flux in the central NPSG, suggests that this estimate for active flux due to migrant decapods may be more important relative to local passive flux in this region than in other areas of the world's oceans. Differences in community structure between this thesis and other studies emphasize the importance of local micronekton migrations to understanding vertical carbon flux in any region. The deep daytime migrations for many shrimp species, as well the relatively high prevalence of decapod species that did not migrate all the way up to the euphotic zone, emphasizes the importance of sampling the entire water column, not just migrations into and out of the euphotic zone, as many previous studies have done. Overall, the active flux estimates produced by this study show that migrant decapods are a significant contributor to downward carbon flux in the central NPSG.

3 Feeding ecology of pelagic decapods in the North Pacific Subtropical gyre

3.1 Introduction

In the previous chapter the active carbon flux due to diel migrant decapods in the NPSG was estimated, with the assumption being made that the decapods were feeding exclusively in their shallow night time depths, with no feeding occurring in the deeper daytime depths. This is a simplifying assumption in all studies to date where the active flux attributed to mesozooplankton, macrozooplankton and micronekton was assessed. Should this assumption prove incorrect, current active flux estimates could potentially be overestimates. As previously outlined, active carbon flux occurs when organisms consume food primarily or entirely at shallow nocturnal depths, but they die, respire, excrete and defecate at all depths (Longhurst, 1991). If the food fueling these fluxes is consumed only near the surface, there would be a net downward transport of carbon (Longhurst, 1991), but if feeding was occurring equally at all depths, there would be no net carbon transport. In fact, carbon flux would likely be an upwards flux in this case, as respiration and excretion occur at slower rates in deeper, cooler waters (Ikeda, 1985; Steinberg et al., 2000).

Pronounced nocturnal feeding, with full stomachs for organisms caught near the surface at night, but little or no food in the stomachs of organisms caught at depth, has been observed for a range of meso- and macrozooplankton species (Hayward, 1980; Longhurst et al., 1989; Stuart and Pillar, 1990). However, nocturnal feeding is not always associated with vertically migrating crustaceans. In a study on the diurnal feeding behaviour of four euphausiid species in the central NPSG, it was found that two strong vertical migrators (*Thysanopoda aequalis* and *Thysanopoda monacantha*) showed increased feeding activity during the night, but it was likely

that some feeding was occurring during the day as well (Hu, 1978). For a moderate migrator (*Thysanopoda pectinata*) there was no indication of preferential nocturnal feeding, instead feeding appeared to be constant throughout all depths and times, with no difference in mean stomach weights between animals caught near the surface at night and animals caught at depth during the day (Hu, 1978). Finally, for *Nematobrachion sexspinosus*, a weak migrator (or possibly a non-migrator), mean stomach weight actually increased at depth during the day (Hu, 1978). Similar results have been found for other crustaceans. In a study on the feeding behaviour of ten sergestid shrimp species near Bermuda, stomachs of two species (*Sergestes sargassi* and *Sergestes pectinatus*) were equally full during the day and night, indicating continuous feeding over a 24-hour cycle (Donaldson, 1975). For the other eight species stomachs were more full at night, but not empty during the day, causing the authors to conclude that some daytime feeding at depth could be occurring (Donaldson, 1975).

Clearly the extent to which pelagic crustaceans feed nocturnally depends strongly on the crustacean species being studied. Current community scale studies on the trophic ecology of pelagic decapods in the central NPSG have been limited. Micronektonic shrimp use mandibular teeth to masticate their prey into small pieces, which has presented a barrier to dietary studies of this group (Brodeur and Yamamura, 2005). The most extensive studies addressing the trophic ecology of pelagic decapods have been performed in the eastern, central and western North Atlantic (Foxton, 1970a, 1970b; Foxton and Roe, 1974; Donaldson, 1975; Fasham and Foxton, 1979), as well as in the eastern Gulf of Mexico (Flock and Hopkins, 1992; Hopkins et al., 1994; Hopkins and Sutton, 1998). The only community scale study addressing the trophic ecology of pelagic decapods in the NPSG focused simply on identifying common

prey items for all sergestid shrimp present in samples, with little numerical analysis (Walters, 1975). It is thus important to study pelagic decapod diets in the NPSG not only to test the assumption of exclusive nocturnal feeding, but to perform basic research on the feeding ecology of these understudied animals.

Elucidating pelagic decapod feeding ecology and active flux is additionally important to establish baselines for a community that is not currently fished commercially. The problem of shifting baselines has been well established in the field of fisheries science, where scientists are often forced to study systems after commercial fishing has commenced, without data on the state of the ecosystem before the onset of fishing (Pauly, 1995). There is no current fishery for pelagic shrimp in the NPSG (Drazen, pers. comm.). However, the phenomenon known as "fishing down the food web" has been established throughout marine ecosystems, with an ongoing gradual transition in landings from large, high trophic level piscivorous fish towards smaller, low trophic level invertebrates and planktivorous fish (Pauly, 1998). It is thus possible that a pelagic shrimp fishery could open in the central NPSG in the future, especially since pelagic decapods are locally abundant, and rich in sergestid shrimp (Maynard et al., 1975), which are desirable for human consumption. While most shrimp fisheries currently target benthic and demersal shrimp (Gillett, 2008), commercially important fisheries for pelagic shrimp exist, especially for sergestid shrimp in the western Pacific (Chikuni, 1985). These include the paste shrimp (*Acetes* spp.) and the Sakura shrimp (*Sergestes lucens*). These Sergestid shrimp fisheries are not necessarily small scale fisheries, as *Acetes japonicus* is the most fished shrimp species in the world by weight, with landings higher than any benthic or demersal shrimp species (Gillett, 2008). The potential for a pelagic shrimp fishery to open in

the NPSG makes it essential to understand the feeding ecology and active flux of local decapods in the communities' current state.

Most previous attempts to study diurnal feeding have focused on changes in mean stomach weight throughout the day (Donaldson, 1975; Hu, 1978; Hayward, 1980; Longhurst et al., 1989; Stuart and Pillar, 1990). While this analysis can reveal the presence of nocturnal feeding, it has difficulty differentiating between exclusive nocturnal feeding and feeding occurring at all depths and times, but with an increase at night. Should mean stomach weight during the night be twice that of daytime stomach weight, this could be due to daytime feeding being half that of night time feeding, or due to exclusive nocturnal feeding, with day time gut content simply being food consumed at night that has not been fully digested. This study will examine diurnal changes in prey composition as well as stomach weight in an attempt to more accurately estimate the percentage of feeding occurring at both shallow night time depths and deep daytime depths. The goals of this research chapter are:

- a) To establish the prey composition of each of the most abundant pelagic decapod species
- b) For each species, determine the distribution of feeding effort across time and depth
- c) To determine whether organism size or taxonomy plays a larger role in diet specialization

3.2 Materials and methods

3.2.1 Field sampling

Samples were collected from October 6th - 12th, 2004, aboard the NOAA research ship *Oscar Elton Sette*, as part of the Micronekton Inter-calibration Experiment (MICE). A total of 56 midwater trawls were conducted off the southwest coast of Oahu, over bottom depths of 700 - 1200 m. Sampling tracks are shown in **Figure 3.1**.

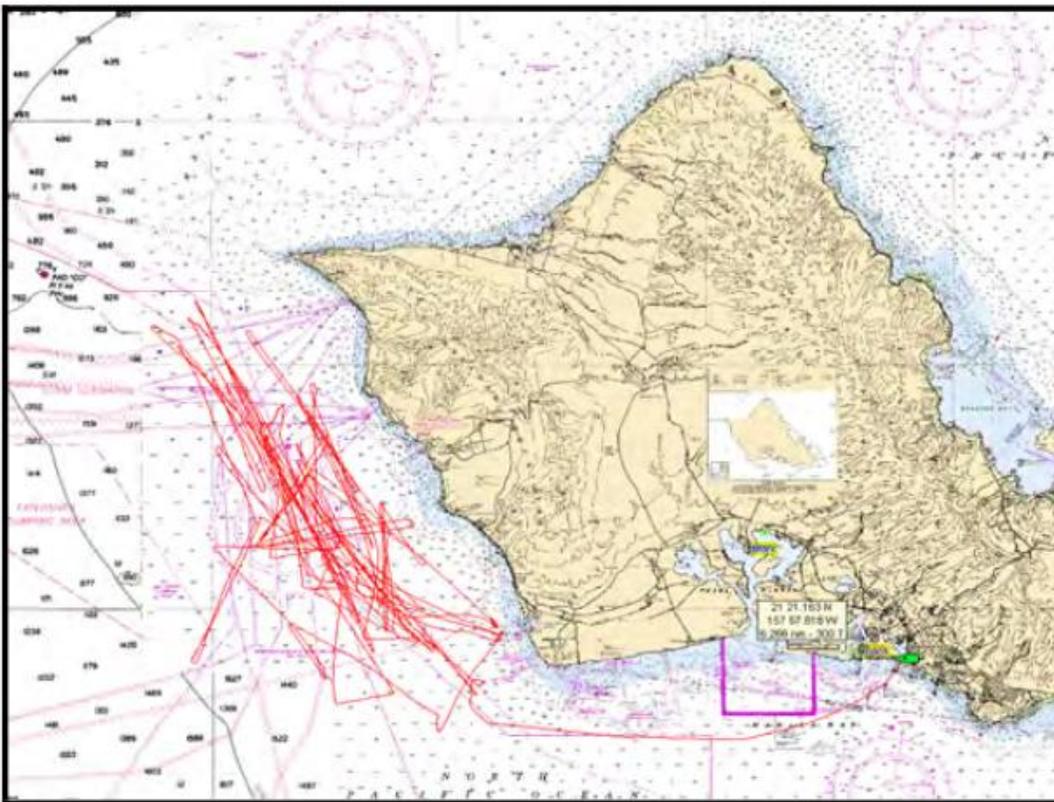


Figure 3.1 Sampling tracks carried out off the southwest coast of Oahu, in October 2004.

Trawls were conducted both at night (from 8:00 pm to 5:00 am local time) and during the day (from 8:00 am to 5:00 pm local time), sampling both the surface backscattering layer (the SSL, located at ~120 m) and the deep backscattering layer (the DSL, located at ~550 m). Three different gears were used, allowing a wide range of macrozooplankton and micronekton

to be sampled. These gears were a 3 m² Isaacs-Kidd Midwater Trawl (IKMT) with a 5 mm mesh size, a 4 m² Hokkaido University Frame Trawl (HUFT) with a 3 mm mesh size, and a 140 m² pelagic Cobb trawl with a mesh size narrowing to 10 mm near the cod end. The number of samples collected with each gear in each depth range are shown in **Table 3.1**.

Table 3.1 Number of trawls conducted at each depth, at each time of day. SSL = shallow backscattering layer, DSL = deep backscattering layer.

Gear	Number of trawls conducted at night in the SSL	Number of trawls conducted at night in the DSL	Number of trawls conducted during the day in the DSL
IKMT	12	1	6
HUFT	13	1	6
Cobb	8	3	6

Trawls were not conducted during the day in the SSL, due to the virtual absence of micronekton in this layer during the day. This was confirmed by aborted trawls that accidentally sampled only the SSL during the day. Samples were sorted into major taxonomic groups (decapods, euphausiids, tunicates, fish, amphipods, copepods, stomatopods, etc.), and certain taxonomic groups (such as fish and squid) were removed from the samples, for use in a separate study. All decapods, as well as all macrozooplankton and mesozooplankton, were preserved in a 10% formalin seawater solution for further analysis in the laboratory.

3.2.2 Laboratory procedures

All decapods in the preserved samples were identified to the species level. The decapod community was very diverse, with 30 different species present in the samples, belonging to 9 different families (**Table 3.2**).

Table 3.2 All pelagic decapod species caught on the 2004 *Oscar Elton Sette* cruise.

Species	Family	Included in analysis?
<i>Acanthephyra smithi</i>	Oplophoridae	Yes
<i>Janicella spinicauda</i>	Oplophoridae	Yes
<i>Neosergestes orientalis</i>	Sergestidae	Yes
<i>Notostomus elegans</i>	Oplophoridae	Yes
<i>Oplophorus gracilirostris</i>	Oplophoridae	Yes
<i>Parasergestes armatus</i>	Sergestidae	Yes
<i>Sergia gardineri</i>	Sergestidae	Yes
<i>Sergia scintillans</i>	Sergestidae	Yes
<i>Stylopandalus richardi</i>	Pandalidae	Yes
<i>Acanthephyra quadrispinosa</i>	Oplophoridae	No
<i>Allosergestes pectinatus</i>	Sergestidae	No
<i>Allosergestes sargassi</i>	Sergestidae	No
<i>Deosergestes erectus</i>	Sergestidae	No
<i>Eupasiphae gilesii</i>	Pasiphaeidae	No
<i>Funchalia taaningi</i>	Penaeidae	No
<i>Gennadas bouvieri</i>	Benthescymidae	No
<i>Gennadas tinayrei</i>	Benthescymidae	No
<i>Heterocarpus ensifer parvispina</i>	Pandalidae	No
<i>Lucifer typus</i>	Luciferidae	No
<i>Nematocarcinus sp.</i>	Nematocarcinidae	No
<i>Neosergestes consobrinus</i>	Sergestidae	No
<i>Parasergestes vigilax</i>	Sergestidae	No
<i>Pasiphaea affinis</i>	Pasiphaeidae	No
<i>Sergestes atlanticus</i>	Sergestidae	No
<i>Sergia bigemmeus</i>	Sergestidae	No
<i>Sergia bisulcatus</i>	Sergestidae	No
<i>Sergia inequalis</i>	Sergestidae	No
<i>Sergia tenuiremis</i>	Sergestidae	No
<i>Systellaspis debilis</i>	Oplophoridae	No
<i>Thalassocaris lucida</i>	Thalassocarididae	No

Of the 30 species caught, only 9 were included in the analysis (**Table 2.2**). Of the species excluded most were simply very rare, while some were too small to perform a gut content analysis using a dissecting microscope (*Lucifer typus* and *Neosergestes consobrinus*), and some were common at a certain depth or time of day, but were not found at other depths and times

of day, making it impossible to analyze diel feeding patterns. This was likely due to the fact that, as seen in the first research chapter, many of the local pelagic decapods migrated to daytime residence depths below 550 m, or to night time depths below 120 m. These depths were chosen for sampling due to maximum acoustic backscattering, indicating a high concentration of organisms, but not necessarily the highest concentrations of decapods.

For the species included in the analysis, up to 75 individuals per species were analyzed, with 15 individuals from each of 5 different depth-time intervals. The 5 depth-time intervals were: individuals caught in the SSL during the early night, from 8:00 pm - 12:30 am (Shallow EN), individuals caught in the SSL during the late night, from 12:30 am - 5:00 am (Shallow LN), individuals caught in the DSL during the early day, from 8:00 am - 12:30 pm (Deep ED), individuals caught in the DSL during the late day, from 12:30 pm - 5:00 pm (Deep LD), and individuals caught in the DSL at any point during the night, from 8:00 pm - 5:00 am (Deep E/LN). Once decapods were identified to the species level, their carapace lengths, total lengths and weights were measured. Carapace lengths were measured in the same manner as in chapter 1, using calipers with a resolution of 0.1 mm, measured from the posterior middorsal margin of the carapace to the posterior edge of the orbit. Total lengths were measured from the posterior margin of the telson to the posterior edge of the orbit. Stomachs were removed, and stomach fullness (as a percentage) was estimated visually. Stomachs were then opened, the food ball was removed, and its wet weight was measured. Prey composition was determined through visual analysis of the food balls with a dissecting microscope.

The gears with the finer mesh nets (the IKMT and HUFT) caught mesozooplankton and macrozooplankton as well micronekton, so many of the potential prey species were caught.

These potential prey species were identified to the species level when possible, dissected, and body parts of taxonomic importance photographed. As mentioned earlier, pelagic decapods use mandibular teeth to masticate their prey into small pieces, so whole prey are rarely found in their guts. It was thus essential to identify the potential prey items, dissect them, and photograph key identifying features that could resist mastication and digestion. For example, the molar process of the mandibles of euphausiids and decapods tend to be distinct from species to species, and especially genus to genus, and they also tend to be present in gut contents, even when the softer body parts have been digested. By creating a library of photographs matching identified euphausiids to their distinct molar processes, it was possible to identify masticated and digested prey in the decapod stomachs. The same process was used for chaetognath grasping hooks, polychaete chaetae, pteropod shells, etc. Some prey items could be more readily identified in decapod stomachs than others: for example, calanoid copepods of the genus *Pleuromamma* are characterized by a black spot on the cephalosome which resists mastication (Foxton and Roe, 1974), while many other copepod genera possessed no such readily identifiable features that were preserved in decapod stomachs.

Once the prey items within an individual stomach were identified to the lowest taxonomic level possible, the percent contribution of each prey item to the overall food ball volume was estimated (for example, a food ball could be 20% *Pleuromamma* sp., 5% Foraminifera, 50% Osteichthyes, 25% *Thysanopoda acutifrons*). The digestion stage of each prey item was also estimated, and ranked on a scale from 1-5 (1: whole animal, virtually undigested; 2: body mostly in one piece, appendages detached if applicable, some digestion of soft parts; 3: soft parts mostly digested, entire animal fragmented; 4: only hard parts

identifiable; 5: only a highly digested, unidentifiable paste remains). The food ball and the decapod were then dried in an oven at 50 °C for 24-72 hours, as described in Chapter 1. Dry weights for the food ball and the decapod were then measured, using a scale with a resolution of 0.1 mg.

3.2.3 Numerical analysis

To assess changes in stomach fullness through different depth/time intervals, the Stomach Fullness Index (SFI) proposed by Hureau (1969) was used (**Equation 3.1**).

$$\text{Equation 3.1 } SFI = 100 * FB_{DW}/Org_{DW}$$

FB_{DW} is the food ball dry weight (mg) and Org_{DW} is the organism's dry weight (mg). The SFI is thus the ratio of food ball dry weight to organism dry weight, expressed as a percentage. The SFI was calculated for each decapod, and the mean SFIs at each depth/time interval were compared using an ANOVA, with a p-value lower than 0.05 indicating a statistically significant difference in SFI at one of more depth/time intervals.

The scale used to measure food ball wet weights (FB_{WW}) and FB_{DW} had a resolution of 0.1 mg, but due to vibrations in the laboratory it was determined that measurements were not accurate to within 0.1 mg. Because of this, all measurements of 0.3 mg or less were considered unreliable. When $FB_{DW} \leq 0.3$ mg (unreliable), but $FB_{WW} > 0.3$ mg (reliable), FB_{DW} was calculated using **Equation 3.2**.

$$\text{Equation 3.2 } FB_{DW} = a * FB_{WW}$$

Where a was a constant determined through a regression analysis. When FB_{WW} measurements were also unreliable ($FB_{WW} \leq 0.3$ mg), FB_{DW} was instead calculated using **Equation 3.3**.

$$\text{Equation 3.3 } FB_{DW} = b * Org_{DW} * Fullness$$

Where *Fullness* is the visually estimated stomach fullness, expressed as a proportion, and b is a constant determined through regression analysis. This equation assumes that FB_{DW} for 100% full stomachs scales linearly with Org_{DW} , which is an assumption also made with the use of the SFI.

Prey composition for each decapod species was calculated in terms of the mean dry weight (μg) of each prey item found in the stomachs. Mean dry weight was calculated by multiplying the FB_{DW} by the percentage contribution of each prey item to the overall food ball volume. This assumes that all prey items have the same density, which is not the case, but it would have been impossible to accurately measure the dry weight of each prey item. For each decapod species the mean prey composition for organisms caught in both the SSL and DSL was calculated, to allow for a comparison between stomach contents during the day and night.

For each pelagic decapod species, two methods were used to estimate the percentage of feeding occurring at depth, one method representing a reasonable upper boundary for this estimate, with the other method representing a reasonable lower boundary for the estimate. Upper and lower boundaries for the estimate of feeding at depth were computed separately for each decapod species. The upper boundary was established using **Equation 3.4**.

$$\text{Equation 3.4 } \textit{Upper boundary} = \frac{SFI_{DSL}}{SFI_{SSL}} \times 100\%$$

Where SFI_{DSL} is the mean SFI in the deep scattering layer, and SFI_{SSL} is the mean SFI in the shallow scattering layer. **Equation 3.4** represents an upper boundary for the estimate of feeding at depth because it assumes that 100% of food ball dry weight for decapods caught in the DSL is due to feeding at depth, as opposed to food consumed in the SSL that has yet to be fully digested.

The lower boundary for the percentage of feeding occurring at depth was established using **Equation 3.5**.

$$\text{Equation 3.5 Lower boundary} = \frac{Prey\ DW_{DSL}}{Prey\ DW_{SSL}} \times 100\%$$

Where $Prey\ DW_{DSL}$ is the DW of all prey taxa occurring exclusively or nearly exclusively in decapods found in the DSL, and $Prey\ DW_{SSL}$ is the DW of all prey taxa occurring in decapods found in the SSL, including both prey taxa found exclusively in the SSL, and prey taxa found in both the SSL and DSL. "Nearly exclusively found in the DSL" was defined as those prey taxa for which DSL dry weight was at least 5 times SSL dry weight. **Equation 3.5** represents a lower boundary for the estimate of feeding at depth because it assumes that, for prey taxa found in considerable quantities during both the SSL and DSL, the prey DW in the DSL stomachs is due exclusively to partially digested SSL feeding, and not at all due to DSL feeding.

In addition to the species specific analyses, the entire stomach content data set was analyzed on the community level using the PRIMER software package (Plymouth Routines in Multivariate Ecological Research, version 6.1.12). Two different analyses were performed using the PRIMER software, the first being a cluster analysis. As the name suggests, cluster analysis puts sites into clusters, such that sites within the cluster are more similar to one another than

sites in different clusters (Clarke and Warwick, 2001). A hierarchical agglomerative method was used, so that each comparison was between two sites, one site and one cluster of sites, or two clusters of sites. A Bray-Curtis Similarity Index was used to quantify similarity. Prey composition data was log transformed, using a $\log(x+1)$ transformation, to reduce bias due to highly abundant prey. Through the cluster analysis a dendrogram was produced, with samples on the x-axis, and similarity levels between samples on the y-axis. Four different cluster analyses were performed. For the first cluster analysis prey composition was averaged by the depth/time interval at which the decapods were caught in (Shallow EN, Shallow LN, Deep ED, Deep LD and Deep E/LN), with each interval representing one "site." For the second cluster analysis prey composition was averaged by the decapod species that consumed the prey (*A. smithi*, *J. spinicauda*, etc.). For the third cluster analysis prey composition was averaged based on the weight of the decapods, specifically into bins of the natural logarithm of the dry weight of the decapods, as measured in mg (bins were $\ln(\text{DW})$ (mg) = 1-2, 2-3, 3-4, etc.). For the fourth cluster analysis, each of the 520 decapods was assigned to one of nine random groups, and the cluster analysis was performed on these randomly assigned groups. This analysis was performed as somewhat of a control, to determine the level of similarity between diets between groups of a similar size to those used in the previous analysis. Nine groups were used, because the species analysis contained nine groups, and the dry weight analysis eight groups.

Following the cluster analysis, an analysis of similarities (ANOSIM) was performed. ANOSIM is a nonparametric, multivariate analysis similar to analysis of variance (ANOVA). Instead of testing for a difference between a set of group means, ANOSIM tests for differences in relative similarities in community composition, in this case using a Bray-Curtis Similarity

matrix (Clarke and Warwick, 2001). The analysis was performed for the same four factors used in the cluster analysis: depth/time interval, decapod species, decapod weight, and randomly assigned groups, though for the ANOSIM the full data set was used, without averaging by factor. For each factor, a test statistic, R, was calculated, as show in **Equation 3.6**.

$$\text{Equation 3.6 } R = \frac{(\bar{r}_B - \bar{r}_W)}{\frac{1}{2}M}$$

\bar{r}_B is the average of rank similarities from all pairs of replicates between different groups, \bar{r}_W is the average of all rank similarities among replicates within groups, $M = n(n - 1)/2$, and n is the total number of groups. The value of R lies between -1 and +1, with a value of 1 indicating that all replicates within a group are more similar to one another than to replicates from other groups, a value of 0 indicating that there is no difference between groups, and a value of -1 indicating that all replicates within groups are less similar to one another than to replicates from other groups (Clarke and Warwick, 2001). A total of 999 random permutations were conducted to assess the significance level of R, with a significance level of 0.05 or lower being considered statistically significant.

3.3 Results

A statistically significant correlation was found between food ball wet weight and food ball dry weight (**Equation 3.7**):

$$\text{Equation 3.7 } FB_{DW} = 0.14 * FB_{WW}$$

For this relationship the R^2 was 0.868, with a p-value $< 2 \times 10^{-16}$ ($t = 24.71$, $DF = 93$). Variance was highest for heavy food balls, but the equation was only used to estimate FB_{DW} for stomachs where $FB_{DW} \leq 0.3$ mg, so estimates should be quite precise (**Figure 3.2**).

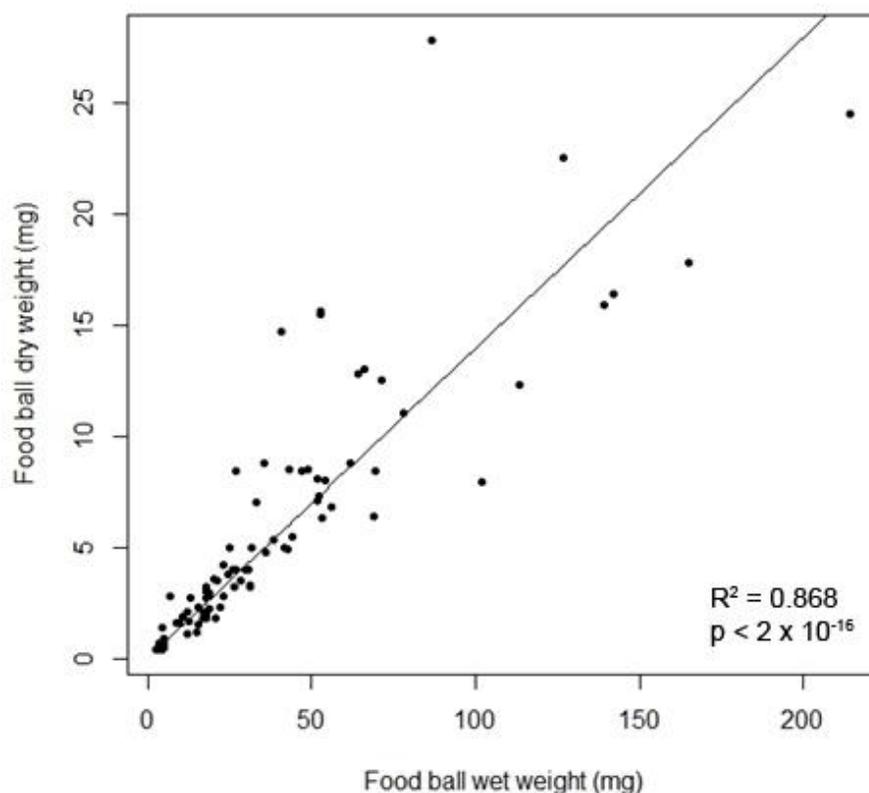


Figure 3.2 Food ball wet weight (mg) vs. food ball dry weight (mg) for all decapod stomach's analyzed from the 2004 *Oscar Elton Sette* cruise. The regression line shown is described in **Equation 3.7**.

A statistically significant correlation was also found between organism dry weight * stomach fullness and food ball dry weight (**Equation 3.8**).

$$\text{Equation 3.8 } FB_{DW} = 0.020 * Org_{DW} * Fullness$$

For this relationship the R^2 was 0.8204, with a p-value $< 2 \times 10^{-16}$ ($t = 20.61$, $DF = 93$). Again, there was more variance for heavy food balls, but in this chapter **Equation 3.8** was only used when $FB_{WW} \leq 0.3$ mg, so the estimates should be reasonably precise (**Figure 3.3**). In Chapter 1,

Equation 3.8 was used for a wide range of organism dry weights and stomach fullness, but it should still provide a reasonable estimate given the high R^2 and low p-value.

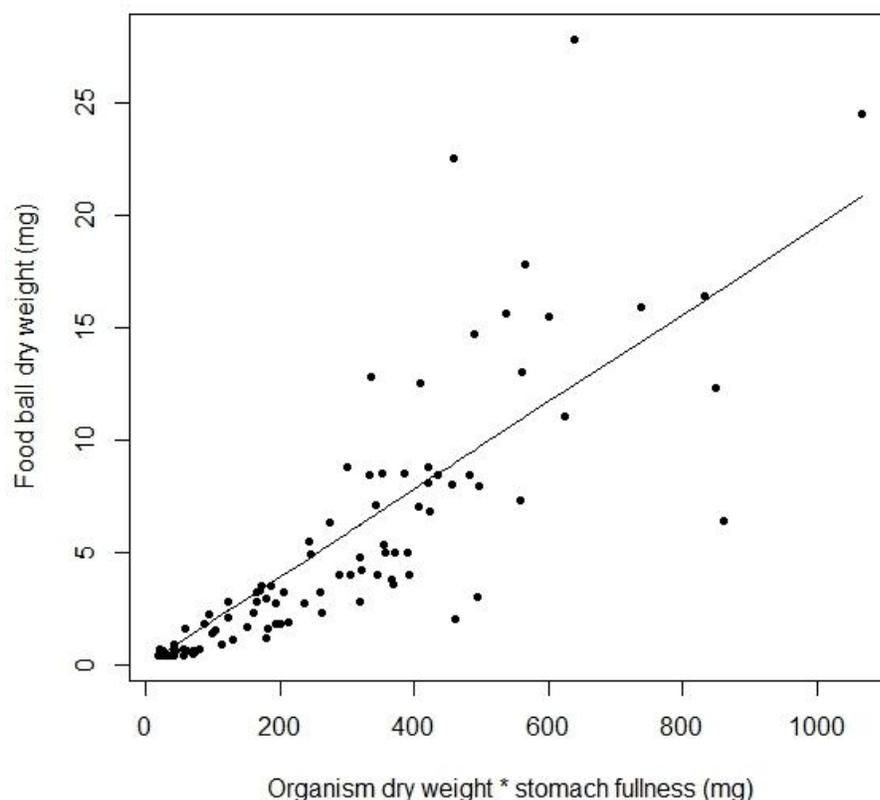


Figure 3.3 Organism dry weight * stomach fullness (mg) vs. food ball dry weight (mg) for all decapod stomach's analyzed from the 2004 *Oscar Elton Sette* cruise. The regression line shown is described in **Equation 2.8**.

Once **Equations 3.7** and **3.8** were used to correct all food ball dry weights too small to be measured accurately by the scale, SFI through the depth/time intervals as well as prey composition during the day and night was calculated. For 6 of the 9 species (*J. spinicauda*, *N. orientalis*, *O. gracilirostris*, *S. gardineri*, *S. scintillans* and *S. richardi*) the full 75 individuals per species were analyzed, at all depth/time intervals. For 2 of the species (*A. smithi* and *P. armatus*), no individuals were caught in either of the shallow intervals (Shallow EN or Shallow LN), likely because they did not migrate up to 120 m, so only individuals from the Deep ED,

Deep LD and Deep E/LN were analyzed. *Notostomus elegans* were caught only in the Deep E/LN interval, but were included in the analysis because of their exceptionally large size, and thus significant contribution to local decapod biomass.

Janicella spinicauda showed a trend of decreasing SFI throughout the day, with SFI peaking in the Shallow EN interval, and progressively lowering at each interval through to Deep E/LN (**Figure 3.4**). However, an ANOVA showed that SFI did not vary significantly between depth/time intervals ($p = 0.0519$, $F = 2.4767$, $DF = 4$ and 70). It should be noted that the p -value was 0.0519 , very close to the 0.05 significance level cut off, so it is possible that the sample size was simply not large enough to detect a statistically significant difference in mean SFI.

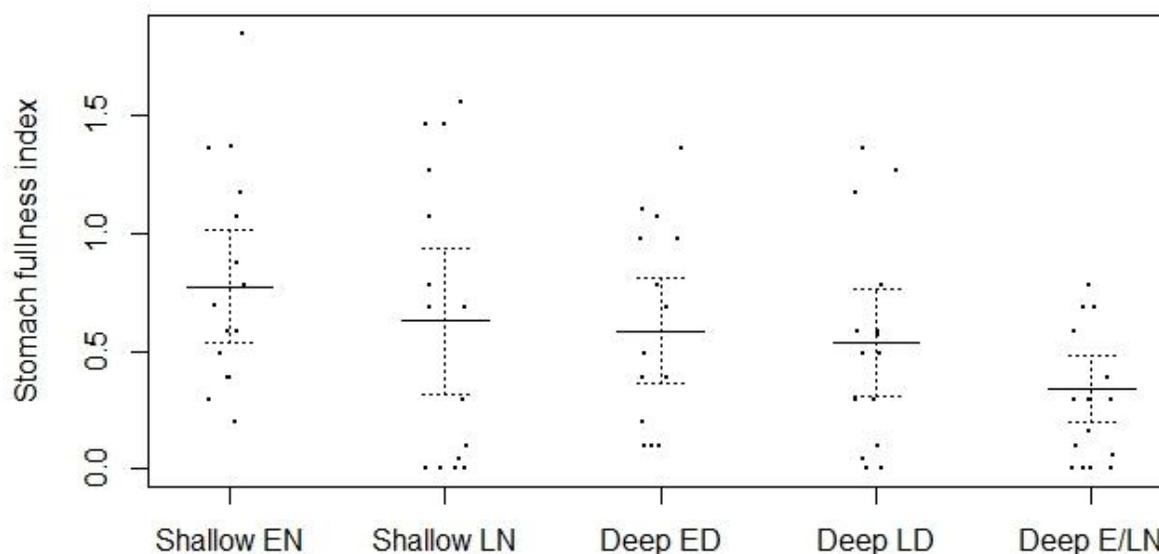


Figure 3.4 *Janicella spinicauda* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Sixteen different prey taxa were found in *J. spinicauda* stomachs, with Osteichthyes (fish) and *Pleuromamma* spp. (a genus of calanoid copepod) being the largest contributors to mean dry weight per shrimp (**Figure 3.5**). For most prey the mean DW per shrimp was higher for shrimp caught in the SSL than for shrimp caught in the DSL. However, two prey taxa were

found only in the stomachs of shrimp caught in the DSL: *Atlanta* spp. (a genus of gastropod) and Decapoda.

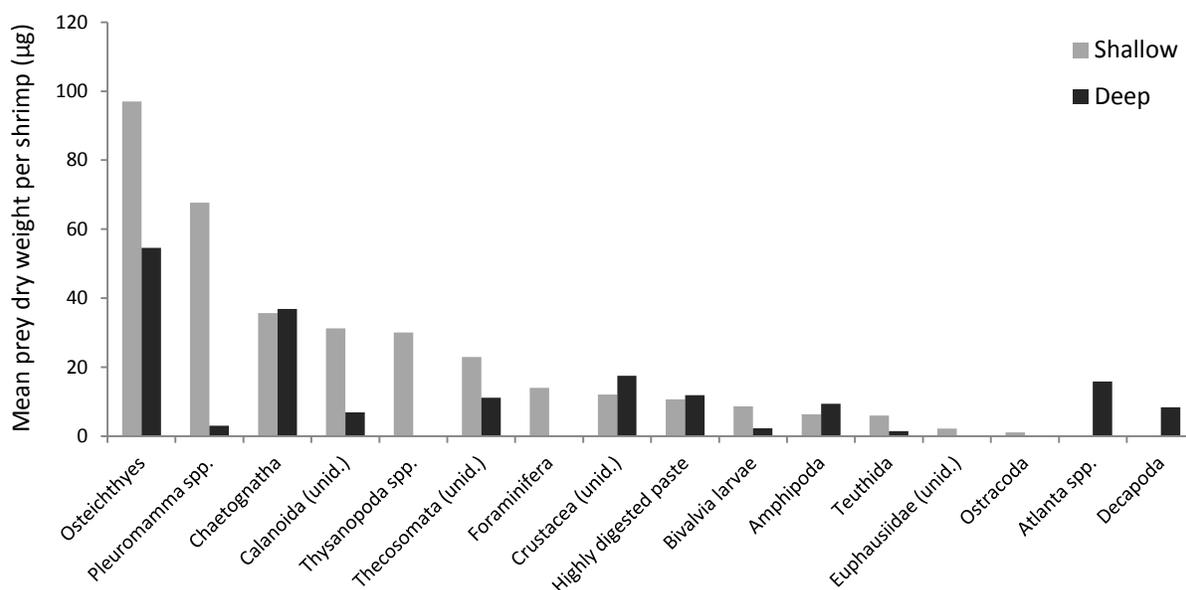


Figure 3.5 *Janicella spinicauda* diet

Neosergestes orientalis had generally high SFI near the surface, and generally low SFI at depth (**Figure 3.6**). An ANOVA showed that SFI varied significantly between different depth/time intervals ($p = 0.0228$, $F = 3.0369$, $DF = 4$ and 70). It is worth noting that there appeared to be a slight increase in SFI from when individuals would be expected to most recently migrate to depth (Deep ED) to when they would be expected to have been at depth for the longest period of time (Deep E/LN), though this trend was not statistically significant (**Figure 3.6**).

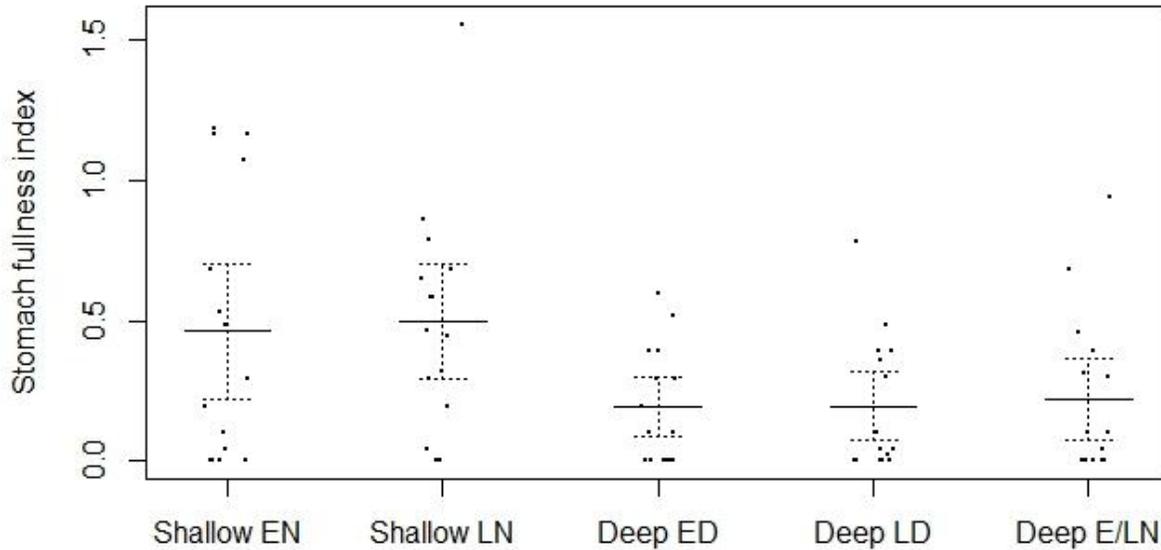


Figure 3.6 *Neosergestes orientalis* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Eleven different prey taxa were found in *N. orientalis* stomachs, with *Nematobrachion* spp. (a genus of krill) and unidentified crustaceans being the largest contributors to mean dry weight per shrimp (**Figure 3.7**). *Pleuromamma* spp., Osteichthyes and *Thysanopoda pectinata* (a species of krill) were all found only in shrimp caught in the DSL, while calanoid copepods were found almost exclusively in such shrimp (**Figure 3.7**). Highly digested paste was found only in shrimp caught in the DSL, though this is not its own a taxa of prey, but simply prey that has been digested so thoroughly that it is unidentifiable.

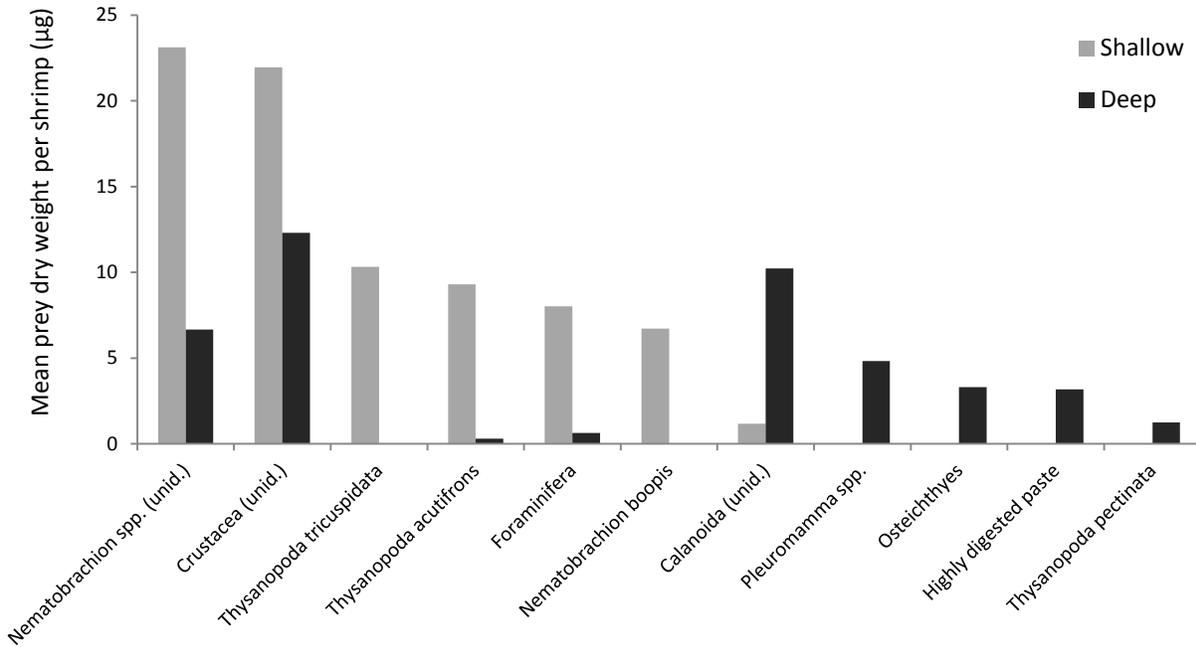


Figure 3.7 *Neosergestes orientalis* diet

Oplophorus gracilirostris peaked in SFI during the Shallow LN interval, and had generally higher SFI near the surface than at depth (**Figure 3.8**). An ANOVA showed that SFI varied significantly between different depth/time intervals ($p = 0.0101$, $F = 3.5936$, $DF = 4$ and 70). Of the three intervals in the DSL, mean SFI was highest for shrimp caught in the Deep E/LN, when they would be expected to have been at depth for the longest period of time, though none of the deep intervals had mean SFIs statistically different from one another (**Figure 3.8**).

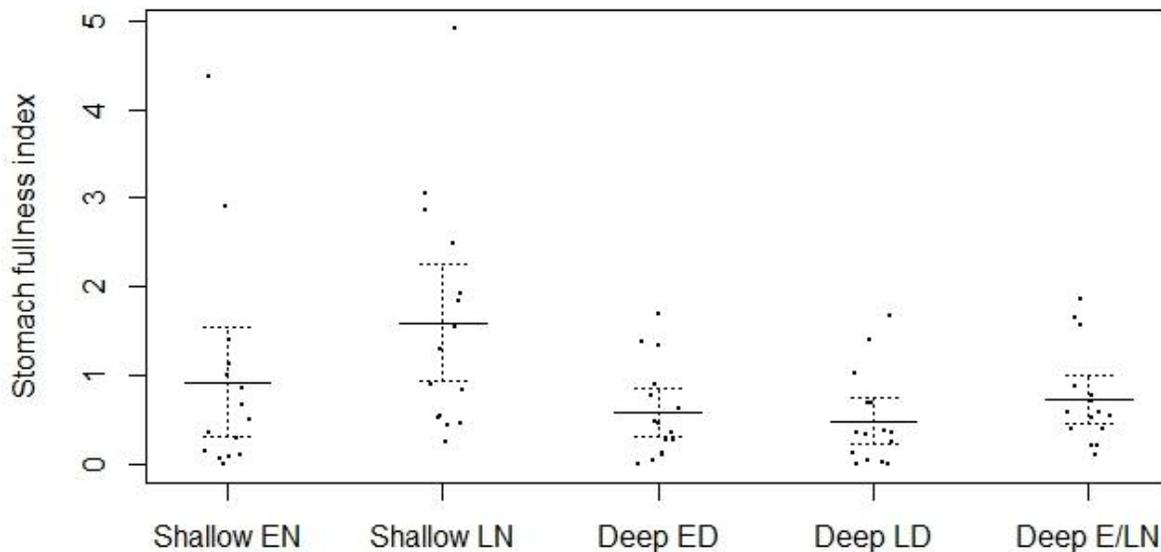


Figure 3.8 *Oplophorus gracilirostris* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Eighteen different prey taxa were found in the *O. gracilirostris* stomachs, with Osteichthyes being by far the largest contributors to mean dry weight per shrimp (**Figure 3.9 a**). As there were many rare prey taxa that were not well displayed by the standard scale (**Figure 3.9 a**), the same data was also displayed in log scale (**Figure 3.9 b**). Eight prey taxa were found only in shrimp caught in the DSL, though all were minor contributors to overall diet in terms of mean dry weight, and another two (Chaetognatha and Euphausiidae) were found almost exclusively in DSL shrimp (**Figure 3.9 b**). Highly digested paste was also found only in shrimp caught in the DSL (**Figure 3.9 b**). Three prey taxa (chaetognaths, amphipods and unidentified krill) were found predominantly in shrimp caught in the DSL (**Figure 3.9 b**).

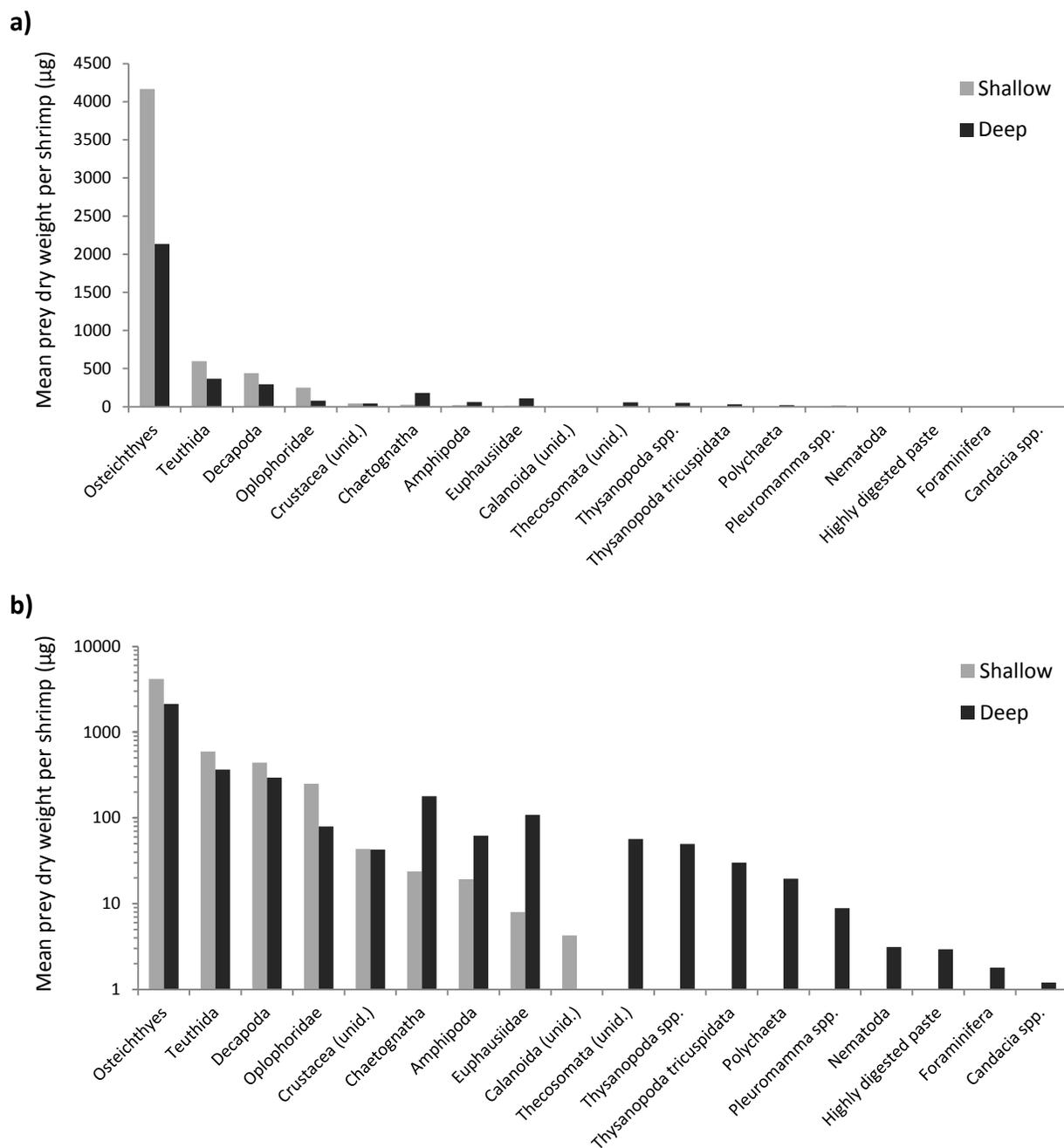


Figure 3.9 *Oplophorus gracilirostris* diet. Both **a)** and **b)** display the same data, but **b)** is shown in log scale to better display the rare prey taxa

Sergia gardineri had generally high SFI near the surface, and generally low SFI at depth, with mean SFI peaking during the Shallow LN interval (**Figure 3.10**). An ANOVA showed that SFI

varied significantly between different depth/time intervals ($p = 0.0210$, $F = 3.0943$, $DF = 4$ and 70).

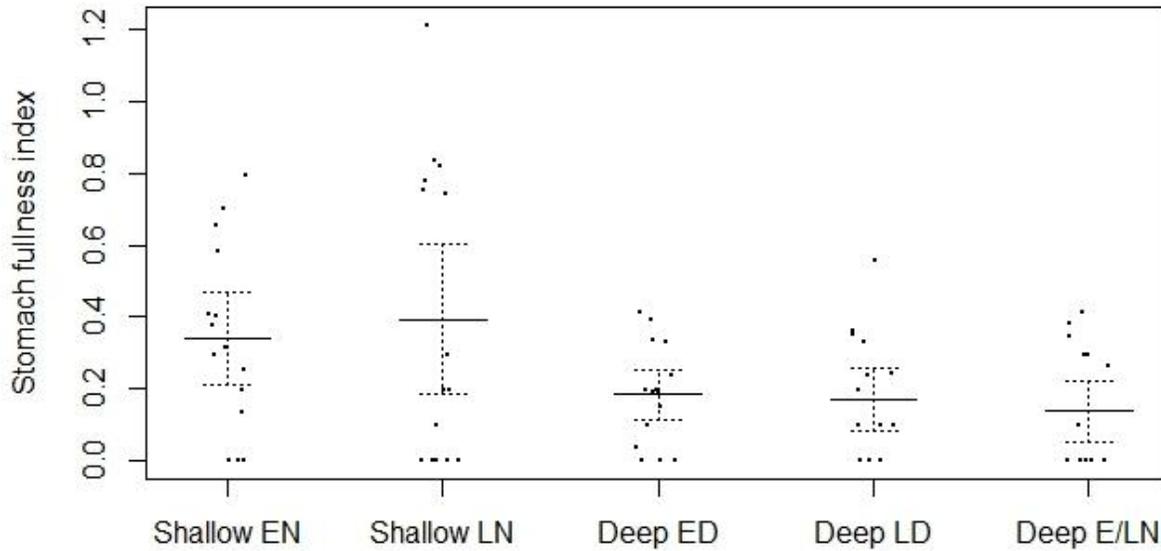


Figure 3.10 *Sergia gardineri* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Ten different prey taxa were found in *S. gardineri* stomachs, with unidentified calanoid copepods being the largest contributors to mean dry weight per shrimp (**Figure 3.11**).

Forminifera were found only in shrimp caught in the DSL, as was highly digested paste (**Figure 3.11**).

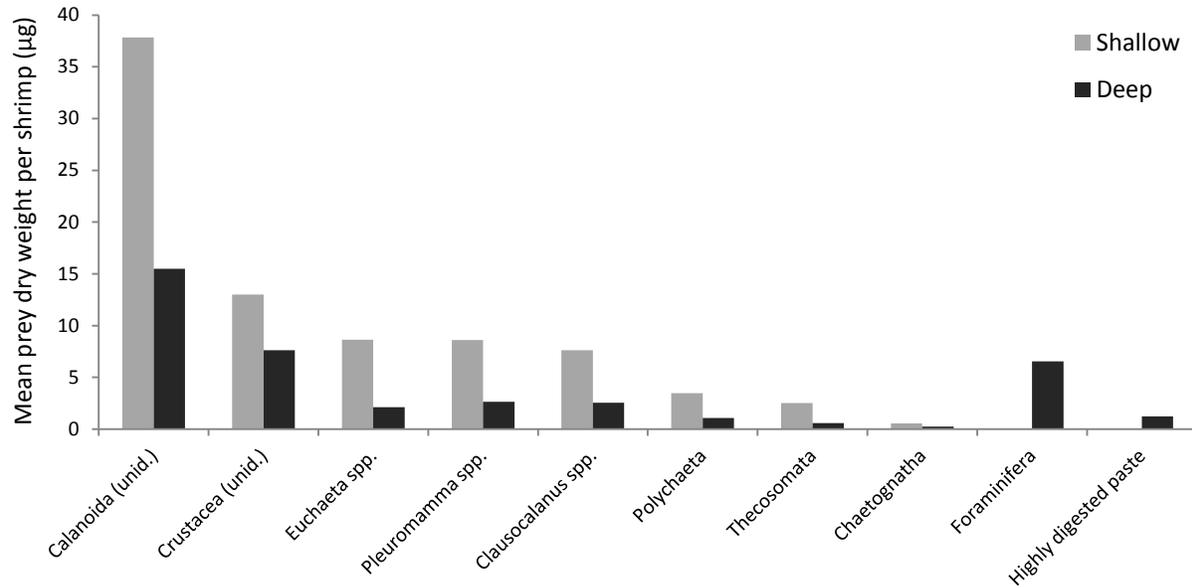


Figure 3.11 *Sergia gardineri* diet

Sergia scintillans had generally high SFI near the surface, and generally low SFI at depth, with mean SFI peaking during the Shallow EN interval (**Figure 3.12**). An ANOVA showed that SFI varied significantly between different depth/time intervals ($p = 0.0175$, $F = 3.3879$, $DF = 4$ and 70). In the DSL, mean SFI was highest during the Deep LD interval, though no intervals in the DSL were statistically different from one another (**Figure 3.12**).

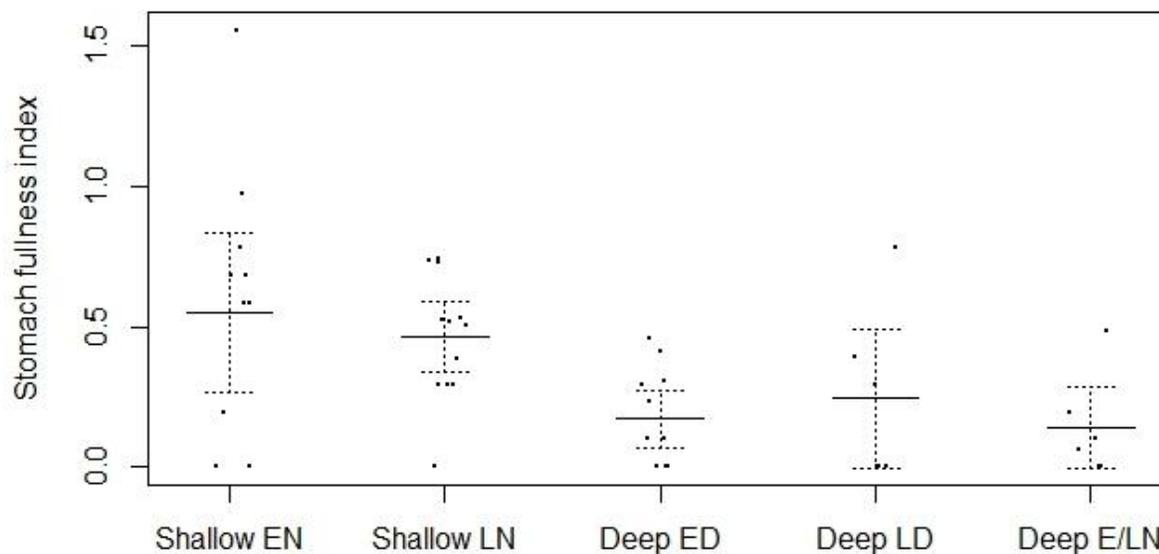


Figure 3.12 *Sergia scintillans* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Eight different prey taxa were found in *S. scintillans* stomachs, with unidentified calanoid copepods being the largest contributors to mean dry weight per shrimp (**Figure 3.13**). Osteichthyes and *Pleuromamma* spp. were found only in shrimp caught in the DSL (**Figure 3.13**).

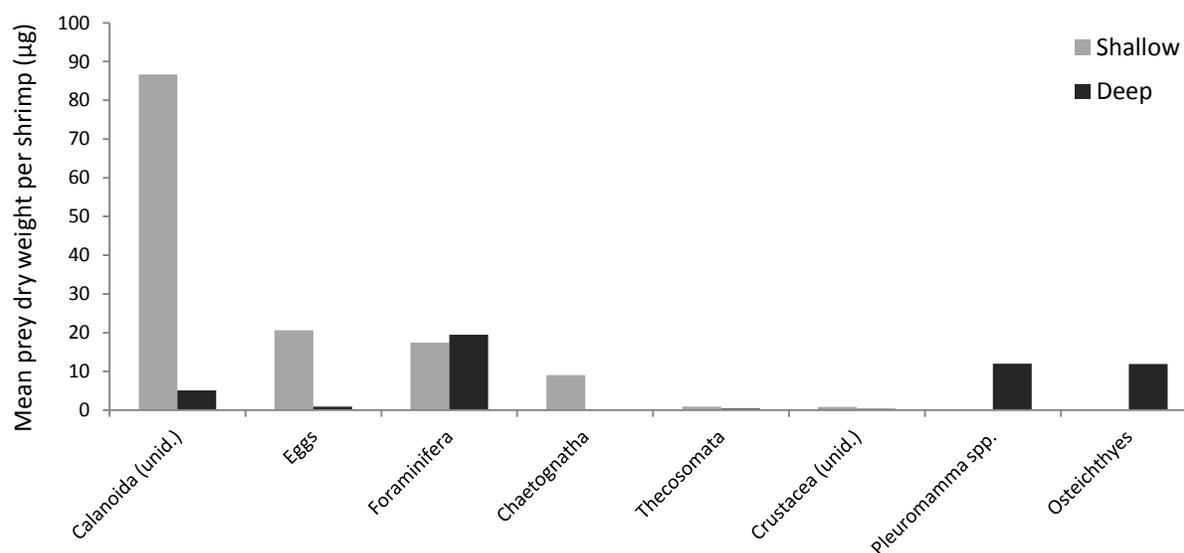


Figure 3.13 *Sergia scintillans* diet

Stylopandalus richardi had low mean SFI at all depth/time intervals except during the Shallow LN, where mean SFI was high (**Figure 3.14**). An ANOVA showed that SFI varied significantly between different depth/time intervals ($p < 0.0001$, $F = 20.2770$, $DF = 4$ and 70).

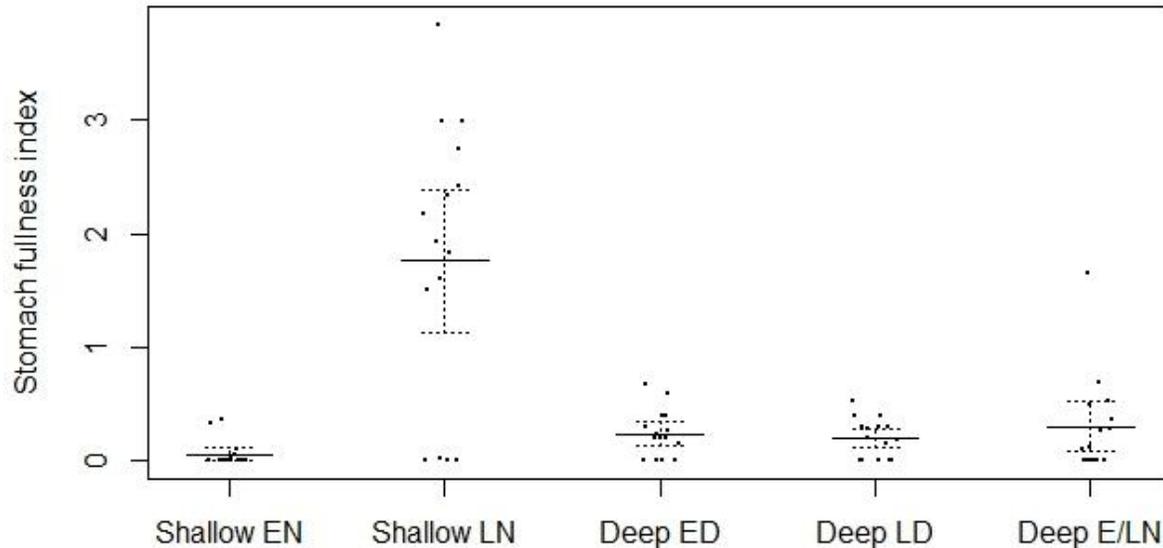


Figure 3.14 *Stylopandalus richardi* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Thirteen different prey taxa were found in *S. richardi* stomachs, with unidentified crustaceans being the largest contributors to mean dry weight per shrimp (**Figure 3.15**).

Thysanopoda acutifrons and unidentified eggs were found only in shrimp caught in the DSL, as was highly digested paste (**Figure 3.15**).

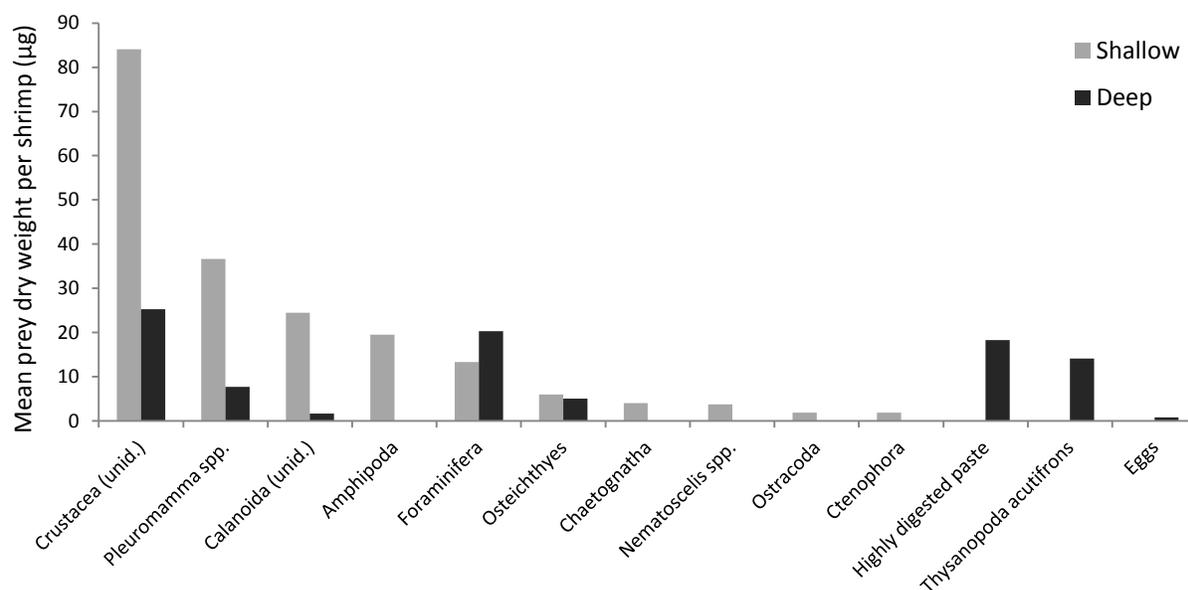


Figure 3.15 *Stylopandalus richardi* diet

The upper and lower bounds for the estimates of feeding at depth, expressed as a percentage of feeding during the day, are shown in **Table 3.3**. Only those species for which stomachs were analyzed from both the SSL and DSL were included. For all six species combined, the mean upper bound for feeding at depth was 44.69% of feeding near the surface, while the mean lower bound for feeding at depth was 9.67% of feeding near the surface. It should be noted that "highly digested paste" was not included as a DSL exclusive prey taxa in these calculations, since it is likely a result of digested SSL feeding, not new DSL feeding.

Table 3.3 Upper and lower boundaries for the estimates of feeding at depth, expressed as a percentage of feeding during the day.

Species	Upper boundary (%)	Lower boundary (%)
<i>Janicella spinicauda</i>	69.57	4.20
<i>Neosergestes orientalis</i>	42.05	24.32
<i>Oplophorus gracilirostris</i>	48.09	8.28
<i>Sergia gardineri</i>	44.82	4.77
<i>Sergia scintillans</i>	36.61	8.82
<i>Stylopandalus richardi</i>	26.98	7.64

As mentioned above, three of the decapod species (*A. smithi*, *P. armatus*, and *N. orientalis*) were caught only in the DSL, likely because they did not migrate into the SSL during the night. *A. smithi* was found during the Deep ED, Deep LD, and Deep E/LN intervals, with very little difference in mean SFI through these intervals (**Figure 3.16**). An ANOVA failed to reject the null hypothesis that mean SFI was identical for all intervals ($p = 0.8891$, $F = 0.1179$, $DF = 2$ and 38).

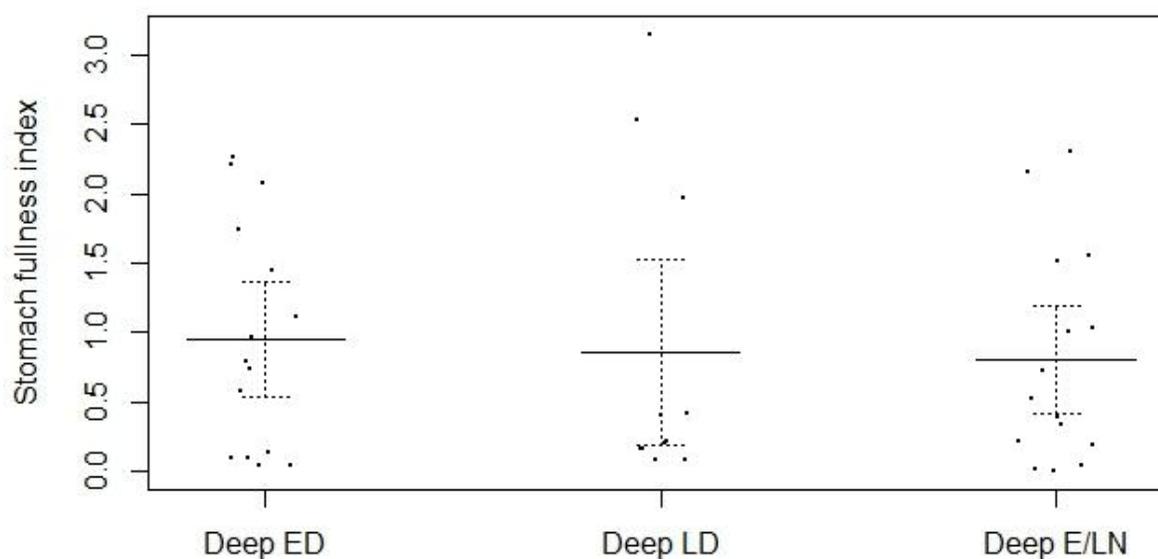


Figure 3.16 *AcanthePHYRA smithi* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Fourteen different prey taxa were found in *A. smithi* stomachs (**Figure 3.17**). Pandalidae (a family of Decapoda) were the largest contributors to the diet by mean dry weight, though unidentified crustaceans, Ophlophoridae (a family of Decapod), Osteichthyes and Polychaeta were all similarly large contributors, while the other 9 prey taxa were relatively rare (**Figure 3.17**).

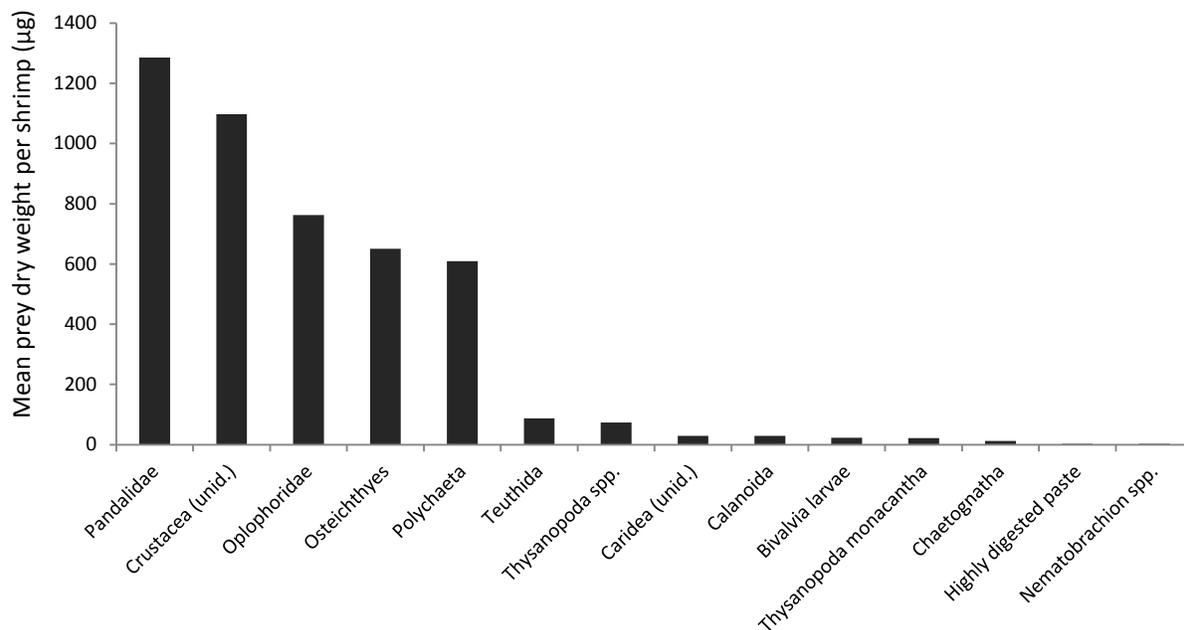


Figure 3.17 *AcanthePHYra smithi* diet

Like *A. smithi*, *P. armatus* was found during the Deep ED, Deep LD, and Deep E/LN intervals, also with very little difference in mean SFI through these intervals (**Figure 3.18**). An ANOVA failed to reject the null hypothesis that mean SFI was identical for all intervals ($p = 0.7852$, $F = 0.2432$, $DF = 2$ and 42). It should be noted that, compared to most other decapod species in this study, mean SFI was low at all depth/time intervals (**Figure 3.18**).

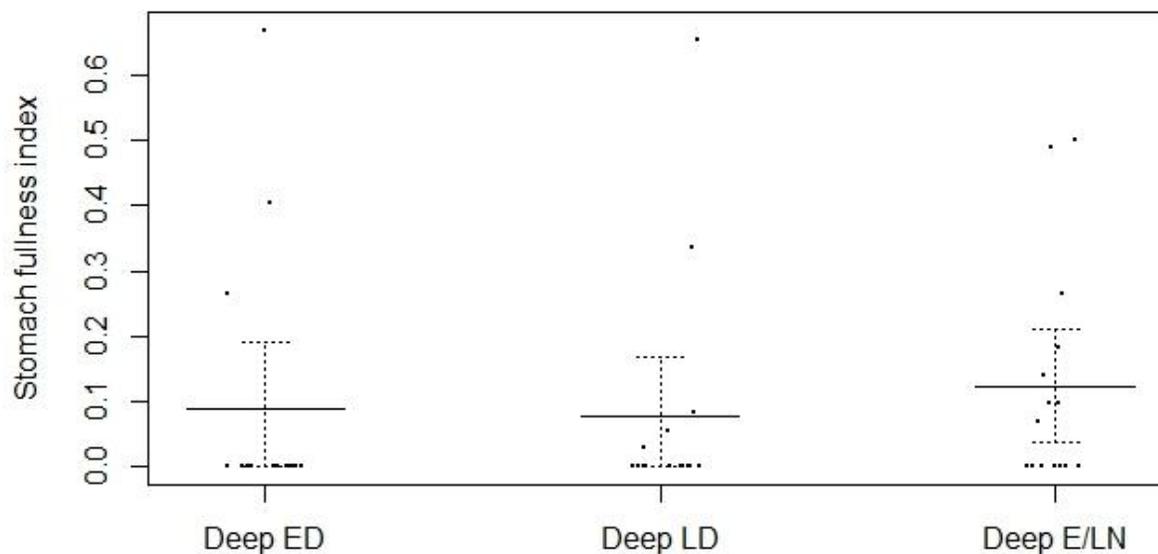


Figure 3.18 *Parasergestes armatus* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Nine different prey taxa were found in *P. armatus* stomachs (**Figure 3.19**). Unidentified calanoid copepods were the largest contributors to the diet by mean dry weight, Osteichthyes the smallest contributors, while all other prey taxa made up similar contributions (**Figure 3.19**).

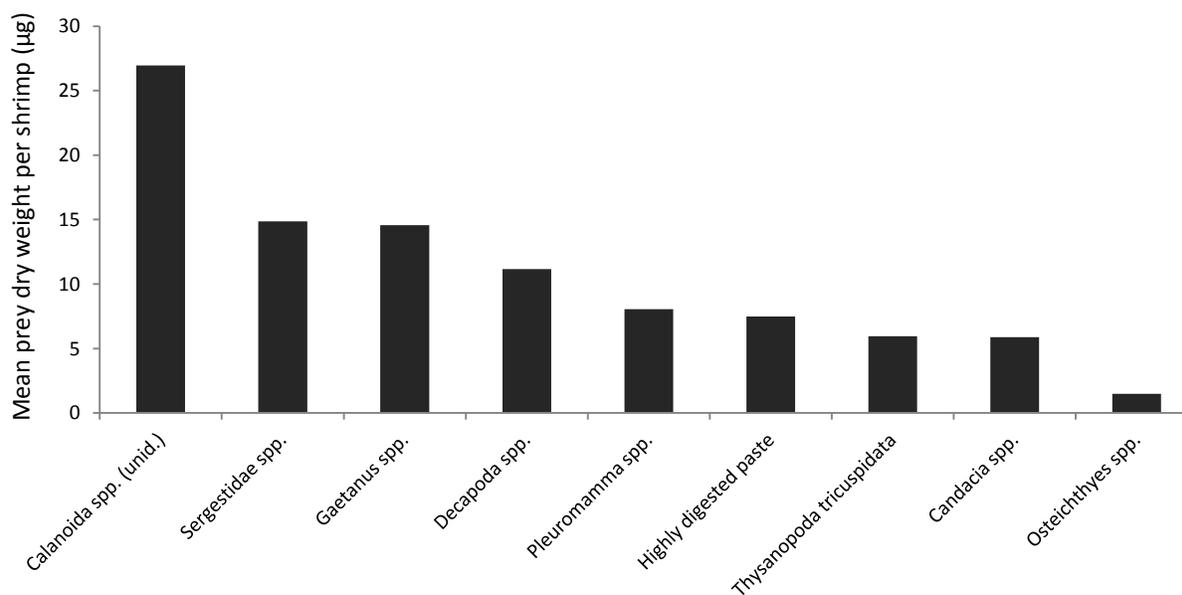


Figure 3.19 *Parasergestes armatus* diet

Notostomus elegans were very rare in the samples, with a total of only 13 specimens collected, but their diet was analyzed regardless as they were still significant contributors to local decapod biomass due to their very large size; *N. elegans* had a mean dry weight of 1511.20 mg per individual, while most other decapod species have mean dry weights in the range of 10-100 mg per individual (**Table 2.3**). *Notostomus elegans* were found only in the DSL at night (**Figure 3.20**), and there was no statistically significant difference in mean SFI from individuals caught during the Deep EN and the Deep LN ($p = 0.9068$, $F = 0.0144$, $DF = 1$ and 11). It should be noted that, compared to most other decapod species in this study, mean SFI was low at all depth/time intervals (**Figure 3.20**).

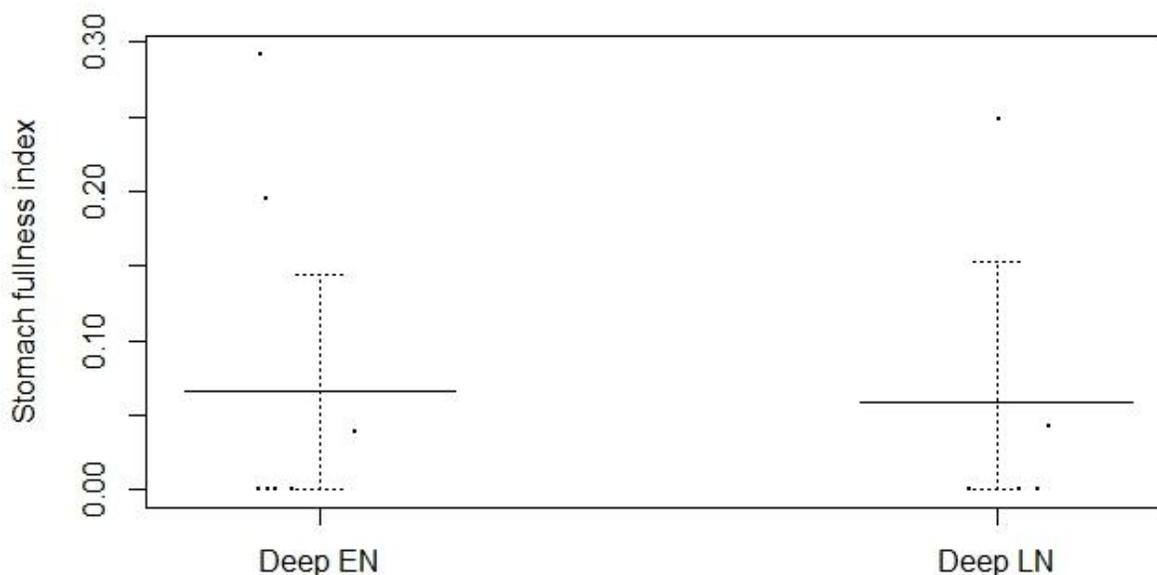


Figure 3.20 *Notostomus elegans* stomach fullness index through its diel vertical migrations. Error bars show 95% confidence intervals for the estimate of the mean.

Only 3 prey taxa were found in *N. elegans* stomachs, with Osteichthyes being the most common (**Figure 3.21**).

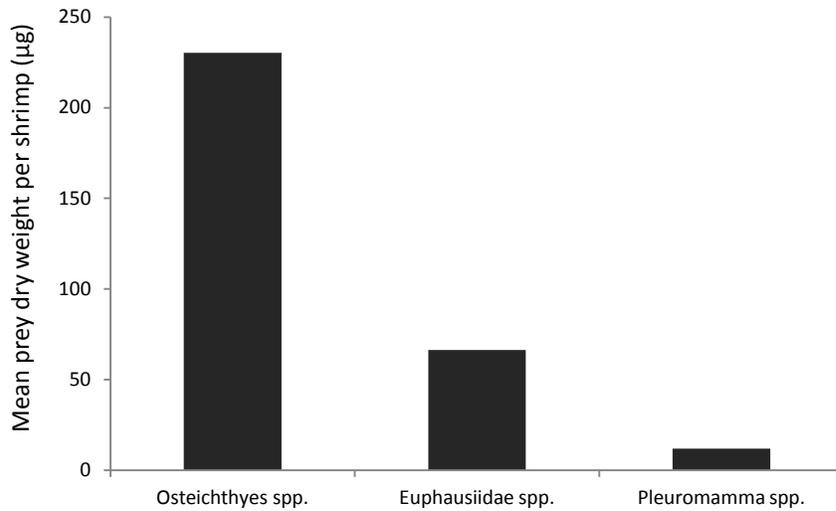


Figure 3.21 *Notostomus elegans* diet

Cluster analysis showed that, for decapod diets averaged by depth/time intervals, diets clustered into two main groups: one group for diets of decapods caught in the SSL, and another for decapods caught in the DSL (**Figure 3.22**). However, even at this highest level of clustering, similarities between diets were high, with a Bray-Curtis Similarity of 66.5% between the diets of the SSL and DSL clusters (**Figure 3.22**). An ANOSIM run on the full data set, with depth/time intervals as the factor being tested, found that there was no significant difference in prey composition between the different intervals ($p = 0.106$, $R = 0.003$).



Figure 3.22 Dendrogram showing Bray-Curtis Similarity in prey composition for decapods caught in 5 different depth/time intervals: in the SSL during the early and late night (Shallow EN and Shallow LN), and in the DSL during the early day, late day, and early/late night (Deep ED, Deep LD and Deep E/LN).

For decapod diets averaged by decapod species, cluster analysis showed diets clustering into two main groups: one group contained only the four Oplophorid decapod species, while the other group contained the four Sergestid decapod species, as well as the Pandalid decapod species (**Figure 3.23**). Diets between species were quite dissimilar, at the highest level of clustering diets had a Bray-Curtis Similarity of just 18.8%, and even for the two species with the most similar diets (*S. gardineri* and *S. scintillans*) Bray-Curtis Similarity was 57.7% (**Figure 3.23**). An ANOSIM run on the full data set, with decapod species as the factor being tested, found that prey composition was significantly different between species ($p < 0.001$, $R = 0.161$).

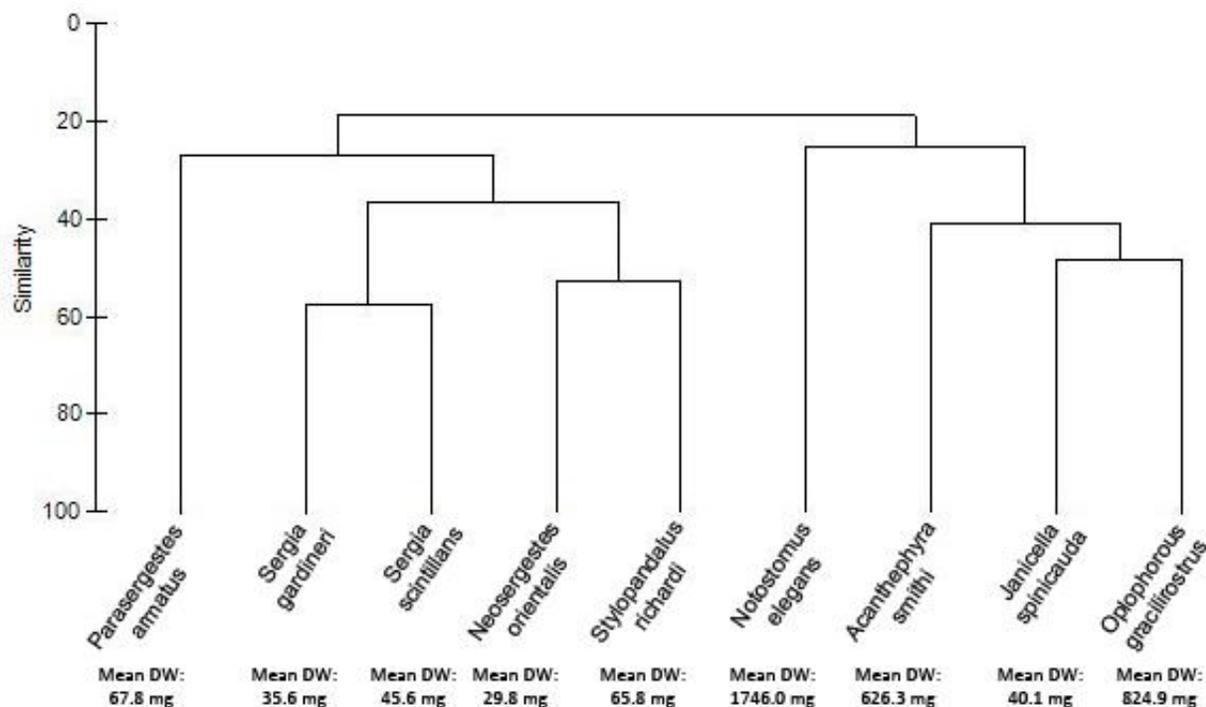


Figure 3.23 Dendrogram showing Bray-Curtis Similarity in prey composition for the 9 different decapod species analyzed in this study. The mean dry weight for one individual of each species is provided.

For decapod diets averaged by $\ln(\text{DW})$ bins, cluster analysis showed diets clustering into two main groups: one group containing decapods with a $\ln(\text{DW})$ of 1-5 mg, the other group containing decapods with a $\ln(\text{DW})$ of 5-9 mg (**Figure 3.24**). Bray-Curtis Similarity at this highest level of clustering was 19.6% (**Figure 3.24**). At lower levels of clustering diets continued to group together by similar dry weights: $\ln(\text{DW})$ bins of 2-3 mg with 3-4 mg, 5-6 mg with 6-7 mg, and 7-8 mg with 8-9 mg (**Figure 3.24**). An ANOSIM run on the full data set, with $\ln(\text{DW})$ bins as the factor being tested, found that prey composition was significantly different between bins ($p < 0.001$, $R = 0.035$).

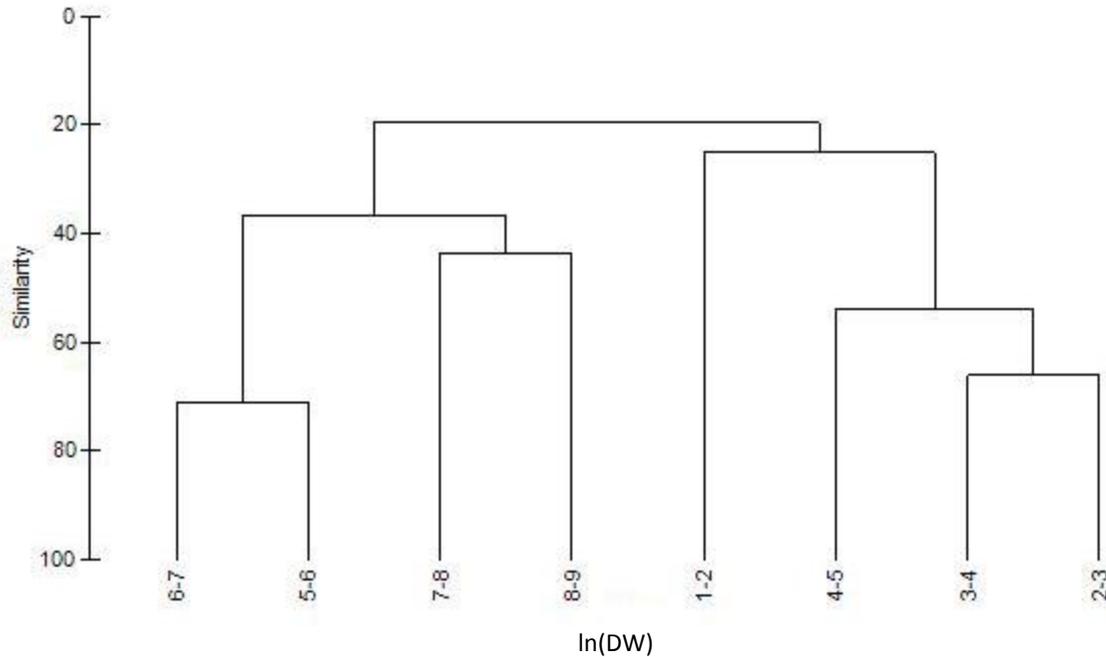


Figure 3.24 Dendrogram showing Bray-Curtis Similarity in prey composition for bins of ln(DW). "1-2" represents the prey composition of all decapods with a ln(DW) of 1-2 mg (and thus a DW of 2.72 - 7.39 mg), "2-3" represents the prey composition of all decapods with a ln(DW) of 2-3 mg (and thus a DW of 7.39 - 20.09 mg), etc.

For decapod diets averaged by 9 randomly assigned groups, cluster analysis showed Bray-Curtis Similarity to range from 78.1% between the most similar groups, to 67.5% at the highest level of clustering (**Figure 3.25**). An ANOSIM run on the full data set, with randomly assigned groups as the factor being tested, found that prey composition was not significantly different between groups ($p = 0.647$, $R = -0.001$).

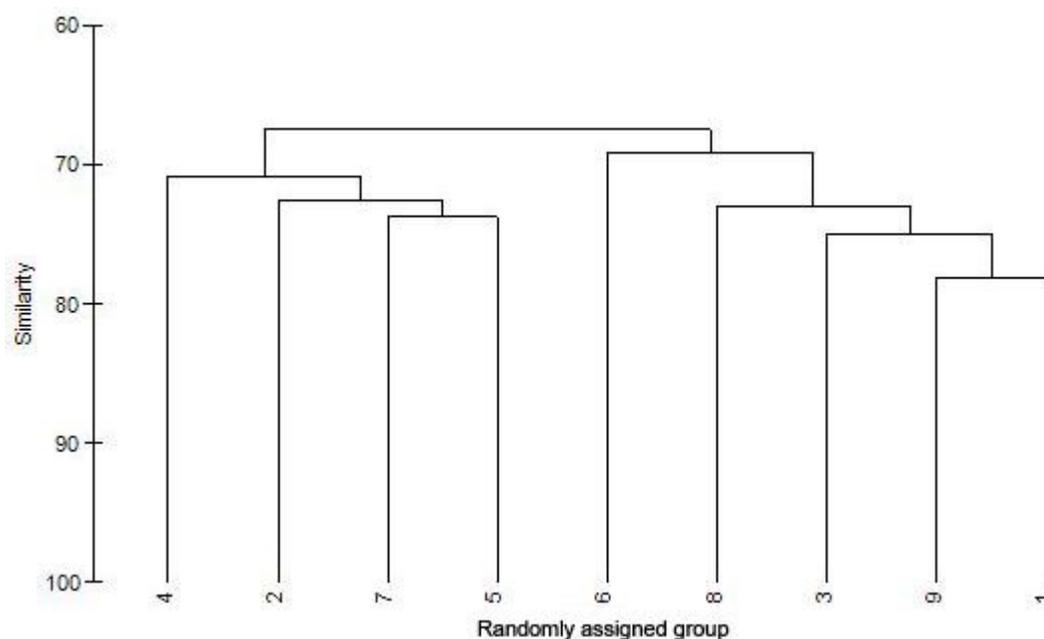


Figure 3.25 Dendrogram showing Bray-Curtis Similarity in prey composition for randomly assigned groups. All 520 decapods analyzed were randomly assigned a group from 1 to 9, thus each group represents the average prey composition for ~58 decapods.

3.4 Discussion

3.4.1 Diurnal feeding

The SFI data indicate intensive nocturnal feeding in the SSL for all decapod species that were found in quantities sufficient for analysis across all depth/time intervals. Only *J. spinicauda* did not have a significantly higher SFI during one of the night time SSL intervals, but there was a trend of decreasing SFI through the intervals, and with the results very close to being significant ($p = 0.0519$), it is likely the case that nocturnal feeding was occurring, but the sample size was not quite large enough to show a statistically significant difference.

While it seems that all decapods were feeding more in the SSL than the DSL, the prey composition data separated by depth shows strong evidence that the decapods were feeding in the DSL as well, as for every species there were between one and eleven prey taxa (not

including highly digested paste) that occurred exclusively or almost exclusively in decapods caught in the DSL. Furthermore, all prey taxa that appeared to have been consumed in the DSL (*Atlanta* spp., *Candacia* spp., Foraminifera, Nematoda, *Pleuromamma* spp., *Thysanopoda acutifrons*, *Thysanopoda pectinata*, *Thysanopoda tricuspidata*, *Thysanopoda* spp., Chaetognatha, Decapoda, Euphausiidae, Osteichthyes, Polychaeta, and Thecosomata), are known to occur in the mesopelagic layer, with the possible exception of nematoda, which could have been consumed as a parasite on another organisms, or from the sediments (Nemoto, 1968; Maynard et al., 1975; Hu, 1978; Baars and Oosterhuis, 1984; Mauchline, 1985; Almogilabin et al., 1988; Forward, 1988; Seapy, 1990; Al-Mutairi and Landry, 2001; Steinberg et al., 2008; Hull et al., 2011). It is thus reasonable that these prey could have been consumed at depth.

The estimates for feeding at depth as a percentage of feeding near the surface ranged from a mean upper boundary of 44.69% to a mean lower boundary of 9.67%. This would mean that the active flux due to decapod migrations calculated in the first research chapter were overestimates, as they assumed no feeding at depth. Instead of 691.9 $\mu\text{gC}/\text{m}^2/\text{day}$ being transported to the mean daytime depth of 710.74 m, the active flux would be 387.7 – 625.0 $\mu\text{gC}/\text{m}^2/\text{day}$. Thus active flux would be reduced from 8.6% of passive flux at the mean night time residence depth (710.7 m) to 4.8 - 7.8%, from 3.4% of passive flux at the mean night time residence depth (261.8 m) to 2.1 - 3.4%, and from 2.7% of passive flux at the base of the euphotic zone (173 m) to 1.5 - 2.4%.

The upper boundary is meant to be a theoretical maximum estimate of feeding at depth, and it is almost certainly a significant overestimate. The upper boundary of the estimate

assumes that all food ingested in the SSL has passed out of the stomach by the time the shrimp were caught in the DSL, and thus that all stomach contents in the DSL were ingested within the DSL. While this could be the case for some prey items, or even parts of certain prey items, the harder to digest prey items and body parts would not be evacuated this rapidly (Clarke, 1980). Likewise, the lower boundary makes a nearly opposite assumption, that any time a prey taxa is found both in shrimp caught in the SSL and shrimp caught in the DSL, 100% of the prey must have been consumed in the SSL, and any of said prey present in stomachs of shrimp caught in the DSL must simply be residual prey from feeding in the SSL. An exception was made only for cases where the mean DW of the prey taxa in the DSL exceed that of the mean DW of the prey taxa in the SSL, as in this case it is far more likely that the prey was consumed in the DSL, not the SSL. Requiring the mean DW of the prey in the DSL to be at least five times that of the same prey in the SSL is an extreme condition, but the lower boundary was meant to be a very conservative estimate, that is almost certainly too low.

One process that could actually cause the lower boundary to be an overestimate of feeding at depth, as opposed to an underestimate, is natural variance. The sample size of 75 stomachs analyzed per species (30 from the SSL, 45 from the DSL) could be small enough that certain prey taxa that show up in the DSL shrimp but don't show up in the SSL shrimp do so simply by chance, as opposed to not showing up in the SSL shrimp because they are consumed only in the DSL. This seems unlikely, however, for three reasons. First, these prey taxa were often found in 3 to 6 DSL stomachs, but no SSL stomachs, thus the probability of them being consumed only in the SSL (with appearances in DSL stomachs due only to slow digestion) seems very low. Second, for cases like *O. gracilirostris*, where 11 of 18 prey taxa (ignoring highly

digested paste) were found exclusively in DSL shrimp, with just 1 prey taxa found exclusively in SSL shrimp, it again seems highly unlikely that chance alone could explain the results. Third, the cluster analysis further supports the hypothesis of feeding in the DSL. For the data set as a whole, the three DSL depth/time intervals clustered together, as did the two SSL depth/time intervals. While there was a high level of similarity between DSL and SSL gut contents on the whole (not surprising, given that many prey items consumed in the SSL could still be getting digested in the DSL, and vice versa), the clustering of diets by depths suggests that different prey were being consumed in the DSL, as opposed to DSL gut contents simply being made up entirely of partially digested prey from the SSL.

3.4.2 *Size vs. taxonomy*

One question that this thesis attempted to answer was whether pelagic decapod diets were controlled solely by the size of the decapod, or whether taxonomy played a role as well. Diets clustered strongly based on both the size and the species of the decapod, and both factors proved strongly significant with respect to dietary composition through an ANOSIM. Compared to the ANOSIM and cluster analysis performed on randomly assigned groups, diets between different species and different weight classes were highly dissimilar, with high R values, indicating that the clustering was not due to chance alone.

While diets clustered strongly based on decapod species, it should be noted that much of this clustering can be explained by decapod size. At the broadest level of clustering there were two groups: one containing only Sergestid and Pandalid species, the other containing only Ophiopodid species (**Figure 3.23**). The Sergestid and Pandalid group was composed exclusively

of relatively small species, each with a mean DW ranging from 29.8 to 67.8 mg/individual (**Figure 3.23**). The Oplophorid group was composed predominant of large species, with three of the four species having mean DWs of 626.3 to 1746.0 mg/individual, but this group also contained *J. spinicauda*, a relatively small species with with a mean DW of 40.1 mg/individual (**Figure 3.23**). *Janicella spinicauda* clustered most strongly with *O. gracilirostris*, a species ~20 times its size in terms of mean DW/individual. While strongly different in terms of size, *J. spinicauda* and *O. gracilirostris* are highly similar in terms of taxonomy and external anatomy, to the point where *J. spinicauda* was previously thought to belong to the genus *Oplophorus* (Chace, 1986). It appears that size alone cannot explain dietary preference in these decapods, with taxonomy likely influencing diet through similar feeding structures between taxonomically close species.

Also worth noting are the R values from the ANOSIM for both species and size. As mentioned in **section 3.2.3**, an R value of 1 indicates that all replicates within a group are more similar to one another than to replicates from other groups (for example, all 75 *J. spinicauda* shrimp would have gut contents more similar to one another than to any other shrimp), while an R value of 0 indicates that there is no difference between groups. When running an ANOSIM with species as the factor being tested, the R value was 0.161, compared to 0.035 with bins of $\ln(\text{DW})$ as the factor, so diets were more similar within species groups than they were within groups organized based solely on organism dry weight. This further emphasizes the point that, while decapod size clearly plays a key role in diet specialization, it cannot explain decapod diets alone, with taxonomy also having a role. Should a given pelagic decapod species be removed

from the ecosystem (through a targeted fishery, ecosystem change, etc.), a similar sized decapod species would not necessarily be able to fill the same niche.

It should be noted that diets were highly dissimilar between species, with just an 18.8% similarity in diet between the two broadest clusters (carideans and sergestids/pandalids), and a 57.7% similarity between the two species with most similar diets (*S. gardineri* and *S. scintillans*). For the randomly assigned groups similarities ranged from 67.5 - 78.1%, so an 18.8% similarity between diets represents very specialized diets. This suggests low levels of competition between species (Clarke, 1980), and helps explain how such a large diversity of decapod species could co-exist, especially when many show overlapping vertical distributions. This pattern of high diversity and low dietary overlap should not be surprising, as it has been observed for diel migrant micronekton myctophids in the central NPSG, while myctophids at high latitudes have been observed to have much more dietary overlap (Clarke, 1980).

3.4.3 Potential sources of error

One main caveat should be mentioned with respect to the dietary analyses in this chapter, which is that stomach content data is not necessarily representative of predator-prey relationships. There are three main sources of error inherent to using stomach content data to estimate natural diets: secondary feeding, feeding in the cod end, and variable rates of digestion for different prey.

Secondary feeding occurs when a predator consumes prey, with the later also having prey in their stomach. When analyzing the stomach of the predator, the prey composition could reflect not only prey consumed directly by the predator, but also secondary prey. For

example, in the eastern North Atlantic it has been observed that copepods of the genus *Pleuromamma* are very common in the stomachs of the decapod *Acantheephyra purpurea*, but that *Pleuromamma* were rare in *A. purpurea* feeding depths at the times when *A. purpurea* were feeding (Foxton and Roe, 1974). It was assumed that *Pleuromamma* were not being consumed directly by *A. purpurea*, but that the decapod was consuming prey such as chaetognaths, euphausiids and fish, which themselves had *Pleuromamma* in their stomachs. As the vertical distributions at the time of sampling were not collected for the potential prey in this thesis, it is impossible to say whether secondary feeding was occurring, and to what extent. The smallest prey found in the stomachs of the largest decapods are the most likely candidates for secondary feeding (Foxton and Roe, 1974), such as bivalve larvae in the stomachs of *A. smithi* or *Pleuromamma* in the stomachs of *N. elegans* and *O. gracilirostris*. Foraminiferans in the stomachs of larger decapods like *O. gracilirostris* were an unusual discovery, and could indicate secondary feeding, but the highly fragile nature of the tests (calcium carbonate shells) makes it unlikely that they could have survived predation by an intermediate predator. While it cannot be determined which food items, if any, were due to secondary feeding as opposed to direct predation, it is a weakness in the analysis worth keeping in mind.

Another potential source of error is feeding within the trawl's cod end. In the cod end of a trawl, organisms are packed together very tightly, and the decapods may have ingested prey that they would not normally ingest. For example, it has been shown that *Sergestes similis* caught by trawls have a higher percentage of euphausiids in their stomachs than *S. similis* found in the stomachs of albacore tuna, suggesting that *S. similis* might have fed preferentially on euphausiids when in the cod end of a trawl (Judkins and Fleminger, 1972). As with secondary

feeding, it is impossible to say to what extent feeding in the cod end occurred in the samples collected in this study, but both processes should be considered as potential sources of error in this study. It should be noted that a previous study on migratory decapods in the subtropical Atlantic found little evidence of feeding in the cod end, so this could potentially be a small source of error (Foxton and Roe, 1974).

Finally, variable digestion rates for different prey taxa must be considered. Prey that are digested quickly are likely underestimated in the diet in terms of both abundance and mass. For example, decapods could be eating significant quantities of entirely gelatinous organisms, but they would rarely show up in the stomachs as they would be digested too rapidly and would quickly become unidentifiable. Many organisms have both softer and harder parts of their bodies. Chaetognaths, for example, have hard grasping hooks, but very soft bodies otherwise, so in the decapod stomachs only grasping hooks were found. While this allows the number of chaetognaths ingested to be easily estimated, the biovolume (and thus biomass) of chaetognaths consumed would be underestimated, as the grasping hooks make up a low percentage of their biovolume. Similarly, for prey that would be hard to digest (such as *Osteichthyes*, with many difficult to digest body parts such as scales, jaw bones, fin rays and eye lenses), their percent contribution to overall diet by biomass could be overestimated, simply because their biovolume would be better preserved in stomachs than the biovolume of most other prey.

2.3.4 *Concluding remarks*

All migrant decapods for which gut content data was available across all five depth/time intervals displayed enhanced feeding at night in the SSL. However, these decapods did not feed entirely in the SSL, but continued to ingest prey in the DSL. It was estimated that feeding in the DSL ranged from 9.67 – 44.69% of feeding in the SSL (by dry weight) for the migratory decapod community as a whole. Thus the active flux estimate in the first research chapter should be reduced from 691.9 $\mu\text{gC}/\text{m}^2/\text{day}$ to 382.7 – 625.0 $\mu\text{gC}/\text{m}^2/\text{day}$. Furthermore, it was determined that decapod diets were diverse from species to species, and were not controlled by decapod size alone, with taxonomy being equally or more important.

4 Overall conclusions

Decapod community structure and vertical migrations in the central NPSG were described, with 19 of 22 species performing diel vertical migrations, to daytime WMDs of 475.00 – 1102.69 m. For all decapod species with a mean DW under 100 mg per individual, decapod weight was positively correlated with daytime WMD, though this relationship did not hold for the largest migratory decapods (*D. erectus* and *A. smithi*), possibly due to a reduced need to avoid visual predators. Migratory decapods were found to be significant contributors to local vertical carbon flux. When assuming 100% feeding near the surface at night, as all past active flux studies have done, decapods were estimated to be transferring 691.9 $\mu\text{gC}/\text{m}^2/\text{day}$ to a mean depth of 710.74 m, which corresponded to 2.7% of the passive flux to the base of the euphotic (173 m), 3.8% of the passive flux at the mean night time feeding depth (261.8 m), and 8.6% of the passive flux at the mean daytime residence depth (710.7 m). However, the assumption of 100% feeding near the surface at night was shown to be incorrect. Decapods fed both in the SSL and the DSL, with feeding in the DSL for the decapod community estimated to lie between a lower boundary of 9.67% and an upper boundary of 44.69% (by weight) of feeding in the SSL, for the migratory decapod community as a whole. Adjusting for DSL feeding, the active flux estimate for decapods was reduced to 382.7 - 625.0 $\mu\text{gC}/\text{m}^2/\text{day}$, or 1.5 - 2.4% of passive flux at the base of the euphotic, 2.1 - 3.4% of passive flux at the night time feeding depth, and 4.8 - 7.8% of passive flux at the daytime residence depth. Decapod diets were determined to vary strongly based on decapod size, but size alone could not explain all dietary variation, with taxonomy playing a role as well. Dietary similarity was low between species, which could help explain how such a large diversity of decapod species could co-exist in one environment despite largely overlapping vertical distributions.

One of the most important contributions of this thesis is to aid in the accurate modeling of global carbon cycles. In such models it is necessary to properly describe carbon sinks, and the strength of the ocean as a carbon sink depends in part on the strength of the biological pump. These findings show that, if active flux due to decapod communities is ignored in such models, estimates of the strength of the biological pump will be underestimates. It was shown that this underestimate would be considerable in the central NPSG, though in other regions of the world it could be less significant. In the central NPSG decapods are abundant and migrate to deep depths (Maynard et al., 1975), while the local passive flux in the central NPSG is weaker than in most other areas of the world's oceans (Francois et al., 2002). Furthermore, light is generally accepted to be the most significant external factor influencing diel vertical migrations, with migrations tending to be deepest and most common when surface irradiance is high, and attenuation with depth low (Forward, 1988). Thus we should expect migrations for decapods, and thus active flux, to be strongest at low latitudes, which is supported by a comparison of the results of this thesis to those of Kitamura et al. (in review). The warmer deep waters at low latitudes would accentuate this latitudinal effect, as respiration at depth would be more rapid (Ikeda, 1985), increasing the active respiratory flux. It is possible that active flux due to decapod migrations is similarly strong in other tropical and subtropical oceans, but it seems likely that decapod active flux at high latitudes would be of less relative importance.

Another important contribution of this thesis is to highlight the importance of estimating feeding at depth to the proper calculation of active fluxes. Previous active flux estimates have assumed no feeding at depth, but this study shows that, at least for pelagic decapods in the central NPSG, there was significant feeding at depth, that reduced estimates of decapod active flux by 9.67 – 44.69% compared to estimates made with the assumption of no

feeding at depth. The question arises whether such a pattern holds true for migratory species other than decapods. While estimates of the percentage of feeding at depth are not available for pelagic mesozooplankton and macrozooplankton, previous studies have shown that some feeding at depth appears to occur for mesozooplankton such as copepods (Baars and Oosterhuis, 1984) and macrozooplankton such as euphausiids (Hu, 1978). It would seem wise to attempt to quantify feeding at depth for all major migratory groups of organisms for which active flux estimates have been made, so as to avoid potentially large overestimates of active flux on a global scale.

This study is the first to attempt to calculate all four active fluxes for a group of organisms (respiratory, excretory, mortality and gut flux). It is also the first active flux study to test the assumption of no feeding at depth, and to attempt to quantify the extent of feeding at depth. Sampling extensively through the water column in both the day and night also allowed for the detection of migrations by species that migrate upwards at night, but not all the way into the epipelagic, which would be missed in many previous active flux studies which have sampled only in the epipelagic.

The comprehensive nature of this study, investigating pelagic decapod diel vertical migrations, active flux, diet, and diurnal feeding allowed for a more complete understanding of the behavior, ecological importance, and contributions to carbon cycling than a conventional, more finely focused study would allow. However, this broad focus meant that, due to time constraints, the number of species studied was relatively narrow. It would have been preferable to perform a similar study for the entire micronekton community, not just the decapods, but given the extent of the research performed on each species this would have been impractical.

The other most significant limitation of this study lies in the sampling procedures. Sampling procedures for the 2004 cruise were designed to calibrate micronekton gears as part of the MICE, not to specifically sample decapods for a dietary analysis. Samples were taken in the SSL and DSL, but many decapods were not present in both layers, thus either night or day samples were missing for many species. As such the number of decapod species for which a diurnal dietary analysis could be carried out was reduced. Similarly, during the 2011 cruise, sampling procedures were a compromise between the goals of this thesis, and the goals of a number of other studies being simultaneously carried out. To determine vertical distributions for all species it would have been ideal to consistently sample at the same depth intervals, but due to the multiple demands of different studies using the same samples, it was not possible to keep consistent depth intervals through the various MOCNESS-10 trawls. Similarly, a larger number of trawls on the 2011 cruise would have yielded higher sample sizes and more accurate vertical distributions for each species, but this was not possible due to monetary constraints.

In terms of future directions for research, the extent to which feeding at depth occurs is highly understudied. While many studies have looked for the presence of preferential feeding at the surface for a variety of migratory organisms, few have attempted to differentiate between preferential and exclusive feeding at the surface, and fewer still have attempted to quantify the extent of feeding at depth. Quantifying this aspect of feeding biology for a wide variety of species is critical to obtaining accurate estimates for the active vertical flux of carbon, as an assumption of exclusive feeding at the surface for all migratory organisms is flawed. While the method presented in this paper provides an estimate of feeding at depth, it is a broad, imprecise estimate. A more precise estimate could be achieved by comparing gut fullness at depth to gut fullness near the surface for migratory organisms, but to also catch live

specimens of said organisms near the surface at night, and measure the rate at which their guts evacuate over time in filtered sea water, with no new prey available. Conditions of this filtered seawater would be made to mimic conditions at the organisms daytime residence depth as closely as possible, and in this manner it would be possible to compare daytime fullness in the environment (where feeding at depth is possible) to fullness after an equal amount of time in filtered seawater (where feeding is impossible), with the difference equalling the feeding at depth. Such experiments could be performed for a wide variety of organisms (mesozooplankton, macrozooplankton and micronekton), with previous active flux estimates corrected accordingly.

Another gap in the literature involves the lack of studies on micronekton active flux in general. As discussed in the introduction of the first research chapter, the micronekton community (and thus the associated active flux) varies widely throughout the world's oceans, but this is just the third study to attempt to quantify the active flux due to any class of micronekton in a given location. As micronekton active flux contributes significantly to vertical carbon flux in the oceans, understanding how this flux varies worldwide is essential, and further studies on micronekton active flux in different ecosystems are necessary.

In conclusion, this study has shown migrant decapods in the NPSG to be a significant contributor to active flux. In this environment decapods almost universally perform diel vertical migrations to deep depths, and feed preferentially, though not exclusively, near the surface at night. Their diets were found to be diverse, and to depend not just on size, but also on taxonomy.

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Appendix 3 Steps in the calculation of respiratory and excretory flux for each migratory decapod species. Abund = abundance; ind = individual; ppln = population; ind = individual; temp = temperature; RO = the rate of respiratory oxygen uptake; RC = the respiratory carbon equivalent; C = carbon.

Species	Abund (ind/m ²)	Biomass (mg DW/m ²)	Biomass per ind (mg DW)	Percent migrating	Temp at day WMD (°C)	RO per ind (µL O ₂ /ind/hr)	RC per ind (µg C/ind/hr)	Daily RC at depth (µg C/ind)	Respiratory C flux for migratory ppln (µg C/m ² /d)	Excretory C flux for migratory ppln (µg C/m ² /d)
<i>Acanthephyra smithi</i>	0.0934	59.3	634.5	100	5.02	5.08	2.64	33.3	3.11	1.01
<i>Allosergestes pectinatus</i>	0.152	1.77	11.7	69.35	6.46	2.00	1.04	13.1	1.38	0.45
<i>Allosergestes sargassi</i>	0.0492	1.57	31.9	100	7.47	2.85	1.48	18.6	0.92	0.30
<i>Deosergestes erectus</i>	0.146	25.3	173.2	92.23	5.04	4.06	2.11	26.6	3.58	1.16
<i>Gennadas bouvieri</i>	0.481	41.8	86.8	100	4.5	3.49	1.81	22.8	11.0	3.57
<i>Gennadas capensis</i>	0.331	35.8	108.2	71.01	3.63	3.62	1.88	23.7	5.57	1.81
<i>Gennadas clavicularis</i>	0.121	8.27	68.1	78.67	5.05	3.33	1.73	21.8	2.08	0.67
<i>Gennadas incertus</i>	0.071	3.69	52.47	100	4.19	3.08	1.60	20.1	1.42	0.46
<i>Gennadas spp.</i>	0.372	22.5	60.4	49.65	4.9	3.22	1.67	21.1	3.90	1.27
<i>Gennadas tinayrei</i>	0.0481	2.75	57.3	80.41	4.75	3.17	1.65	20.8	0.80	0.26
<i>Janicella spinicauda</i>	0.105	4.38	41.5	87.82	7.21	3.04	1.58	19.9	1.84	0.60
<i>Neosergestes consobrinus</i>	0.132	1.43	10.8	55.44	5.91	1.91	0.99	12.5	0.92	0.30
<i>Neosergestes orientalis</i>	0.146	4.20	28.7	100	6.67	2.72	1.42	17.8	2.61	0.85
<i>Parasergestes armatus</i>	0.277	19.1	68.9	100	5.92	3.38	1.75	22.1	6.13	1.99
<i>Sergestes atlanticus</i>	0.0727	1.72	23.7	88.22	5.67	2.52	1.31	16.5	1.06	0.34
<i>Sergia bigemmeus</i>	0.118	10.5	89.1	89.67	4.19	3.49	1.82	22.9	2.43	0.79
<i>Sergia gardineri</i>	0.560	20.4	36.4	76.43	4.8	2.82	1.46	18.5	7.89	2.6
<i>Sergia scintillans</i>	0.0916	4.12	45.0	76.72	5.07	3.00	1.56	19.6	1.38	0.45
<i>Stylopandalus richardi</i>	0.167	12.2	72.8	88.05	5.9	3.42	1.78	22.4	3.30	1.07
Total flux									61.31	19.90

Appendix 4 Prey consumed by the 9 decapod species studied in Chapter 2. Values shown are the mean dry weight (μg) of each prey item in the stomach of one decapod.

Prey	<i>Acantheephyra smithi</i> (n = 41)	<i>Janicella spinicauda</i> (n = 75)	<i>Neosergestes orientalis</i> (n = 75)	<i>Notostomus elegans</i> (n = 13)	<i>Oplophorus gracilirostris</i> (n = 75)	<i>Parasergestes armatus</i> (n = 49)	<i>Sergia gardineri</i> (n = 75)	<i>Sergia scintillans</i> (n = 46)	<i>Stylopandalus richardi</i> (n = 75)
Amphipoda		8.2			45.1				7.8
<i>Atlanta</i> spp.		9.5							
Bivalvia larvae	22.9	4.8							
Calanoida	28.7	16.7	6.6		1.7	26.9	24.4	45.9	10.8
<i>Candacia</i> spp.	29.3				0.4	5.9			
Caridea	29.3								
Chaetognatha	12.5	36.4			117.1		0.4	4.5	1.6
<i>Clausocalanus</i> spp.							4.6		
Crustacea	1097.6	15.3	16.2		43.0		9.8	0.2	48.8
Ctenophora									0.7
Decapoda		5.0			353.0	11.2			
Eggs								10.8	0.1
<i>Euchaeta</i> spp.							4.7		
Euphausiidae		0.9		66.3	68.5				
Foraminifera		5.6	3.6		0.6		3.9	18.4	17.5
<i>Gaetanus</i> spp.						14.6			
Highly digested paste	3.2	11.4	1.9		1.8	7.5	0.7		11.0
<i>Nematobrachion boopis</i>			2.7						
<i>Nematobrachion</i> spp.	2.8		13.2						
Nematoda					1.9				
<i>Nematoscelis</i> spp.									1.5
Oplophoridae	762.2				148.0				
Osteichthyes	650.5	71.6	2.0	230.2	2947.2	1.5		5.9	5.4
Ostracoda		0.4							0.7
Pandalidae	1285.1								
<i>Pleuromamma</i> spp.		28.9	2.9	12.0	5.3	8.1	5.0	6.0	19.3
Polychaeta	609.4				11.7		2.0		
Sergestidae						14.9			
Teuthida	87.8	3.3			458.0				
Thecosomata		15.9			34.2		1.4	0.2	
<i>Thysanopoda acutifrons</i>			3.9						8.5
<i>Thysanopoda monacantha</i>	22.0								
<i>Thysanopoda pectinata</i>			0.7						
<i>Thysanopoda</i> spp.	73.9	12.0			29.9				
<i>Thysanopoda tricuspidata</i>			4.1		18.1	5.9			