A NOVEL APPROACH TO ESTIMATE ACTIVE CARBON FLUX USING THE
MICRONEKTON BIOMASS SPECTRA

by

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Abstract

Micronekton play a critical role in global carbon cycling, actively transporting carbon between the surface and deep ocean during diel migrations. Carbon transport is mediated through respiration, gut flux, excretion and mortality of migrating organisms. Because marine ecological processes are strongly size dependent, it was proposed that active carbon transport can be measured from biomass spectra. The micronekton community was sampled during the Micronekton Intercalibration Experiment (MIE-1) in October of 2004 off the south west coast of Oahu. Sampling was conducted during both day and night in the epipelagic (0 – 120 m) and mesopelagic (550 – 650 m) layers, using three micronekton sampling gears (Cobb trawl, Isaacs-Kidd Midwater trawl, Hokkaido University Frame Trawl) and an acoustic echosounder (hull-mounted, dual-frequency, split-beam Simrad EK60). Micronekton species composition and size spectra varied depending on the depth and time of day. We estimated total migratory micronekton abundance and biomass to be \(~487\) ind.m\(^{-2}\) and \(~6,014\) mgC m\(^{-2}\), respectively, assuming that \(~16\)% of micronekton remained within the epipelagic zone during the day. A biomass/production size dependent model based on the biomass spectra theory was developed to predict active carbon transport of micronekton. The model was robust against changes in respiration, excretion and mortality, but relatively sensitive to changes in the gut flux. The model estimated that vertically migrating micronekton exported approximately 88.5 mgC m\(^{-2}\) day \(^{-1}\) to \(~450\) m depth in this region. This estimate was substantially higher than the majority of past estimates, and comparable to recent total global carbon export estimates. The model output suggests that micronekton play a key role in active carbon cycling, and that their contribution to carbon cycling may have been underestimated. Therefore, behavioural and physiological responses of these organisms to changes in oceanic conditions may affect the efficiency and strength of the biological pump potentially reducing atmospheric CO\(_2\) sink to the deep-ocean.
Preface

The work presented in this dissertation represents original, unpublished work conducted independently by the author, L. Kwong.
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<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>BMSS</td>
<td>Biomass size spectra</td>
</tr>
<tr>
<td>CW</td>
<td>Carbon weight</td>
</tr>
<tr>
<td>DOC</td>
<td>Dissolved organic carbon</td>
</tr>
<tr>
<td>DSL</td>
<td>Deep-sea backscattering layer (centered at ~550 m)</td>
</tr>
<tr>
<td>DVM</td>
<td>Diel vertical migration</td>
</tr>
<tr>
<td>DW</td>
<td>Dry weight</td>
</tr>
<tr>
<td>GPT</td>
<td>Gut passage time</td>
</tr>
<tr>
<td>ISF</td>
<td>Index of stomach fullness</td>
</tr>
<tr>
<td>MIE</td>
<td>Micronekton Intercalibration Experiment</td>
</tr>
<tr>
<td>NBSS</td>
<td>Normalized biomass size spectra</td>
</tr>
<tr>
<td>Ni</td>
<td>Nominal size</td>
</tr>
<tr>
<td>NMI</td>
<td>Nautical miles</td>
</tr>
<tr>
<td>OMZ</td>
<td>Oxygen minimum zone</td>
</tr>
<tr>
<td>POC</td>
<td>Particulate organic carbon</td>
</tr>
<tr>
<td>SSL</td>
<td>Shallow backscattering layer (centered at ~120 m)</td>
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</tbody>
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To my family.
1 General introduction

Micronekton are actively swimming organisms that range in size from 20 to 100 mm and are heterogeneously distributed throughout the World’s mesopelagic realm (Brodeur et al., 2004; Kloser et al., 2009; Young et al., 2015). They comprise a highly diverse group of organisms encompassing fishes (e.g., myctophids, gonostomatids), crustaceans (e.g., euphausiids, decapods, mysids, stomatopods), and cephalopods (e.g., gonatids, enopleuthids) and are one of the largest unexploited animal biomasses (Brodeur et al., 2004).

The mesopelagic zone extends from the base of the euphotic zone (~200 m) to 1000 m depth (Irigoien et al., 2014). This zone is light limited lacking autochthonous production and is considered food-poor. Therefore, micronekton inhabiting this zone must derive their nutrients from the highly productive epipelagic zone. The majority of micronekton are known to undergo extensive vertical migrations either diurnally, based on light intensity, or seasonally, based on changes in temperature and productivity (Maynard et al., 1975; Williams and Koslow, 1997; Cade and Benoit-Bird, 2015). During daily movements, or diel vertical migrations (DVM), micronekton feed in the highly productive surface waters during the night, and migrate downward during the day where they reside to avoid predation (Enright, 1977; Hernández-León et al., 2010; Iwasa, 1982) and improve metabolism (Prosser and Brown, 1961; McLaren, 1963, 1974; Enright, 1977; Hernández-León et al., 2010; Iwasa, 1982). While at depth, micronekton metabolize surface derived nutrients releasing organic matter via respiration, excretion, defecation (gut flux) and mortality (Angel and Pugh, 2000; Ariza et al., 2015; Ducklow et al., 2001; Hernández-León et al., 2001; Kobari et al., 2008; Longhurst et al., 1990; Steinberg et al., 2000; Turner, 2002; Zhang and Dam, 1997). By connecting the surface waters to the deep ocean and linking lower and upper trophic levels, migrating organisms inhabiting the mesopelagic zone play a key role in controlling marine productivity globally. The permanent inhabitants (non-vertical migrators) of the mesopelagic realm depend on the passive sinking of epipelagic particles as well as migratory zooplankton (organisms < 20 mm) and micronekton (Hannides et al., 2013; Choy et al., 2016). Therefore, these vertical migrations play a critical role in global carbon cycling, actively transporting organic matter from the
epipelagic to the mesopelagic zone (Ariza et al., 2015), a process referred to as active carbon transport/flux. It has been hypothesized that the mesopelagic zone may play a significant role in sequestering atmospheric carbon to the deep ocean (Angel, 1989; Longhurst and Harrison, 1989; Bianchi et al., 2013a; Davison et al., 2013; Hudson et al., 2014). The importance of vertically migrating micronekton and the mesopelagic zone to biogeochemical cycling is becoming increasingly more apparent. However, its role in biogeochemical models remains largely unresolved (Tsubota et al., 1999; Hansen and Visser, 2016).

Past studies have focused primarily on active carbon transport via respiration, excretion, gut flux and/or mortality of mesozooplankton, individual species (Darnis and Fortier, 2012; Kobari et al., 2008), individual groups (i.e., zooplankton or micronekton; Hidaka et al., 2001) or specific size ranges (Ariza et al., 2015; Davison et al., 2013; Hernández-León et al., 2001). Unlike zooplankton, micronekton have the ability to migrate to the lower part (500 -1000 m; Baird et al., 1975) of the mesopelagic zone, and due to their long gut passage time (4 – 10 hours; Pakhomov et al., 1996) they are able to metabolize/excrete their gut contents at those depths. Neglecting micronekton may underestimate carbon export to the deep ocean by up to 70% (Buesseler et al., 2007; Davison et al., 2013; Falkowski et al., 2003; Martz et al., 2008; Hernández-León et al., 2010; Usbeck et al., 2003; Wexels Riser et al., 2010).

In addition to their importance in global carbon cycling, micronekton also provide an important source of energy and nutrients for myriad marine organisms ranging from larger invertebrates to whales (Brodeur and Yamamura, 2005; Nowacek et al., 2011). For example, in the North Pacific, micronekton are thought to contribute significantly to the food supply of foraging salmon during the fall and winter when surface productivity is low (Khoruzhiy et al., 2014; Zavolokin et al., 2014). Therefore, micronekton biomass dynamics may determine the distribution of top predators in the water column (Menkes et al., 2015). Aside from Antarctic krill (Euphausia superba), a highly abundant and economically important species of euphausiid (Flores et al., 2014), micronekton as a whole are understudied. This is primarily due to the fact that no commercial fishery exists for micronekton, a tremendous effort is required when sampling the deep ocean, and these organisms are difficult to catch quantitatively. These patchily distributed, yet abundant
organisms comprise the most ecologically and functionally important components of the poorly studied mesopelagic zone.

Currently, there is little understanding of key processes at the micronekton level, including secondary production estimates and the contribution of these organisms to global carbon export to the deep ocean (Basedow et al., 2014). Similar to terrestrial systems, the structure of marine pelagic food webs is largely size dependent (Sheldon et al., 1972, 1977; Platt and Denman, 1978; Silvert and Platt, 1980; Cousins 1985; Platt, 1985). This observed pattern has been formalized as the Biomass Spectra Theory, in which the abundance or normalized biomass of organisms is plotted against organism size (e.g. length or biomass) producing a linear graph with a slope close to -1. The size distribution shows that larger organisms are much rarer than smaller organisms. The application of size spectra is of particular interest, as the shape can be used to determine community respiration, mortality, excretion, growth and gut flux rates (Zhou and Huntley, 1997; Kerr and Dickie, 2001; Zhou, 2006; Zhou et al., 2010), which directly influence active carbon flux. Thompson et al. (2013) and Rodriguez and Mullin (1986a) found that when migrating zooplankton ascend to the epipelagic zone during the night to feed, the resulting microzooplankton size spectra display a flatter slope. However, in the presence of a greater abundance of myctophids and gonostomatids, two of the most abundant micronektonic fishes, Suthers et al. (2006) observed steeper epipelagic zooplankton biomass spectra regardless of the time of day. These steeper size spectra resulted due to high predation on larger zooplankton. As such, the biomass spectra theory provides an exciting venue to assess carbon transport from the epipelagic zone to the mesopelagic zone, as the corresponding biomass size spectra reflect changes in biomass of vertically migrating zooplankton and micronekton.

We hypothesized that patterns of active carbon transport via vertical migrations of zooplankton and micronekton are correlated to body size, and thus can be inferred from the biomass size spectra. The main objectives of this thesis were twofold. First, to investigate the dynamics of micronekton size spectra between the epi- and mesopelagic layers, and to compare micronekton densities obtained using nets and biomass spectra. Second, to develop a size based biomass / production model to quantify total migratory flux and active carbon transport of vertically migrating micronekton.
This hypothesis was tested on the southwest coast of Oahu, where previous studies have documented micronekton DVM (e.g., Benoit-Bird et al., 2008; Domokos et al., 2010; Maynard et al., 1975). These studies suggested that micronekton DVMs are the result of food availability and predation in this region (Benoit-Bird and Au, 2006; Benoit-Bird et al., 2001; Davison 2011). Although the concept of active carbon transport has previously been studied in this region, these studies have focused on the contribution of single zooplankton groups (e.g., Kobari et al., 2008, Stukel et al., 2013), certain fluxes (e.g., Kobari et al., 2013; Stukel et al., 2013), and/or certain size classes of zooplankton and micronekton (e.g., Steinberg et al., 2008). To date, no studies have considered the whole micronekton community. With changes in ocean circulation, temperature, acidity and oxygen minimum zone depth related to climate change, it is crucial that we gain a better understanding of the contribution of micronekton to carbon cycling.
2 The biomass size spectra

2.1 Introduction

There exists a deterministic distribution of individuals among body classes in both terrestrial and aquatic ecosystems (Brown, 1995; Gaston and Blackburn, 2000; Kerr and Dickie, 2001), such that there is a predictable decrease in the abundance of individuals with increasing body size. The relationship between abundance and body size dates back to the work of Elton (1927); however, it was first described in aquatic communities by Sheldon et al. (1972), and was later formalized as the biomass spectra theory by Kerr and Dickie (2001). The assumptions of the biomass size spectra, as presented by Kerr and Dickie (2001), state that 1) the system is in steady state, 2) predation is the only source of mortality, 3) large organisms eat only smaller organisms, 4) there is a constant input of energy to the smallest size classes in the spectrum, and 5) the flow of energy is unidirectional (from smaller to larger size classes). The log-transformed biomass spectra (i.e. log\(_{10}\) normalized biomass against log\(_{10}\) biomass [biomass = body mass]), referred to as the normalized biomass size spectra (NBSS), returns a linear regression with a slope close to -1 when in steady-state, regardless of the fact that different communities vary both temporally and spatially (Kerr and Dickie, 2001). In contrast, the non-normalized biomass size spectra yield a slope of 0 when in steady state (Sheldon et al. 1972; Tseitlin, 1986; Kerr and Dickie, 2001). However, it is recognized that a perfect steady-state does not exist in the ocean, but that all systems are approaching, or have just been disrupted from, their steady-state. As such, this assumption is met and this theory can be applied to our system as well as others. When dissected, size spectra reveal a series of biomass ‘domes’. Each of these ‘domes’ represents different groups of organisms/trophic positions (i.e., phytoplankton, zooplankton, nekton, etc.; Boudreau and Dickie 1992; Sprules et al. 1991; Thiebaux and Dickie, 1992, 1993; Sprules et al., 2001). Thus, by comparing size spectra spatially and temporally ecologists can effectively discern food web level changes.

Since first being formalized, several studies have conformed to the biomass spectra theory, displaying the classic decrease in the abundance of individuals with increasing body size in a variety of different pelagic systems (e.g., Beers et al., 1982; Echevarria et al., 1990; Platt et al., 1984; Rodriguez and Mullin, 1986a,b; Schwinghamer 1981, 1985;
Sheldon et al., 1972; Sprules et al., 1983; Sprules and Knoechel, 1984; Sprules and Munawar, 1986; Warwick, 1984; Witek and Krajewska-Soltys, 1989). Studies have focused primarily on pelagic communities, including organisms ranging from bacteria to small fishes (Platt et al., 1984; Rodriguez and Mullin, 1986a; Clement et al., 2015; Genin, 1986). Since the 1970’s the biomass size spectra approach has been used to assess fisheries productivity (e.g., Sheldon et al., 1977; Borgmann et al., 1984; Moloney and Field, 1985), pollution/anthropogenic effects (e.g., Thomann, 1979, 1981; Greisbach et al., 1982; Borgmann and Whittle, 1983; Sabeel and Vanreusel, 2015), and ecosystem health (e.g., Macpherson et al., 2002).

The biomass spectra theory has provided an ataxonomic (Platt, 1985; Quiñones, 1994; Rodríguez, 1994) approach for ecologists to effectively describe food web attributes using only the elevation (i.e. y-intercept) and slope. This simplifies the food web to a degree that is much more manageable, while integrating both top-down and bottom-up effects. Simply stated, the slope of the biomass size spectra of a given community can be used to infer transfer efficiency (Gaedke, 1993), while the y-intercept can be used to infer food web capacity or productivity (Sweeting et al., 2009; Boldt et al., 2012, Murry and Farrel, 2014). Biomass transfer between predator and prey is a continuous process, rather than a discrete process, and the proportion of prey and predator are reflected in the biomass size spectra. Therefore, we can infer transfer efficiency by looking at the slope of the size spectra. For example, where the slope is shallower (closer to 0) the difference between prey and predator biomass is lower, suggesting that energy is being transferred more efficiently. In contrast, where the slope is steeper (more negative), the difference between prey and predator biomass is greater, meaning that energy is being transferred less efficiently. On the other hand, the y-intercept can be used to infer productivity as it directly reflects the production in the smallest size class. For example, if we compare two different size spectra for the same size range with the same slope but different y-intercepts, the one with the higher intercept has higher production than the one with the lower intercept. This is also demonstrated by the total biomass, which can be calculated by taking the area underneath the curve (biomass size spectra). The area underneath the biomass size spectra with a higher intercept will be greater than that with a lower intercept. As such, the biomass of one trophic level may be used to predict the biomass in another trophic level and vice versa.
In addition, the biomass size spectra can be used as an indicator of ecosystem health, perturbation (human induced or natural), and fisheries effects (Sweetings et al., 2009; Shin et al., 2005; Law et al., 2009; Jennings and Dulvy, 2005; Petchey and Belgrano, 2010; Murry and Farrel, 2014), as physiological and ecological parameters scale with size (Genin, 1986).

Body size (e.g. length, weight) is one of the most fundamentally important properties of an organism. This is because it is directly related to lifespan, home range size and life history. Furthermore, rate processes such as growth, mortality, excretion, respiration, gut flux, and trophic status scale with size (Garcia-Munoz et al., 2014; Zhou and Huntley, 1997; Zhou, 2006). These rates are of particular importance when it comes to assessing biological and biochemical processes within marine ecosystems. Because transfer efficiency is indicated by slope of the biomass size spectra and rates scale with size, the biomass size spectra can be used to calculate these rate processes for entire communities.

In this chapter, we assess trends in taxonomic composition and differences in biomass size-spectra of micronekton in the epipelagic and mesopelagic during the day and night on the southwest coast of Oahu Island, Hawaii. We produce biomass size spectra for micronekton ranging from 20-100 mm in size. The main goal of this chapter is to assess the differences in micronekton taxonomic composition and biomass size spectra during diel vertical migrations. Although previous studies have estimated differences in biomass size spectra by depth or time of day, these studies have focused primarily on mesozooplankton (i.e., organisms less than 20 mm in size) (e.g., Quiñones et al., 2003; Rodriguez and Mullin, 1986a; Suthers et al., 2006), while the current study assess changes in micronektonic biomass size spectra. Furthermore, this chapter acts as a precursor to the next chapter which uses the biomass size spectra, produced here, to estimate active carbon transport.
2.2 Methodology

2.2.1 Field sampling

Sampling was carried out onboard the National Oceanic and Atmospheric Administration (NOAA) research ship Oscar Elton Sette (R/V Sette) during October 6-12, 2004 off the southwest coast of Oahu Island as part of the first Micronekton Sampling Intercalibration Experiment (MIE-1; Pakhomov and Yamamura, 2010). Bottom depth ranged from 700 to 1200 m in the study area (Figure 2.1).

![Map of survey area](image.png)

Figure 2.1. Survey area of MIE-1 on the southwest coast of Oahu Island, Hawaii, in October 2004, showing the trawl locations by type.

A total of 54 tows were carried out using three different gears: Cobb trawl (16 tows), Isaacs-Kidd Midwater Trawl (IKMT; 19 tows) and Hokkaido University Frame Trawl (HUFT; 19 tows) (Figure 2.1). Nets were deployed at random (by gear type) during the night (between 20:00 and 05:00 local time) and day (between 08:00 and 17:00 local time) (Figure 2.2). All tows were conducted directly behind the vessel inside the ships wake.
Figure 2.2. Trawl locations separated by time of day for the a) Cobb trawl, b) IKMT and c) HUFT during the MIE-1 on the southwest coast of Oahu Island, Hawaii.

During sampling the lunar phase was waning from last quarter to new moon. Sampling was not conducted during the crepuscular (05:00-08:00 and 17:00-20:00 h), as micronekton were in flux during this period. Net deployment was dictated by the presence of pronounced backscattering layers, that were detected using the RV Sette hull-mounted, dual-frequency, split-beam Simrad EK60 echosounder, operating at 38 and 120 kHz frequencies (Figure 2.3; Domokos et al., 2010). Nighttime sampling consisted of oblique trawls, during which nets were deployed to a depth of the bottom of the surface backscattering layer (SSL; ~100-120 m) and then slowly brought to the surface. In contrast, day nets were deployed to a depth of deep-sea backscattering layers (DSL) between 450 and 650 m, and towed horizontally. During nighttime of October 10-13 all three nets were horizontally deployed to the DSL. Since each replicate hit a different depth within the DSL (with the exception of the IKMT and HUFT at night in the DSL), and the average abundance and biomass were taken for each gear, we assume that our estimates are representative of this layer. The depth of each trawl was determined using a depth sensor.
Figure 2.3. The EK-60 38 kHz echogram in the top 750 m during the MIE-1 on the southwest coast of Oahu Island, Hawaiʻi, displaying the shallow scattering layer (SSL) and the deep scattering layer (DSL) during the day (left) and night (right), separated by a pronounced vertical migration.

Each trawl varied in mouth and mesh size (Figure 2.4). The Cobb trawl, which is a type of otter trawl, had a mouth area of approximately 140 m$^2$, equipped with a mesh size of 152 mm stretched from the mouth to a cod end of 10 mm lined with 3.2 mm knotless nylon delta mesh netting. The HUFT, which is a rigid frame trawl, had a 4 m$^2$ mouth and 3 mm mesh size. The IKMT, which is also a rigid frame trawl, had a 3 m$^2$ mouth and 5 mm mesh size. The volume filtered was calculated based on the nominal mouth opening of the net and the distance travelled. Distance travelled was calculated by taking the latitude/longitude once the net reached the target depth and once the net reached the end of the tow (before retrieval). For oblique tows the wire angle was used to estimate the distance traveled in the same manner. The average duration of each tow was one hour. Trawls were towed at 2.5-3.5 knots and volume filtered varied between 14,630-24,259 m$^3$, 10,744-15,307 m$^3$, and 637,829-832,980 m$^3$ for HUFT, IKMT and Cobb, respectively. The abundance was determined by dividing the number of individuals by the volume filtered and expressed as ind.m$^{-3}$. This was used to convert to the abundance in the water column (ind.m$^{-2}$) by multiplying by the average thickness of the backscattering layers (100-120 m) during the night and day.
Figure 2.4. Sampling gears used during the MIE-1 on the southwest coast of Oahu Island, Hawaii. From left to right: The Cobb trawl, HUFT and IKMT.

Macroplankton and micronekton catch abundance between the sampling depth and surface layer during the day was minimal, as the majority of these organisms inhabit waters below 400 m depth (e.g., Maynard et al., 1975; Williams and Koslow, 1997). This was confirmed using acoustics (Domokos et al., 2010) and by two oblique tows (HUFT and Cobb trawl), which were aborted for technical reasons before reaching DSL.

Samples were sorted onboard in the cold room immediately after each tow. Rare and large species were individually counted, measured, and weighed from the entire sample and preserved in 6% formalin seawater solution. The remaining sample was either analyzed entirely for macroplankton and micronekton species (only a few IKMT and HUFT samples) or subsampled (all Cobb trawl samples and the majority of the IKMT and HUFT samples). Generally, ½ or ¼ of each sample, by wet weight, was used for onboard sorting into the major taxonomic groups (i.e. fishes, decapods, euphausiids, tunicates, etc.). The total subsample was weighed, the main taxonomic groups counted, and preserved in 6% formalin seawater solution. After sub-sampling, the remaining sample was preserved in 6% formalin seawater solution for subsequent laboratory taxonomic analyses. Fishes, decapods, and squids were identified to the species level, counted, and measured. The remaining zooplankton were identified to major taxonomic groups (e.g., chaetognaths, copepods, molluscs, etc.). Individuals were counted and measured to the nearest mm in either the entire sample, or ¼ subsample. Samples were sorted onboard in the cold room immediately after each tow. Rare and large species were individually counted, measured and weighed from the entire sample and preserved in 6% formalin seawater solution. The remaining sample was either analyzed entirely for macroplankton and micronekton species (only a few IKMT and HUFT samples) or subsampled (all Cobb trawl samples and the majority of the IKMT and HUFT samples).
2.2.2  **Gear intercomparison and calibration**

An intercomparison between gears was conducted for the total catch composition; organisms less than 20 mm and greater than 100 mm were omitted due to under sampling. Length frequency curves were constructed for each sampling gear and sampling time/depth by averaging organism densities expressed as individuals per m$^2$ among all samples for the size intervals of 1, 5 and 10 mm.

To quantify the differences among gears, size-dependent pairwise ratios of the total (e.g., total abundance of Cobb trawl : total abundance of HUFT), fish, and crustacean abundance were calculated for micronekton in 1 mm size bins. Reconstructions of the IKMT abundance were conducted, as it represents one of the most widely used sampling gears historically (Kashkin and Parin, 1983; Wiebe and Benfield, 2003). Therefore, successful reconstruction of IKMT catch abundance will allow for comparisons of past global catches. To reconstruct the IKMT abundances using the HUFT and Cobb trawl, the pairwise ratios were averaged into 3, 5, and 10 mm bins for total, fish and crustacean abundance. These averaged ratios were then applied to the HUFT and Cobb trawl abundance for each size bin. These size bins were selected to reduce the high between-gear ratio variability and stay within narrow size intervals. Because organisms were measured to the closest mm, 3 mm size bins were used instead of 1 mm size bins as they would provide a perfect 1:1 relationship. Total abundance according to size class was then calculated using average pairwise ratios for the 20 mm to 100 mm size classes. The full results of this study are presented in Kwong et al. (In Review).

2.2.3  **Length weight conversions**

After calibrating the length-specific abundance for each trawl, total lengths were converted to carbon weight (mg) using three different approaches. Where available, all reported values of length and weight (i.e., dry, wet or carbon) for the species, genus, or family, depending on the degree of taxonomic identification and availability, were compiled and length to weight relationships (LWR) were developed. Alternatively, length was converted to carbon weight using conversion factors available in the literature or using FishBase Bayesian LWR from Froese (2006). All conversions are reported in Appendix A. If no direct carbon conversion was available in the literature for the given species, the average
of the genus or group was used. Similar to density, carbon weight was divided by the volume filtered to give carbon weight in mgC per m$^3$. This was then converted to carbon weight in mgC per m$^2$ by multiplying the average thickness of the backscattering layers during the night and day by the carbon weight (in mg m$^{-3}$).

To convert calibrated length frequency composition figures into carbon weight biomass size spectra, two linear regressions were developed. The log-transformed organism length (mm) was plotted against the log-transformed carbon weight (mg) for all individuals observed during the survey (Figure 2.5).

Figure 2.5. Log transformed organism length (mm) to carbon weight (mg) relationship for various taxonomic groups observed during the MIE-1 on the southwest coast of Oahu, Hawaii.

Aside from gonostomatids, all other micronektonic organisms conformed to the length-weight regression expressed in Equation 2.1 (Figure 2.5).

Equation 2.1 \[ \log_{10} \text{cw} = 2.308 \times \log_{10} l - 1.975 \]
Where \(cw\) is the carbon weight of an individual (mg), and \(l\) is length of an individual (fish: standard length, other micronekton: total length; mm). Gonostomatids exhibit a unique body form, such that their long slender body results in a significantly different (ANCOVA: \(F= 55.613; p < 0.005\)) length-weight relationship (slope and intercept) than that of other micronektonic organisms. As such, a separate linear regression was developed for this group (Equation 2.2).

\[
\log_{10} cw = 3.157 \times \log_{10} l - 6.782
\]

The proportion of gonostomatids for length intervals of 1 mm were determined and the carbon weight for each length was calculated by weighting the proportion of each equations contribution in calculating the carbon weight for that length interval.

To correct for avoidance, escapement and targeted sampling during the daytime in the mesopelagic Equation 2.3 was applied. We assume that the whole water column was represented during sampling. Therefore, the amount of carbon weight during the daytime in the mesopelagic should be equivalent to the amount of carbon weight during the nighttime in the mesopelagic and epipelagic such that:

\[
DM = NM + NE
\]

For each carbon weight size class in mg, \(DM\) is the abundance of micronekton individuals during the daytime in the mesopelagic, \(NM\) is the abundance of micronekton individuals during the nighttime in the mesopelagic, and \(NE\) is the abundance of micronekton individuals during the nighttime in the epipelagic. Abundance-carbon weight size spectra and normalized biomass size spectra (Platt and Denman, 1977, 1978) were first plotted for each individual trawl, and then as the total biomass size spectra using the intercomparison study by Kwong et al. (2016). Statistical analyses were performed using RStudio (R Core Team, 2016).

2.2.4 Biomass size spectra – abundance and nominal size class

Biomass size spectra may take various forms. Here, biomass size spectra were first plotted as biomass (mgC) against average abundance (ind.m\(^{-2}\)). From there, the total abundance of
micronektonic, and the abundance of micronekton in each size class (Chapter 3), was calculated by integrating the biomass size spectra such that:

\[ N_{W_{i+1}} = \int_{i}^{i+1} N(w) \, dx \]

Where \( N_{W_{i+1}} \) is the abundance of individuals in a given size class, \( N(w) \) is the abundance of individuals as a function of weight, \( i \) is the lower limit of the size class and \( i+1 \) is the upper limit of the size class. For total abundance, integration was conducted for all micronektonic organisms with carbon weights ranging from 0.125 to 8192 mgC. In order to calculate total carbon weight, and in Chapter 3 rates of respiration, mortality, excretion, and gut flux, using the biomass spectra theory, nominal size classes for each size spectra were calculated according to the discrete model from Blanco et al. (1998):

\[ W_{N_i} = W_i \left( \frac{c^{b+1}-1}{(c-1)(b+1)} \right)^{\frac{1}{b}} \]

Where \( W_{N_i} \) is the nominal size class (in mg of carbon weight \( CW_{N_i} \) or dry weight \( DW_{N_i} \)) that represents all organisms within this size bin, \( W_i \) is the lower limit of the size class (mg), \( b \) is the slope of the size spectra, and \( c \) is that rate of geometric increasing of classes (=2). As such, the nominal size class represents a weighted mean size class for the given size range.

To plot the normalized biomass size spectra (NBSS), the biomass was normalized (NB) such that:

\[ NB = \frac{\text{biomass in body mass interval } \Delta w \text{ (mgC m}^{-2}\text{)}}{\text{body mass interval } \Delta w \text{ (mgC)}} \]

Where \( w \) is the biomass in carbon weight of an individual micronekton in mg. The NBSS was then plotted as biomass (mgC), which is equivalent to body mass, against normalized biomass (mgC m\(^{-2}\) \( \Delta \)mgC\(^{-1}\)).
2.3 Results

2.3.1 Catch composition

Micronekton made up between 1-71% of the total numbers and 23-84% of the total biomass captured by the three gears (Table 2.1). Gonostomatids, “other fishes” (fish belonging to the families Acanthuridae, Bothidae, Bregmacerotidae, Blennidae, Engraulidae, Evermannellidae, Malacosteidae, Melamphaidae, Opisthoprodtidae, Phosichthyidae, Serrivomeridae, Sternophtyidae, Stomiidae, Trichiuridae), gelatinous zooplankton and euphausiids consistently comprised the majority of micronektonic organisms (20 – 100 mm) for all three gears. The contribution of all other groups to the average abundance generally never exceeded 8% (Figure 2.6). Myctophids, decapods, “other fishes”, cephalopods, and euphausiids consistently contributed the most in terms of biomass in all samples (Figure 2.6).

The highest total abundance and biomass of micronekton was observed at night in the mesopelagic for the IKMT (39.2 ind.m$^{-2}$; 320.8 mgC m$^{-2}$) and the Cobb trawl (7.4 ± 6.8 ind.m$^{-2}$; 271.8 ± 237.3 mgC m$^{-2}$) (Figure 2.6; Table 2.2). The lowest total abundance (0.4 ± 0.2 and 5.2 ± 1 ind.m$^{-2}$) and biomass (8.9 ± 4.3 and 46.2 ± 21.6 mgC m$^{-2}$) for the Cobb trawl and IKMT, respectively, were documented during the day in the mesopelagic layer (Figure 2.6; Table 2.2). Nighttime epipelagic total abundance (Cobb: 2.9 ± 1.8 ind.m$^{-2}$, IKMT: 7.9 ± 2.9 ind.m$^{-2}$, HUFT: 2.8 ± 0.8 ind.m$^{-2}$) and biomass (Cobb: 71.8 ± 39.3 mgC m$^{-2}$, IKMT: 62.5 ± 22.7 mgC m$^{-2}$, HUFT: 24 ± 8.6 mgC m$^{-2}$) were relatively modest for all three trawls when compared to the mesopelagic during the day and night (Figure 2.6; Table 2.2).

HUFT abundance was significantly (ANOVA; p = 0.04) greater than the Cobb trawl during the day in the mesopelagic (HUFT = 15.2 ± 6.5 ind.m-2; Cobb = 0.4 ± 0.2 ind.m-2). No other significant differences (ANOVA; p > 0.07; See Appendix A) were observed among the three trawls for micronekton abundance or biomass (day/night or epipelagic/mesopelagic).

In general, abundance of the three different gears were dominated by similar taxonomic groups depending on the depth and time of day (Figure 2.6; Table 2.2). During the day in the mesopelagic zone, all three trawls were numerically dominated by
gonostomatids (IKMT: 47%, HUFT: 66%, Cobb: 30%; Table 2.3), while the Cobb trawl also captured several “other fishes” (29%; Figure 2.6a). For the Cobb trawl biomass, myctophids (35%), the majority of which were *Diaphus suborbitalis*, and “other fishes” (32%) contributed most during the day in the mesopelagic zone, while “other fishes” (47%), primarily *Sternoptyx* spp., contributed the most for the HUFT (Figure 2.6a; Table 2.3). Mean IKMT biomass was dominated by decapods (21%), euphausiids (20%), “other fishes” (20%), and cephalopods (20%).

At night in the mesopelagic zone, “other fishes” dominated all three trawls (IKMT: 64%, HUFT: 72%, Cobb: 34%; Figure 2.6b; Table 2.3). The Cobb trawl and IKMT also had high abundances of gonostomatids (24%) and gelatinous zooplankton (26%), respectively (Figure 2.6b; Table 2.3). The Cobb trawl biomass was dominated by decapods (41%), myctophids and “other fishes” (49%). The HUFT abundance and biomass was dominated by “other fishes”, while the IKMT abundance and biomass was composed primarily of decapods and “other fishes” (Figure 2.6b; Table 2.3).

At night in the epipelagic, gelatinous zooplankton were the most abundant group for all three trawls (IKMT: 35%, HUFT: 71%, and Cobb: 43%; Figure 2.6c; Table 2.3). Within the gelatinous group, chaetognaths were most abundant in Cobb and HUFT samples. For the Cobb trawl, “other fishes” (25%) were also abundant. The Cobb trawl micronekton biomass was dominated primarily by cephalopods (45%) and myctophids (31%), namely *Triphoturus nigrescens*. The HUFT caught mostly decapods (35%) and stomatopods (31%), while the IKMT caught myctophids (32%), euphausiids (20%), other fish (14%), and cephalopods (13%) (Figure 2.6c; Table 2.3). A shift in the most abundant groups, from gonostomatids during the day in the mesopelagic to “other fishes” at night in the mesopelagic, was observed for all three trawls (Figure 2.6; Table 2.3). The relative biomass proportions of *D. suborbitalis* and *Sternoptyx* sp. in the mesopelagic were reduced during the night. Similarly, myctophid biomass became less prevalent at night in the mesopelagic and more prevalent in the epipelagic layer in all three gears (Figure 2.6).
Figure 2.6. Micronekton (20 to 100 mm) total abundance (individuals m$^{-2}$), percent abundance, total biomass (mgC m$^{-2}$), and percent biomass of major contributing taxonomic groups for the a) daytime mesopelagic, b) nighttime mesopelagic, and c) nighttime epipelagic for three different sampling gears. Bars indicate ± SEM, where no bars are present no replicates were available.
Table 2.1. Average percent contribution ± standard error of the mean (SEM) of each size range (<20 mm, 20-100 mm, >100 mm) in terms of abundance (A) and biomass (B) to total catch by trawl type during the day and night in the mesopelagic (M) and epipelagic (E) zones, during the MIE-1 in October 2004 off Oahu Island, Hawaii.

<table>
<thead>
<tr>
<th>Trawl</th>
<th>Day/night</th>
<th>Zone</th>
<th>N</th>
<th>Total mean A (ind.m^{-2})</th>
<th>B (mgC m^{-2})</th>
<th>&lt;20 mm % A</th>
<th>&lt;20 mm % B</th>
<th>20-100 % A</th>
<th>20-100 % B</th>
<th>&gt;100 % A</th>
<th>&gt;100 % B</th>
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<tbody>
<tr>
<td>Cobb</td>
<td>D</td>
<td>M</td>
<td>6</td>
<td>0.5±0.3</td>
<td>12.5±5</td>
<td>28±5</td>
<td>4±2</td>
<td>71±5</td>
<td>84±7</td>
<td>1±0</td>
<td>12±7</td>
</tr>
<tr>
<td>HUFT</td>
<td>D</td>
<td>M</td>
<td>6</td>
<td>118.4±44</td>
<td>221.7±121</td>
<td>90±4</td>
<td>39±6</td>
<td>10±4</td>
<td>43±8</td>
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<td>19±8</td>
</tr>
<tr>
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<td>D</td>
<td>M</td>
<td>6</td>
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<td>93±12</td>
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<td>30</td>
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<td>52</td>
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Table 2.2. Total abundance (A: ind.m^{-2}) and biomass (B: mgC m^{-2}) for the total micronekton catch (20-100 mm) and the corresponding percent contribution of total fish and total crustaceans.

<table>
<thead>
<tr>
<th>Trawl</th>
<th>Parameter</th>
<th>Total</th>
<th>% Total Fish</th>
<th>% Total Crustacea</th>
</tr>
</thead>
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<td>A</td>
<td>0.1</td>
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<td>27</td>
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<tr>
<td></td>
<td>B</td>
<td>8.9</td>
<td>67</td>
<td>21</td>
</tr>
<tr>
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<td>79</td>
<td>6</td>
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<td></td>
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<td></td>
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Table 2.3. Percent total abundance (A) and biomass (B) for major taxonomic groups captured in the mesopelagic (M) and epipelagic (E) zones during the MIE-1. Including organisms ranging from 20 – 100 mm in size only.

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2.3.2 *Diel vertical migration*

Approximately 208 taxa of macroplankton and micronekton were captured during the MIE-1 (Pakhomov et al., 2010). Our data was separated into 126 taxonomic groups of micronekton (Table 2.4). Of these, 80 groups of micronekton were observed only in the mesopelagic or epipelagic. Species observed in both the epipelagic and mesopelagic were assumed to undergo vertical migrations, and are presented in Table 2.4. In total, 46 taxonomic groups of micronekton were found to undergo vertical migrations between the epipelagic and mesopelagic realms. Furthermore, 73 taxonomic groups occurred in the epipelagic realm, while 99 groups occurred in the mesopelagic realm (Table 2.4). A total of 27 taxonomic groups were captured only in the epipelagic realm, and therefore were likely not participating in DVM.

Table 2.4. Species captured during the MIE-1 off the southwest coast of Oahu. The presence of each taxonomic group in the epipelagic and mesopelagic, along with whether or not migration was observed during the study and/or previous studies (Y=yes; N=No; N/A=Not available).

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<td>Notolychnus validivae</td>
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<td>12,23</td>
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<td>Symbolophorus evermanni</td>
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<td>14</td>
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<td>Mysidacea</td>
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<tr>
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<td>23</td>
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<td>25</td>
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<tr>
<td>Bremmaceros atlanticus</td>
<td>Other Fish</td>
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<td>15</td>
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</tr>
<tr>
<td>Bremmaceros nectabanus</td>
<td>Other Fish</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bremmaceros sp.</td>
<td>Other Fish</td>
<td>Y N N N</td>
<td>15</td>
<td></td>
<td></td>
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<tr>
<td>Brotulotenaia</td>
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<td>Chauliodus sloani</td>
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<td>12,27</td>
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<td>Grouping</td>
<td>Epi-</td>
<td>Meso-</td>
<td>Migration (this study)</td>
<td>Migration (literature)</td>
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<tr>
<td>Chauliodus sp.</td>
<td>Other Fish</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>N†</td>
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<tr>
<td>Coccorella atlantica</td>
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<td>Cubiceps sp.</td>
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<td>N</td>
<td>N</td>
<td>N†</td>
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<td>Dananeph oculatus</td>
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<td>Y</td>
<td>N</td>
<td>N†</td>
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<tr>
<td>Dananeph sp.</td>
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<td>N</td>
<td>Y</td>
<td>N</td>
<td>N†</td>
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<td>Y</td>
<td>N</td>
<td>Y‡</td>
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<td>N</td>
<td>N</td>
<td>Y‡</td>
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<tr>
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<td>Other Fish</td>
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<td>Y</td>
<td>N</td>
<td>N/A</td>
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<td>N</td>
<td>N†</td>
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<td>Y</td>
<td>N</td>
<td>Y†</td>
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<td>Idiacanthus fasciola</td>
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<td>Y</td>
<td>N</td>
<td>N†</td>
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<td>Y</td>
<td>N</td>
<td>N</td>
<td>Y‡</td>
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<td>N/A</td>
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<td>Y</td>
<td>N</td>
<td>N†</td>
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<tr>
<td>Malacosteus niger</td>
<td>Other Fish</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>N†</td>
</tr>
<tr>
<td>Melampheas longivelis</td>
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<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y‡</td>
</tr>
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<td>Melanostomias niger</td>
<td>Other Fish</td>
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<td>Y</td>
<td>N</td>
<td>N/A</td>
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<tr>
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<td>Y</td>
<td>N</td>
<td>N/A</td>
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<tr>
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<td>Other Fish</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>N†</td>
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<td>Nesiarchus nasutus</td>
<td>Other Fish</td>
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<td>N</td>
<td>N</td>
<td>N‡</td>
</tr>
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<td>Opisthoproctus soleatus</td>
<td>Other Fish</td>
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<td>Y</td>
<td>N</td>
<td>N†</td>
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<tr>
<td>Paralepidad</td>
<td>Other Fish</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>Y†</td>
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<tr>
<td>Photonectes sp.</td>
<td>Other Fish</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>Y‡</td>
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<tr>
<td>Photostomias guerneri</td>
<td>Other Fish</td>
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<td>N</td>
<td>N</td>
<td>Y*‡,15†</td>
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<td>Rhinecanthus sp.</td>
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<td>N</td>
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<td>Y</td>
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<td>Y</td>
<td>N</td>
<td>N*†</td>
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<td>Scopelogadus misolepis</td>
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<td>Y</td>
<td>N</td>
<td>N/A</td>
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<tr>
<td>Scopelosaurus hoedti</td>
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<td>Y</td>
<td>N</td>
<td>N</td>
<td>Y*†</td>
</tr>
<tr>
<td>Serrivomer sp.</td>
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<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N*‡</td>
</tr>
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<td>Spernophyta diaphana</td>
<td>Other Fish</td>
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<td>Y</td>
<td>N</td>
<td>N*†,14,16†</td>
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<td>Spernophyta sp.</td>
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<td>Y</td>
<td>N</td>
<td>N*†,14,16†</td>
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<td>N</td>
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<td>N</td>
<td>N</td>
<td>N*‡</td>
</tr>
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<td>Y</td>
<td>Y</td>
<td>Y*†</td>
</tr>
<tr>
<td>Valenciennellus sp.</td>
<td>Other Fish</td>
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<td>Y</td>
<td>N</td>
<td>N*‡</td>
</tr>
<tr>
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<td>Other Fish</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>N*‡</td>
</tr>
<tr>
<td>Vinciguerria nimbaria</td>
<td>Other Fish</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y*†</td>
</tr>
<tr>
<td>Vinciguerria poweria</td>
<td>Other Fish</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>Y*†</td>
</tr>
<tr>
<td>Zanclus cornutus</td>
<td>Other Fish</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>N/A</td>
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References:
1. Young, 1978
2. Watanabe et al., 2006
3. Steinberg et al., 2000
4. Podeswa and Pakhomov, 2015
5. Andersen et al., 1992
7. Steinberg et al., 2008
8. Kaartvedt et al., 2007
9. Wang et al., 1995
11. Alldredge and King, 1980
12. Roe and Badcock, 1984
13. Badcock and Merret, 1976
15. Hopkins et al., 1981
16. Loeb, 1979
17. Tanaka et al., 2013
18. Hulsey, 1992
19. Roa, 2010
20. Pearcey et al., 1977
22. Sassa et al., 2002
23. Stickney and Torres, 1989
24. Roe et al., 1984
25. Leis, 1991
27. Olivar et al., 2012
28. Kajihara et al., 1988
29. Voss, 1954
30. van Utrecht, 1982
2.3.3 Micronekton biomass size spectra

Abundance size spectra (i.e., biomass against average abundance) were plotted for each individual trawl type for the daytime in the mesopelagic, nighttime in the mesopelagic, and nighttime in the epipelagic (Figure 2.7). Strong linear relationships were observed between average abundance of individuals and carbon weight for all three gears (Figure 2.7).

During the daytime in the mesopelagic, the slope of the HUFT size spectrum was significantly different (ANCOVA; \( p = 2E-16 \)) to that of the Cobb trawl and IKMT. However, no significant difference (ANCOVA; \( p = 0.1 \)) was observed between the Cobb trawl and IKMT size spectra. During the nighttime in the mesopelagic the IKMT size spectrum returned significantly different (ANCOVA; \( p = 7E-13 \)) slope compared to the Cobb trawl and the HUFT. There was no significant difference (ANCOVA; \( p = 0.17 \)) in the size spectra slopes for the latter two gears. Visually, the least variability in slope and intercept was observed during the nighttime in the epipelagic (Figure 2.7). The IKMT abundance size spectrum slope was significantly different (ANCOVA; \( p < 0.03 \)) from that of the Cobb trawl and HUFT, which had similar (ANCOVA; \( p = 0.752 \)) size spectra slopes.

Although the gears had overlapping catch size distributions, they differed in how effectively they captured different sizes of organisms (Figure 2.7). For example, some size classes were only captured by either the Cobb or IKMT or HUFT gears. Overall, the Cobb trawl consistently captured a greater size range of micronekton, but captured fewer smaller organisms. At night in the mesopelagic, the IKMT was more effective at capturing micronekton than the HUFT, as displayed by the overall higher intercept and shallower slope. Overall, the three gears were the most similar during the night in the epipelagic, although the Cobb trawl again captured more organisms in the larger size classes (Figure 2.7).
After applying the intercomparison from Kwong et al. (In Review), the abundance size spectra were plotted. Significant linear relationships between average abundance of individuals and carbon weight were observed for the day in the mesopelagic (R^2=0.87), night in the mesopelagic (R^2=0.89), and night in the epipelagic (R^2=0.89) (Figure 2.8).

The abundance size spectrum had the highest y-intercept (1.96), and steepest slope (-1.61) during the night in the epipelagic (Figure 2.8). Daytime mesopelagic size spectrum returned the lowest y-intercept (1.14), and a moderate slope of -1.29 (Figure 2.8).
Nighttime mesopelagic size spectrum returned a relatively high y-intercept (1.93), and shallow slope (-1.05). It was assumed that the size spectra during the daytime at depth should be equivalent to the sum of the nighttime meso- and epipelagic size spectra. After correcting the daytime mesopelagic biomass size spectrum, the spectrum exhibited a higher overall y-intercept (2.45; Figure 2.8; Equation 2.3). However, the slope of the size spectrum remained steeper than that of the nighttime mesopelagic.

All four size spectra intercepts were significantly different (ANCOVA; p < 0.0017). The slope of the biomass size spectrum during the night in the epipelagic was significantly different from that of the nighttime mesopelagic (ANCOVA; p = 0.007), but showed no significant difference from the daytime mesopelagic (corrected [p = 0.07] and uncorrected [p = 0.81]) size spectra. No significant difference was observed between the night and day (corrected and uncorrected) mesopelagic size spectra (ANCOVA; p > 0.11).

![Figure 2.8](image)

Figure 2.8. Size spectra expressed as biomass (mgC) against average abundance (ind. m⁻²) for the daytime mesopelagic, nighttime mesopelagic, nighttime epipelagic, and daytime mesopelagic corrected (sum of nighttime epipelagic and mesopelagic abundance by size).

In all cases the calculated total abundance and biomass using the size spectra was higher than that of the total catch (Table 2.5). The largest difference in size spectra and trawl catch abundance was observed during the nighttime in the mesopelagic, as abundance using the size spectrum (804 ind. m⁻²) was more than double the total catch estimate (292.2
ind. m$^{-2}$). Large differences were also observed between the corrected daytime mesopelagic abundance and trawl catch (852.5 ind. m$^{-2}$). Differences between the abundance estimated using the size spectra and trawl catch were minimal during both the nighttime in the epipelagic and daytime in the mesopelagic, 61 ind. m$^{-2}$ and 36.3 ind. m$^{-2}$ respectively. In contrast, biomass estimates using the size spectra were at least 10 times greater than trawl catch biomass (Table 2.5). The greatest difference observed was during the nighttime in the mesopelagic, during which the size spectrum estimate of biomass was 309 times that of the trawl catch biomass. Size spectra estimates of abundance were the highest during the nighttime in the mesopelagic. However, once corrected the daytime mesopelagic size spectrum became the highest. Regardless of this correction, the greatest biomass estimated using the size spectrum was at night in the mesopelagic, more than 10 times that of the corrected daytime mesopelagic biomass.

Table 2.5. Abundance and biomass of organisms calculated by way of biomass size spectra (BMSS) and total catch during the night in the epipelagic and mesopelagic, and during the day in the mesopelagic. Corrected daytime mesopelagic catch is included.

<table>
<thead>
<tr>
<th>Time of day</th>
<th>Zone</th>
<th>Abundance (ind. m$^{-2}$)</th>
<th>Biomass (mgC m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>BMSS</td>
<td>Catch</td>
</tr>
<tr>
<td>Night</td>
<td>Epipelagic</td>
<td>531.0</td>
<td>470.0</td>
</tr>
<tr>
<td>Night</td>
<td>Mesopelagic</td>
<td>804.0</td>
<td>292.2</td>
</tr>
<tr>
<td>Day</td>
<td>Mesopelagic</td>
<td>83.5</td>
<td>47.2</td>
</tr>
<tr>
<td>Corrected – Day</td>
<td>Mesopelagic</td>
<td>1614.8</td>
<td>762.3</td>
</tr>
</tbody>
</table>

2.3.4 Normalized biomass size spectra (NBSS)

Similar to the abundance – carbon weight size spectra, the nighttime epipelagic NBSS had the steepest slope (-1.40), followed by the corrected daytime NBSS (-1.12). The y-intercept of the daytime mesopelagic (uncorrected) NBSS was significantly lower (ANCOVA; p < 0.003) than all other size spectra, although the slope was only significantly different (ANCOVA; p = 0.02) from the nighttime epipelagic values. The nighttime epipelagic slope was significantly steeper (ANCOVA; p = 0.014) than the nighttime mesopelagic. No other significant differences were observed among NBSS (ANOVA; p > 0.08).
Figure 2.9. Normalized biomass size spectra expressed as biomass (mgC) against normalized biomass (mgC m⁻² ΔmgC⁻¹) for the daytime mesopelagic, nighttime mesopelagic, nighttime epipelagic, and daytime mesopelagic corrected (sum of nighttime epipelagic and mesopelagic abundance by size).
2.4 Discussion

2.4.1 Micronekton composition, abundance and biomass

Micronekton catches were similar to those previously reported around the Hawaiian Islands (Maynard et al., 1975; Drazen et al., 2011) and around other tropical Pacific Islands (Suntsov and Domokos, 2013), which were dominated by myctophids. In several other studies carried out in similar oceanographic settings the nighttime epipelagic micronekton could also be dominated by decapods (Maynard et al., 1975; Reid et al., 1991; De Forest and Drazen, 2009; Suntsov and Domokos, 2013), and cephalopods (Hidaka et al., 2003). The overall contribution of cephalopods to total biomass was relatively high in our study. Although gears used in this study have previously been reported to capture cephalopods (e.g., Williams and Koslow, 1997; Drazen et al., 2011; Suntsov and Domokos, 2013), they are generally thought to under sample this group due to avoidance and spatio-temporal patchiness (Haury et al., 1978; Wormuth and Roper, 1983). The relative contribution of gelatinous zooplankton to total abundance was higher than reported by Maynard et al. (1975). These organisms are particularly vulnerable to under sampling as they are often fragmented and enmeshed in trawls (Williams and Koslow 1997; Graham et al., 2003). Numerically, gonostomatids (primarily Cyclothone spp.) dominated the mesopelagic realm during the day (De Forest and Drazen, 2009; Drazen et al., 2011). However, we found that because of their slender bodies they contributed minimally to total biomass. Thus, mesopelagic biomass was primarily composed of myctophids, decapods, cephalopods and “other fishes” (Maynard et al., 1975; Davison et al., 2013).

Using the International Young Gadoid Pelagic Trawl (IYGPT) off southern Tasmania, with a mouth and mesh comparable to that of the Cobb trawl, Williams and Koslow (1997) found that fishes and gelatinous zooplankton made up 45% and 41% of the total abundance, respectively. Also consistent with our findings, they found that 77% of the total micronekton catch were fishes, and of these myctophids comprised 61% of the abundance and 48% of the biomass.

Mesopelagic abundance shifted from being dominated by gonostomatids, euphausiids and Sternoptyx spp. during the daytime to being dominated by a variety of other mesopelagic fishes during the night. Since most gonostomatids remain within 300-
700 m depth (Miya and Nemoto, 1986) and *Sternoptyx* spp. are non-migratory (Loeb, 1979; Hopkins and Baird, 1985; Davison, 2011) their relative proportion should therefore increase at night in the mesopelagic in the presence of DVM. However, the relative proportion of these mesopelagic fishes decreased at night, while the relative proportion of other mesopelagic fishes increased. These results suggest that there is likely a component of diel horizontal migration (Benoit-Bird et al., 2001), mesopelagic layering, and/or deep-sea flux of deeper mesopelagic fishes and/or bathypelagic fishes (Domokos et al., 2010). Benoit-Bird et al. (2001) observed the horizontal migration of the mesopelagic community onto inshore/shallow areas during the night on the west coast of Oahu, resulting in a discrepancy between day/night total abundance and biomass within the mesopelagic zone. Furthermore, Domokos et al. (2010) identified several thin layers with varying backscatters in both the surface scattering layer (SSL; epipelagic) and deep scattering layer (DSL; mesopelagic), suggesting that each layer was composed of different taxa. Because the epipelagic tows were oblique, sampling the whole epipelagic realm, they are likely reliable estimates. In contrast, mesopelagic tows were horizontal, meaning that a portion of the mesopelagic community may have been missed. However, because the thickness of the DSL decreased during the night (i.e., the thin layers became somewhat compressed) the nighttime estimates are likely reliable, while the daytime estimates may have underestimated micronekton species composition, abundance and biomass.

The acoustic results report that the nighttime SSL contained the highest densities of micronekton followed by the daytime DSL, the nighttime DSL and the daytime SSL (Domokos et al., 2010). Also, biomass was the greatest in the daytime DSL, followed by the nighttime SSL, nighttime DSL, and daytime SSL. Contrary to our findings, the nighttime DSL abundance and biomass off the southwest coast of Oahu was lower than the daytime DSL. Domokos et al. (2010) also found that in regions where the bottom depths were 800-1000 m the DSL extended deeper than in areas greater than 1000 m depth. This suggests that perhaps vertically migrating deep-sea organisms were becoming trapped by the bottom topography in shallower areas, while in deeper areas these organisms were able to make it to their daytime residence depth, resulting in a thinner DSL. Thus, confirming that deep-sea flux of deeper mesopelagic and/or bathypelagic fishes from below 1000 m into shallower layers during the night may have occurred.
2.4.2 Biomass size spectra

A linear relationship between abundance/normalized biomass and body size of micronekton off the south west coast of Oahu was identified. These results confirm the findings of several other studies documenting this empirical model (i.e., Platt et al., 1984; Quiñones et al., 2003; Rodriguez and Mullin, 1986a). Similar to Quiñones et al. (2003) and Rodriguez and Mullin (1986a), the NBSS reported in terms of carbon weight, returned more negative slopes than the typically reported -1.0, which is consistent with Platt et al. (1984). This difference between the carbon weight and volume NBSS has also been reported for the bacterioplankton to microplankton size spectrum (Geider, 1988). Contrary to Quiñones et al. (2003), which assessed the size spectrum from bacteria to mesozooplankton, the nighttime epipelagic biomass size spectrum (abundance-biomass size spectra and normalized biomass size spectra) was significantly different than the nighttime mesopelagic and daytime mesopelagic spectra. Specifically, the nighttime epipelagic biomass size spectrum slope was steeper and the intercept higher than the mesopelagic biomass size spectra. This is consistent with previous studies which found that as depth increases the slope (Rodriguez and Mullin, 1986a; Sweeting et al., 2009) and intercept (Quiñones et al., 2003) both decrease. Thus, while smaller organisms are more important at the surface, larger organisms are more important at depth.

Previous studies have also reported that in the epipelagic layer the slope of the zooplankton biomass size spectrum becomes shallower and the intercept decreases during the night (Rodriguez and Mullin, 1986a; Thompson et al., 2013). In contrast, Suthers et al. (2006) found that in the presence of high abundances of myctophids and gonostomatids, the slope of the zooplankton NBSS becomes steeper during the night. Nevertheless, it is difficult to discern whether or not these studies (i.e., Rodriguez and Mullin, 1986a; Thompson et al., 2013; Suthers et al., 2006) are consistent with the present study, as no daytime epipelagic size spectrum is available for comparison, and the size spectra presented in this study includes micronekton ranging from 20 to 100 mm in length.

Approximately 16% of micronekton on the southwest coast of Oahu remain in the epipelagic zone during the day based on acoustic data (Domokos et al., 2010; Kwong et al., In Review). It should be noted that the acoustic data was targeted towards small fishes with swim bladders and is independent of size. Therefore, this approximation (i.e.,
Domokos et al., 2010; Kwong et al., In Review) must be used with caution. Nevertheless, when considering the whole community, the influx of micronekton into the epipelagic, in theory, may result in a shallowing of the size spectrum. The differences between these size spectra (i.e., Rodriguez and Mullin, 1986a; Thompson et al., 2013; Suthers et al., 2006) may also be attributed to biomass ‘domes’ described by Sprules and Goyke (1994). When dissected, biomass size spectra reveal a series of biomass domes, which represent different groups of organisms and/or trophic levels (i.e., phytoplankton, zooplankton, nekton, etc.; Dickie et al., 1987; Thiebaux and Dickie, 1992, 1993; Boudreau and Dickie, 1992; Sprules and Goyke, 1994; Sprules et al., 2001). Therefore, depending on the size range of organisms captured the overall slope of the size spectrum may vary substantially when only a small portion of the community is considered in the analysis. In addition, differences in the slope and intercept between the epi- and mesopelagic zones may reflect ontogenetic changes. For example, one species may inhabit near shore nursery habitat when they are small, while larger individuals may inhabit cold deep waters (Macpherson and Duarte, 1991; Sweeting et al., 2009). When assessed in a single system the size spectrum can still effectively be used to evaluate differences in biomass and abundance across time and depth. However, caution must be taken when comparing size spectra for a limited size range.

A large discrepancy exists between the size spectra calculated abundance and biomass and trawl based estimates of actual catch abundance and biomass. In general, the discrepancy between biomass estimates using actual trawl catches and acoustics are at least 7-10 fold (Koslow et al., 1997; Kloser et al., 2009; Kaardvedt et al., 2012; Irigoien et al., 2014), which is similar to what we have arrived at after reconciling actual trawl micronekton biomass and biomass spectra estimated biomass. We attribute this difference to gaps in the size spectra, which were assumed to be areas in which biomass exists but is not efficiently captured, as well as the aforementioned biomass domes. Previous studies argue that these gaps in data points are actually areas of zero biomass (e.g., Tittel et al., 1998), or that these gaps can be filled by benthic biomass (e.g., Witek and Krajewska-Soltys, 1989). Tittel et al. (1998) argued that if these gaps are indeed areas of zero biomass they represent empty niches, and will likely only exist for a short period of time. This study demonstrated that the three different gears sampled with variable efficiency across the
micronekton size spectrum (at times not overlapping). As previously mentioned, the size spectra produced here is the result of a gear intercalibration (Kwong et al., In Review). This inter-calibration was conducted using 5 mm length intervals. Therefore, for an observation to be captured in the final size spectra, organisms must have been captured at all lengths for both the IKMT and Cobb and/or the IKMT and HUFT, which was not the case. By producing size spectra for each gear type, this study demonstrated that the data points for each gear did not exactly overlap. We considered the calibration valid as there were enough points of overlap between the gears to “link” their respective catches. Therefore, the abundance and biomass calculated using the size spectra was assumed to be accurate, as the gaps in the size spectra represented areas in which biomass exists but is not efficiently captured by one or even all gears. In combination with multiple gears, the use of size spectra may reduce net sampling bias commonly associated with larger micronekton net avoidance (Kaartvedt et al., 2012; Kwong et al., In Review).

2.4.3 Diel vertical migration

Total migratory micronekton was assumed to be approximately equivalent to the nighttime epipelagic abundance and biomass, as the majority of these organisms (>90%) inhabit waters below 400 m depth (Domokos et al., 2010; Maynard et al., 1975; Williams and Koslow, 1997). Consistent with several other studies, myctophids (primarily Triphoturus nigrescens) made up the largest portion of migratory micronekton biomass (Davison, 2011; Drazen et al., 2011; Suntsov and Domokos, 2013; Hopkins and Lancraft, 1984; Maynard et al., 1975), followed by euphausiids and decapods (Ariza et al., 2015). Although percent contribution of decapod biomass in the epipelagic layer at night was relatively high, decapod biomass increased in the mesopelagic at night (Angel and Baker, 1982). Because the DSL was identified using acoustics, which was targeting larger micronekton and fishes with swim bladders (Domokos et al., 2010), decapods were likely under sampled during the daytime in the mesopelagic compared to fishes.

When calculating migratory micronekton abundance and biomass using the size spectrum and the total catch, large discrepancies were observed. Total migratory abundance and biomass calculated using the size spectrum were ~1.2 and ~14 times greater than net estimates, respectively. Indeed, net-based estimates of micronekton abundance
and biomass consistently underestimated their true densities in the water column (Koslow et al., 1997; Kloster et al., 2009; Pakhomov and Yamamura, 2010; Kaartvedt et al., 2012).

Acoustically estimated nighttime total relative abundance and biomass in the water column during our study were 504 ± 44 m² nmi⁻² and 1330 ± 89 m² nmi⁻² (nmi= nautical miles), respectively (Domokos et al. 2010). In theory, these values should correspond to the relative abundance and biomass in the water column during the day, which is equivalent to the daytime SSL plus the daytime DSL, 340 ± 42 m² nmi⁻² and 990 ± 75 m² nmi⁻², respectively. These discrepancies were attributed to mesopelagic layering (Domokos et al., 2010), diel horizontal migration (Reid et al., 1991; Benoit-Bird et al., 2001) and/or deep-sea flux originating from the deeper mesopelagic and bathypelagic zones (Kwong et al., In Review). Using relative micronekton densities calculated acoustically, one can assume that the relative abundance and biomass of migratory micronekton moving into the SSL during the night should be equivalent to the nighttime SSL minus the daytime SSL. Domokos et al. (2010) assessed the relative migratory abundance and biomass to be 251 ± 27 m² nmi⁻² and 603 ± 84 m² nmi⁻², respectively. Consistent with Klevjer et al. (2016) in a variety of oceanographic regimes including our study area this accounted for 50 ± 11% and 45 ± 11% of total micronekton abundance and biomass. This should also be equivalent to the relative abundance and biomass of the daytime DSL minus the nighttime DSL, e.g. 87 ± 81 m² nmi⁻² and 263 ± 131 m² nmi⁻², respectively. Since this is not the case, there is likely a portion of migratory micronekton appearing in the nighttime SSL that did not originate from the DSL. This supports the aforementioned hypothesis that there is a component of diel horizontal migration and/or deep-sea flux occurring in the sampling area.

Based on the acoustics, ~16% of the micronekton abundance and biomass resided within the epipelagic layer during the day, and did not undergo DVM (Domokos et al., 2010). When correcting estimates of migratory abundance and biomass, calculated using the size spectra, the abundance and biomass of migratory micronekton during this study were ~487 ind. m⁻² and ~6,014 mg C m⁻², respectively. Based on the size spectra, 30% and 18% of the total micronekton abundance and biomass were undergoing DVM ascending into the epipelagic zone. These estimated proportions are much lower than the acoustic estimates (i.e., abundance = 50 ± 11%; biomass = 45 ± 11%), and previous studies reporting that ~43% of micronekton abundance (Maynard et al., 1975) and ~50% of total
micronekton biomass vertically migrated (Maynard et al., 1975; Williams and Koslow, 1975). Because only two frequencies were used in the acoustic surveys, both of which were targeting large fishes with swim bladders, the densities of non-fish groups were likely underestimated. Furthermore, only the 38 kHz output was used for DSL calculations of micronekton density, as sound attenuates more rapidly at higher frequencies (Domokos et al., 2010). Since smaller organisms scatter sound at higher frequencies, their presence in the DSL was likely undetected by the acoustics (Domokos et al., 2010). Therefore, the acoustic estimates likely represent the relative proportion of mesopelagic fishes with swimbladders that are undergoing DVM, while the size spectra estimates are representative of total migrating micronekton values. The acoustic results showed that the DSL was composed of several thin backscattering layers, suggesting that each layer may have been composed of different species or sizes of organisms. Thus, targeted horizontal DSL sampling may have underestimated total micronekton densities (Domokos et al., 2010). It was assumed that the nighttime epipelagic abundance and biomass estimates in this study were accurate, and can be used to infer migratory micronekton abundance and biomass.

Total migratory abundance and biomass predicted using the biomass spectra theory (~487 ind.m$^{-2}$ and ~6,014 mgC m$^{-2}$) were approximately two fold higher than in Hidaka et al. (2001) from the western equatorial North Pacific. In 2001, Al-Mutairi and Landry assessed migratory zooplankton to be ~142 mgC m$^{-2}$ in Hawaiian waters. However, because this study assessed mesozooplankton biomass, it is not directly comparable to the values reported in the current study. In a similar oligotrophic region, Ariza et al. (2015) reported mean total migratory biomass of 467 ± 187 mgC m$^{-2}$, in which micronekton made up 201 ± 61 mgC m$^{-2}$ or ~43% of migratory biomass. In general, estimates of migratory micronekton abundance and biomass using the biomass spectra theory were substantially higher than estimates based solely on the catch data.

2.4.4 Concluding remarks

This study demonstrated that micronekton species composition and size spectra vary by depth and time of day off the southwest coast of Oahu Island. The DVM of these organisms was apparent in the changes in relative proportions of dominant micronekton taxa, as well as changes in the slope and elevation of the size spectra. The discrepancy between day and
night mesopelagic abundance and biomass and relative species contribution may have been due to deep-sea influx, mesopelagic layering and/or diel horizontal migration in this region. Differences in the efficiencies of the three different gears in capturing different sized organisms demonstrated that gaps in the inter-calibrated micronekton size spectra represent areas in which biomass exists but were not captured. Overall, estimates of micronekton migratory flux using the biomass spectra theory greatly exceeded previous contemporary net estimates likely due to avoidance, escapement and patchiness. Thus, it is possible that the use of size spectra in predicting micronekton abundance and biomass reduces bias associated with net sampling. To test this hypothesis, future studies must combine multiple acoustic frequency data and multiple sampling gears. Nevertheless, the size spectra elevation and slope may be used to assess carbon transport via vertically migration zooplankton and micronekton from the epipelagic to mesopelagic zone.
3 Active carbon transport using the biomass size spectra

3.1 Introduction

Oceans play a critical role in global carbon cycling absorbing ~48% of the anthropogenic CO₂ from the atmosphere into surface waters, and pumping carbon both passively and actively to the deep ocean (Sabine et al., 2004). The concentration of CO₂ in the deep ocean is higher than that of the surface mixed layer (Volk and Hoffert, 1985). There are three carbon pumps in the ocean that effectively maintain this vertical concentration gradient: the solubility pump, the carbonate pump, and the soft-tissue pump, (Volk and Hoffert, 1985). The solubility pump, is driven by differences in CO₂ temperature dependent solubility. Collectively, the carbonate pump and the soft-tissue pump constitute the biological pump, which is responsible for maintaining approximately 70% of the vertical concentration gradient (Volk and Hoffert, 1985). The biological carbon pump involves the utilization of CO₂ by phytoplankton during photosynthesis in the ocean’s surface waters to produce organic and calcium carbonate particles. A portion of the resulting particles are subsequently transported to the mesopelagic zone (200 – 1000 m depth) either via gravitational settling (passive carbon transport) or active biotransport (active carbon transport/flux) (Broecker, 1983; Steinberg et al., 2000; Volk and Hoffert, 1985). This transported carbon is then returned to its dissolved inorganic form through decomposition and dissolution occurring beyond the euphotic zone in the deep ocean (Volk and Hoffert, 1985). The biological carbon pump sequesters atmospheric carbon to the deep ocean impacting climate and thus global warming (Volk and Hoffert, 1985). Alternatively, a portion of this carbon may be re-introduced to the food web through consumption of organic matter by larger organisms in the deep ocean. Because aerobic metabolism and decomposition involve consumption of oxygen, the mesopelagic zone vertically coincides with the oxygen minimum zone (OMZ; Bianchi et al., 2013a). Changes in oceanic conditions driven by climate change are suggested to impact the efficiency of all three pumps, affecting atmospheric carbon concentrations (Volk and Hoffert, 1985).

Zooplankton and micronekton play a key role in both active and passive carbon transport. Passive carbon transport (i.e. particulate organic carbon [POC] flux) can occur via phytoplankton sinking directly as marine snow, and after passing through the
zooplankton guts as compact fecal pellets (Ducklow et al., 2001; Turner, 2002). As POC sinks it is gradually fragmented, degraded, consumed and respired (Buesseler et al., 2008). The result being that with depth particulate organic carbon (POC) attenuates (Figure 3.1). Mesopelagic bacteria and zooplankton are known to play a pivotal role in particle transport and attenuation (Buesseler et al., 2008; Steinberg et al., 2008). However, the carbon demands of the mesopelagic community are notably higher than the sinking flux of POC (Koppelmann and Weikert, 1999; Steinberg et al., 2008). Thus, the mesopelagic carbon budgets are largely being met through carnivory on vertically migrating plankton (Steinberg et al., 2008; Hannides et al., 2013; Choy et al., 2016). Other sources of organic carbon in the mesopelagic realm may include mesopelagic production (e.g., chemoautotrophy; Reinthaler et al., 2010) or lateral transport (coastal to open ocean; Michaels et al., 1994; Burd et al., 2010).

Figure 3.1. Hypothetical POC flux and attenuation with depth. Inspired by Giering et al., 2014.
Active carbon transport refers to organic matter that is transported by zooplankton and micronekton species (Ducklow et al., 2001; Hidaka et al., 2001; Ariza et al., 2015) when they migrate below the mixed layer (Angel and Pugh, 2000; Bordeur et al., 2005; Steinberg et al., 2000), diurnally (Angel and Pugh, 2000; Longhurst, 1976; Ringelberg, 1964), seasonally or ontogenetically (Clarke, 1983; Bailey and Robison, 1986; Kobari et al., 2008). Diel vertical migration is a known mechanism for minimizing exposure to visual predators (Hernández-León et al., 2010; Iwasa, 1982; Vuorinen, 1987; Zaret and Suffern, 1976). Organisms remain below the euphotic zone during the day, and migrate to the surface waters during the night to feed (Ariza et al., 2015). By consuming phytoplankton and other non-migrating zooplankton at night, and subsequently metabolizing this material during the day at depth, zooplankton and micronekton release carbon via respiration, excretion, defecation and mortality (Angel and Pugh, 2000; Ariza et al., 2015; Ducklow et al., 2001; Hernández-León et al., 2001; Kobari et al., 2008; Longhurst et al., 1990; Steinberg et al., 2000; Turner, 2002; Zhang and Dam, 1997).

Longhurst et al. (1990) measured the respiratory flux of zooplankton undergoing diel vertical migrations (DVM) for the first time, noting that it added between 5 and 20% to the current estimates of vertical carbon flux. In doing so, Longhurst and his colleagues set in motion the concept of quantifying active carbon transport by vertically migrating marine organisms such as plankton and nekton. Since then, active carbon transport has been identified as a significant contributor to downward carbon transport (Dam et al., 1995).

Spatial estimates of passive to active carbon transport ratios in the water column are all recent, highly variable (ranging from 3 to 70%) and limited, while temporal estimates are generally absent (Table 3.1-1). This is likely a reflection of spatial heterogeneity in the distribution, productivity and composition of plankton/micronekton as well as limitations of methodological approaches (Ducklow et al., 2001; Longhurst et al., 1990; Dam et al., 1995; Zhang and Dam, 1997; LeBorgne and Rodier, 1997; Rodier and Le Borgne, 1997; Morales, 1999; Steinberg et al., 2000; Al-Mutairi and Landry, 2001). For example, in Hawaiian waters, Al-Mutairi and Landry (2001) found that active flux ranged from 6 to 25% of mean POC flux. Davison (2011) reported that fish mediated export represent 95% of the passive carbon transport to 400 m, while other studies reported ranges
of 1-73% (Hudson et al., 2014). Podeswa (2015) found that decapods alone may account for 5-8% of the passive flux to ~700 m depth in the North Pacific Subtropical Gyre. Micronekton respiratory flux alone may contribute 28-55% of the passive flux at 160 m depth (Table 3.1).

Past studies have generally focused primarily on active carbon transport via respiration, excretion, gut flux and/or mortality of individual species (Darnis and Fortier, 2012; Kobari et al., 2008), individual groups (i.e., zooplankton or micronekton; Hidaka et al., 2001) or specific plankton size ranges (Ariza et al., 2015; Davison et al., 2013; Hernández-León et al., 2001; Table 3.1). The inclusion of micronekton is critical, as these organisms, unlike mesozooplankton, migrate to the lower part (500 – 1000 m, Baird et al., 1975) of the mesopelagic zone and due to their long gut passage time (4 – 10 hours; Pakhomov et al., 1996) may metabolize / excrete their gut contents at those depths. Thus, by neglecting active carbon transport, carbon export to the deep ocean is under estimated, in some cases by up to 70% (Buesseler et al., 2007; Davison et al., 2013; Falkowski et al., 2003; Martz et al., 2008; Hernández-León et al., 2010; Usbeck et al., 2003; Wexels Riser et al., 2010). To accurately quantify active carbon transport via zooplankton and micronekton, it is crucial that the whole community be assessed, including small and large migrants (Darnis and Fortier, 2012). Factors such as excretion, respiration, mortality and gut flux must all be taken into consideration (Davison et al., 2013; Ducklow et al., 2001). These ecological process rates are known to be size dependent (e.g. Peters, 1983, Shin et al., 2005).

Body size (e.g. length, weight) of any organism is directly related its lifespan, home range size and life history. Furthermore, rate processes such as growth, mortality, excretion, respiration, gut flux, and trophic status scale with size (Garcia-Munoz et al., 2014; Zhou and Huntley, 1997; Zhou, 2006). These rates are of particular importance when it comes to assessing biological and biochemical processes within marine ecosystems. Because transfer efficiency is reflected by the slope of the biomass size spectra (Gaedke, 1992) and rates scale with size (Garcia-Munoz et al., 2014; Zhou and Huntley, 1997; Zhou, 2006), the biomass spectra theory can be used to calculate community level fundamental rates and therefore to assess carbon transport from the epipelagic to mesopelagic zone.
The aim of this chapter is to quantify active carbon transport of micronekton by developing a biomass/production size dependent model based on the fundamentals of the biomass spectra theory. We believe that in combination with optical and acoustic methods, this model may provide an approach to estimate spatially and temporally resolved active carbon transport and would decrease the uncertainty associated with active carbon transport incorporation into biogeochemical models.
Table 3.1. Summary of studies assessing active carbon transport via zooplankton and/or micronekton, including tow type, size range and additional flux measurements conducted. In the flux measurements column, “M” refers to migratory, “R” to respiratory, “G” to gravitational, “MR” to mortality, “E” to excretory, “GF” to gut flux, “I” to ingested,

<table>
<thead>
<tr>
<th>Gear(s)</th>
<th>Fluxes Measured</th>
<th>Taxa</th>
<th>Organism Size Range (mm)</th>
<th>Active Flux (mgC m(^{-2}) day(^{-1}))</th>
<th>Active vs. passive flux</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25 m(^2) Double WP-2 with 100 µm mesh 5 m(^2) MOHT with 4 mm mesh</td>
<td>M, R, G</td>
<td>Euphausiids, Chaetognaths, Myctophids, Sergestids</td>
<td>1-50 mm</td>
<td>6.36 ± 2.89</td>
<td>R: 23-71% of POC to 150 m</td>
<td>Ariza et al., 2015</td>
</tr>
<tr>
<td>1 m(^2) RMT1 with 0.32 mm mesh 8 m(^2) RMT8 with 4.5 mm mesh</td>
<td>M</td>
<td>Micronekton</td>
<td>&gt;0.32 mm</td>
<td>12.5-58</td>
<td>-</td>
<td>Angel and Pugh, 2000</td>
</tr>
<tr>
<td>1 m(^2) plankton net with 0.2 mm Nitex mesh</td>
<td>M, E, MR, R</td>
<td>Zooplankton</td>
<td>0.2-5 mm &gt;5 mm</td>
<td>1-9.2</td>
<td>5.6-25% of POC flux at 150 m</td>
<td>Al-Mutairi and Landry, 2001</td>
</tr>
<tr>
<td>0.25 m(^2) MOCNESS with 64 µm mesh</td>
<td>M, R</td>
<td>Copepods</td>
<td>200-2000 µm</td>
<td>6-41</td>
<td>18-70% of the POC flux at 150 m</td>
<td>Dam et al., 1995</td>
</tr>
<tr>
<td>0.50 m(^2) Hydrobios® multinet sampler with 200 µm mesh 1 m(^2) square aperture with 200 µm mesh net</td>
<td>M(^3), R, I</td>
<td>Calanus hyperboreus, C. glacialis</td>
<td>200-1000 µm &gt;1000 µm</td>
<td>100-132% of POC to 100 m</td>
<td>-</td>
<td>Darnis and Fortier, 2012</td>
</tr>
<tr>
<td>3 m(^2) IKMT with 1.7 mm mesh 5 m(^2) MOHT with 1.7 mm mesh</td>
<td>M, R, E</td>
<td>Micronekton Large zooplankton</td>
<td>2-10 cm</td>
<td>22-24</td>
<td>Fish export 95% of POC to 400 m</td>
<td>Davison, 2011; Davison et al., 2013</td>
</tr>
<tr>
<td>LHPR net with a 200 µm mesh</td>
<td>M, GF, R</td>
<td>Zooplankton</td>
<td>500-1000 µm &gt;1000 µm</td>
<td>1.92-4.29</td>
<td>R: 16-45% of POC to 150 m GF: 3-25% of POC to 150 m</td>
<td>Hernández-León et al., 2001</td>
</tr>
<tr>
<td>2 m(^2) ORI net with 200 µm mesh ~400 m(^2) midwater otter trawl (TANSYU) with 100 cm mesh at mouth decreasing to 8 mm at the cod end</td>
<td>R, M, GF, MR</td>
<td>Mesozooplankton Micronekton</td>
<td>200-2000 µm &gt;8 mm</td>
<td>9.97 – 23.53 15.2 – 29.9</td>
<td>18.2%-42.9% of POC flux at 150 m (mesozooplankton) 27.7-54.6% of POC flux at 150 m (micronekton)</td>
<td>Hidaka et al., 2001</td>
</tr>
<tr>
<td>36 m(^2) double-warp, midwater trawls with 6 mm mesh; 20-35 m vertical mouth, 110 m door-spread Akra trawl with 22 mm mesh</td>
<td>M, E</td>
<td>Myctophids</td>
<td>11-67 mm</td>
<td>0.04-2.78</td>
<td>1-73% of POC to 1000m</td>
<td>Hudson et al., 2014</td>
</tr>
<tr>
<td>Gear(s)</td>
<td>Fluxes Measured</td>
<td>Taxa</td>
<td>Organism Size Range (mm)</td>
<td>Active Flux (mgC m⁻²day⁻¹)</td>
<td>Active vs. passive flux</td>
<td>Source</td>
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<tr>
<td>25 cm diameter double CalVET net with 53 µm mesh; 40 cm diameter WP2 nets (x3) with 200 µm mesh; 80 cm diameter double Bongo net with 500 µm mesh</td>
<td>M, R</td>
<td>Zooplankton</td>
<td>1000 – 2000 µm &gt;2000 µm</td>
<td>0.6-2.4</td>
<td>-</td>
<td>Isla et al., 2015</td>
</tr>
<tr>
<td>40 cm diameter triple WP-2 with 200 µm mesh</td>
<td>R, E</td>
<td>Zooplankton</td>
<td>&gt; 200 µm</td>
<td>7.1-28.8</td>
<td>-</td>
<td>Isla et al., 2004</td>
</tr>
<tr>
<td>60 cm diameter triple WP-2 with 200 µm mesh</td>
<td>E, R, M</td>
<td>Zooplankton</td>
<td>&gt; 200 µm</td>
<td>2.2-30.3</td>
<td>-</td>
<td>Isla and Anadon, 2004</td>
</tr>
<tr>
<td>1.0 m² IONESS with 335 µm mesh</td>
<td>G, R</td>
<td>Copepods</td>
<td>&gt; 100 µm</td>
<td>3.9-16.6</td>
<td>-</td>
<td>Kobari et al., 2008</td>
</tr>
<tr>
<td>1.0 m² IONESS with 335 µm mesh</td>
<td>R, E</td>
<td>Mesozooplankton</td>
<td>&gt; 335 µm</td>
<td>2-7</td>
<td>10-52% of POC flux to 150 m</td>
<td>Kobari et al., 2013</td>
</tr>
<tr>
<td>Triple WP-2 with 200 µm mesh Hydobios MPS II with 200 µm mesh 35 cm diameter triple net with 35 µm mesh¹¹</td>
<td>R, E, M</td>
<td>Mesozooplankton Microzooplankton</td>
<td>200-2000 µm 35-200 µm</td>
<td>3.8-7.9</td>
<td>4-8% of the POC flux at the base of the euphotic zone</td>
<td>Le Borgne and Rodier, 1997</td>
</tr>
<tr>
<td>1 m² BIONESS with 200-243 µm mesh</td>
<td>R, M</td>
<td>Mesozooplankton Micronekton</td>
<td>200-2000 µm</td>
<td>3-107</td>
<td>13-53% of POC flux across the pycnocline</td>
<td>Longhurst et al., 1990</td>
</tr>
<tr>
<td>LHPR ¹²</td>
<td>R, M</td>
<td>Copepods</td>
<td>-</td>
<td>0.75</td>
<td>-</td>
<td>Longhurst and Williams, 1992</td>
</tr>
<tr>
<td>3.14 m² mouth, 500 µm mesh</td>
<td>R, E, GF</td>
<td>-</td>
<td>-</td>
<td>0.382-0.625</td>
<td>4.8-7.8% of POC to 710.7 m</td>
<td>Podeswa, 2012</td>
</tr>
<tr>
<td>LHPR with 200 µm mesh</td>
<td>R</td>
<td>Zooplankton</td>
<td>&gt; 200 µm</td>
<td>-</td>
<td>53% of POC flux to 150 m</td>
<td>Packard and Gomez, 2013</td>
</tr>
<tr>
<td>MOCNESS-10 with a 10 m² mouth opening and 6 mm mesh</td>
<td>R, M, MR, G, E</td>
<td>Decapods</td>
<td>~30-80 mm</td>
<td>2.6</td>
<td>-</td>
<td>Schukat et al., 2013</td>
</tr>
<tr>
<td>1 m² single (9 nets) and double (18 nets) MOCNESS with 333 µm mesh</td>
<td>R</td>
<td>Decapods</td>
<td>~30-80 mm</td>
<td>2.6</td>
<td>-</td>
<td>Schukat et al., 2013</td>
</tr>
<tr>
<td>2 m diameter 500 µm mesh net</td>
<td>M, R, G, GF, E</td>
<td>Copepods Euphausiids</td>
<td>~0.5-12 mm</td>
<td>0.94</td>
<td>3% of POC to 150 m</td>
<td>Schuetzer and Steinberg, 2002</td>
</tr>
<tr>
<td>2 m diameter 500 µm mesh net</td>
<td>M, R, E</td>
<td>Mesozooplankton Macrozooplankton</td>
<td>&gt; 500 µm</td>
<td>0-9.9</td>
<td>0-38.6% of the POC flux at 150 m</td>
<td>Steinberg et al., 2000</td>
</tr>
<tr>
<td>1 m² MOCNESS with 335 µm mesh</td>
<td>R, MR, E</td>
<td>Mesozooplankton Macrozooplankton</td>
<td>&gt; 335 µm</td>
<td>16-46</td>
<td>-</td>
<td>Steinberg et al., 2008</td>
</tr>
<tr>
<td>Gear(s)</td>
<td>Fluxes Measured</td>
<td>Taxa</td>
<td>Organism Size Range (mm)</td>
<td>Active Flux (mg C m(^{-2}) day(^{-1}))</td>
<td>Active vs. passive flux</td>
<td>Source</td>
</tr>
<tr>
<td>------------------------------------------------------------------------</td>
<td>-----------------</td>
<td>-------------------------------------------</td>
<td>--------------------------</td>
<td>---------------------------------------------</td>
<td>-------------------------</td>
<td>--------------------------------</td>
</tr>
<tr>
<td>1 m(^2) MOCNESS with 202 µm mesh</td>
<td>R</td>
<td>Copepods, Euphausiids, Chaetognaths, Hyperiids</td>
<td>&gt; 202 µm</td>
<td>2.4-47.1</td>
<td>1.9-40.5% of POC to 100 m</td>
<td>Stukel et al., 2013</td>
</tr>
<tr>
<td>0.25 m(^2) VMPS with 330 µm mesh</td>
<td>M, R, MR</td>
<td>Copepods</td>
<td>&gt; 330 µm</td>
<td>8</td>
<td>-</td>
<td>Takahashi et al., 2009</td>
</tr>
<tr>
<td>105 m(^2) five-net multiple plankton sampler with 100 mm mesh at wings, decreasing to 20 mm, 10 mm and then 7 mm at the cod end</td>
<td>M</td>
<td>Micronekton</td>
<td>20-300 mm</td>
<td>0.94-4.06</td>
<td>-</td>
<td>Williams and Koslow, 1997</td>
</tr>
<tr>
<td>0.25 m(^2) MOCNESS with 64 µm mesh</td>
<td>M, R, MR</td>
<td>Mesozooplankton</td>
<td>200-2000 µm</td>
<td>0.59-1.06</td>
<td>31-44% of POC flux at the base of the euphotic zone</td>
<td>Zhang and Dam, 1997</td>
</tr>
<tr>
<td>LHPR with 200 µm mesh</td>
<td>M, R, G</td>
<td>Zooplankton</td>
<td>&gt; 200 µm</td>
<td>8.28</td>
<td>53% of POC to mesopelagic zone</td>
<td>Yebra et al., 2005</td>
</tr>
</tbody>
</table>
3.2 Methodology

Organism size has long been used as a scaling factor for myriad biological processes including respiration, excretion, gut flux and mortality (Fenchel, 1974; Zeuthen, 1953; Peterson and Wroblewski, 1984). Here, these size dependent rates were calculated using the nighttime epipelagic biomass size spectrum for the whole micronektonic community (20-100 mm) from Chapter 2 (Figure 2.8) as the input.

3.2.1 Nominal size class

Organisms were grouped into log₂ size bins based on carbon weight (Table 3.2). Nominal size classes, as dry weight ($DW_{Ni}$) or carbon weight ($CW_{Ni}$) were then calculated for each size bin using Equation 2.5, following Blanco et al. (1998). These values were then used to calculate respiration, mortality, excretion and gut flux in the following sections. Equation 2.4 was then used to determine the abundance of organisms in each nominal size class. To determine the biomass (mgC) in each nominal size class, the abundance was multiplied by the carbon weight nominal size class.

Table 3.2 Nominal size classes (mg) calculated according to the lower and upper limit (mgC) of each size bin and the slope (-1.61) of the abundance carbon weight size spectrum at night in the epipelagic (Figure 2.8). Where $CW_{Ni}$ is the carbon weight nominal size class and $DW_{Ni}$ is the dry weight nominal size class calculated using the carbon weight to dry weight ratio ($CR$) for all organisms in the data set (0.4286 ± 0.0001SEM).

<table>
<thead>
<tr>
<th>Lower Limit (mgC)</th>
<th>Upper Limit (mgC)</th>
<th>$CW_{Ni}$ (mg)</th>
<th>$DW_{Ni}$ (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.125</td>
<td>0.25</td>
<td>0.178</td>
<td>0.000416</td>
</tr>
<tr>
<td>0.25</td>
<td>0.5</td>
<td>0.356</td>
<td>0.000831</td>
</tr>
<tr>
<td>0.5</td>
<td>1</td>
<td>0.713</td>
<td>0.00166</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>1.425</td>
<td>0.00333</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>2.850</td>
<td>0.00665</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>5.701</td>
<td>0.0133</td>
</tr>
<tr>
<td>8</td>
<td>16</td>
<td>11.402</td>
<td>0.0266</td>
</tr>
<tr>
<td>16</td>
<td>32</td>
<td>22.804</td>
<td>0.0532</td>
</tr>
<tr>
<td>32</td>
<td>64</td>
<td>45.608</td>
<td>0.106</td>
</tr>
<tr>
<td>64</td>
<td>128</td>
<td>91.215</td>
<td>0.213</td>
</tr>
<tr>
<td>128</td>
<td>256</td>
<td>182.430</td>
<td>0.426</td>
</tr>
<tr>
<td>256</td>
<td>512</td>
<td>364.861</td>
<td>0.851</td>
</tr>
<tr>
<td>512</td>
<td>1024</td>
<td>729.722</td>
<td>1.703</td>
</tr>
<tr>
<td>1024</td>
<td>2048</td>
<td>1459.443</td>
<td>3.405</td>
</tr>
<tr>
<td>2048</td>
<td>4096</td>
<td>2918.886</td>
<td>6.810</td>
</tr>
<tr>
<td>4096</td>
<td>8192</td>
<td>5837.773</td>
<td>13.621</td>
</tr>
</tbody>
</table>
3.2.2 Respiration

The concept that respiration rate is related to body size was first initiated by Sarrus and Rameaux (1839). More recently, Ikeda (1985) presented an empirical allometric relationship between respiration and carbon weight for a variety of zooplankton and micronekton exposed to ambient temperatures ranging from -1.4 to 30 °C. To determine respiratory carbon, it was first necessary to calculate respiratory rate of oxygen uptake according to Ikeda (1985), as follows:

Equation 3.1 \[ \ln RO_{W_Ni} = 0.5254 + 0.8354 \ln CW_{Ni} + 0.0601T \]

Where \( RO_{W_Ni} \) is the respiratory rate of oxygen uptake (\( \mu \text{LO}_2/\text{organism/hr} \)), \( CW_{Ni} \) is the carbon weight for nominal size class \( Ni \) in mg and \( T \) is the environmental temperature (°C). To convert this value to daily respiration at depth, \( RO_{W_Ni} \) was multiplied by the hours spent at depth (\( TD \)), which was 9 hours per day as determined using acoustics (Domokos et al., 2010). Respiratory carbon equivalent for an individual in a given nominal size class the following equation was used:

Equation 3.2 \[ R(CW_{Ni}) = RO \times RQ \times \left( \frac{12}{22.4} \right) \]

Where, \( RQ \) is the respiratory quotient (0.97 according to Gnaiger (1983)), 12 is the molar weight of carbon (g/mol), and 22.4 is the molar volume (mol/L) of an ideal gas at standard pressure and temperature. To calculate the total community respiration (\( \mu \text{gC m}^{-2} \text{ day}^{-1} \)), respiration was calculated for each nominal size class (Table 3.2-1) and multiplied by the abundance of organisms in each nominal size class using Equation 2.4 with the lower and upper limits of each nominal size class present in Table 3.2-1. These values were then added together to calculate total community respiration (\( \bar{R} \)), as follows:

Equation 3.3 \[ \bar{R} = \sum_{i=1}^{N} (N_{W_Ni} \times R(CW_{Ni})) \]
3.2.3 Mortality

Although the relationship between size and mortality is unclear, mortality rate has been proven to decrease with increasing size (Pearcy, 1962; Cushing, 1974; Ursin, 1967; Peterson and Wroblewski, 1984). Peterson and Wroblewski (1984) derived a size-dependent model for determining mortality rate based on Silvert and Platt (1980), which assumed that predation scales in a perfectly isometric fashion. The Zhang and Dam (1997) adaption of Peterson and Wroblewski (1984) was used to estimate natural mortality:

\[
DM(DW_{Ni}) = (5.26 \times 10^{-3} \text{day}^{-1}) \times DW_{Ni}^{-0.25}
\]

Where, \(DM(DW_{Ni})\) is the mortality rate (day\(^{-1}\)) of an individual, \((DW_{Ni})\) is the nominal size class in dry weight (g) (Table 3.2-1). Hourly weight-specific mortality (hour\(^{-1}\)) \(HM(DW_{Ni})\), was then calculated by dividing \(DM(DW_{Ni})\) by 24 h d\(^{-1}\). To determine the total downward flux due to mortality, \(M(CW_{Ni})\), in mgC m\(^{-2}\) day\(^{-1}\) for organisms in nominal size class \(DW_{Ni}\) the following equation was then applied:

\[
M(CW_{Ni}) = B(CW_{Ni}) \times HM(DW_{Ni}) \times TD \times CR
\]

Where, \(CW_{Ni}\) is the nominal size in carbon weight (mg) class equivalent of \(DW_{Ni}\), calculated using the carbon weight to dry weight ratio (CR) which calculated using all organisms in the data set to be 0.4286 ± 0.0001 (SEM). \(B(CW_{Ni})\) is the total carbon biomass of organisms in given nominal size class (i.e., abundance*\(CW_{Ni}\)), which was calculated using Equation 2.4 and Equation 2.5. \(TD\) is the number of hours per day spent at depth (9 hours). \(M(CW_{Ni})\) was then converted from mg to µg, and the total daily mortality flux of the community (\(\dot{M}\)) in µgC m\(^{-2}\) day\(^{-1}\) was calculated by adding the mortality for each nominal size class together (Table 3.2-1) using the following equation:

\[
\dot{M} = \sum_{i=1}^{N} M(CW_{Ni})
\]

3.2.4 Excretion

Since dissolved organic carbon (DOC) excretion data for fishes are lacking (Hudson et al., 2014), the relationship between CO\(_2\) respiration to DOC excretion reported by Steinberg et al. (2000) was used to estimate DOC excretion for all macrozooplankton and
micronekton. Steinberg et al. (2000) found that DOC excretion was on average 31% of CO$_2$ respiration (µgC respired), and found similar variation, depending on environmental temperature and organism weight, across crustacean species. Therefore, excretion (E($CW_{N_i}$)) was taken to be $0.31 \times (N_{W_{N_i}} \times R(CW_{N_i}))$, for each nominal size class ($N_{W_{N_i}}$) in carbon weight (mg), and total daily excretory flux of the community ($\hat{E}$) in µgC m$^{-2}$ day$^{-1}$ was calculated by adding the excretion for each nominal size class (Table 3.2-1) together using the following equation:

Equation 3.7  
\[ \hat{E} = \sum_{i=1}^{N} E(CW_{N_i}) \]

3.2.5 Gut Flux

Gut flux refers to the non-digested food in the gut which is transported from the epipelagic to the mesopelagic by vertically migrating zooplankton and micronekton. To determine gut flux the following information was required: temperature (mesopelagic $\approx -6.3^\circ$ C; epipelagic $\approx 25.5^\circ$ C), assimilation efficiency, Gut Passage Time (GPT), and Index of Stomach Fullness (ISF). Assimilation efficiency was calculated by averaging values from the literature for fishes, cephalopods, decapods, copepods, chaetognaths, and ctenophores. The average assimilation efficiency was calculated to be $85 \pm 0.00017$ SEM, with a range of 70-88%. The gut passage time and carbon weight values for various zooplankton and micronekton were compiled from the literature and a linear relationship was found (Figure 3.2). GPTs in the literature were recorded over several different temperatures and carbon weights. Therefore, a temperature coefficient ($Q_{10}$) of 2, 2.5, and 3 were used to developed a relationship between rate of gut passage (hour$^{-1}$) and weight (mgC) at 6.3 $^\circ$ C. The relationship between rate of gut passage and animal size was strongest using a $Q_{10}$ of 2 (Figure 3.2). Therefore, we calculated rate of gut passage (1/GPT) for each carbon weight nominal size class ($CW_N$) according to the following equation:

Equation 3.8  
\[ \frac{1}{GPT} = 1.238 \times CW_N^{-0.301} \]
Figure 3.2. Rate of gut passage (hour⁻¹) for organisms ranging from 0.12 mg to 600 mg carbon weight. Sources: Cameron (1973), Kjeldson et al. (1975), Reeve (1980), Murtaugh (1984), Hawkins et al. (1980), Arrhenius and Hansson (1994), Atkinson et al. (1996), Perissinotto and Pakhomov (1996), Gurney et al. (2002), Bernard and Froneman (2004), Pakhomov (unpublished data).

Although gut passage times were only available for organisms ranging from 0.0001 mgC to 600 mgC we assumed that the relationship would hold true for larger size classes, as carbon weight explained 52% of the variation in rate of gut passage.

Index of stomach fullness (ISF) was then calculated by compiling ISF and carbon weight values from the literature. Because it was not possible to determine which values in the literature represented a full stomach, a regression was calculated using only the maximum values for each 5 mg size bin (Figure 3.3). Although carbon weight only explained 52% of the variation in ISF, this equation was accepted as no other estimate of ISF and gut flux exist in the literature. As such, the following equation was used to determine the ISF for each nominal carbon weight size class (CWᵣ):

Equation 3.9  

\[ ISF(\%) = 4.7511 e^{-0.016 \cdot CWᵣ} \]
Figure 3.3. Maximum Index of stomach fullness (ISF) for organisms ranging from 0.01 mg to 110 mg carbon weight. Sources: Ajiad and Pushchaeva (1992), Brandner et al. (2013), Fockedey and Mees (1999), Froneman et al. (2000), Hajisame et al. (2003), Pakhomov et al. (1996), and Podeswa (2012).

Assuming that micronekton feed for 8 to 10 h d⁻¹ (Pakhomov et al., 1996), mean specific daily ration or ingestion rate ($C_w$) expressed as a percentage, was calculated using Baikov’s relation (Baikov, 1935; Eggers, 1977), where $C_w = ISF \times 24/T$, where $T$ is the gut passage time in hours, and samples were collected over 24 hour stations. The acoustic data showed that micronekton during the present study were feeding for approximately 9 hours per day, and as such we modified Baikov’s relation as follows:

$$\text{Equation 3.10} \quad C_w = ISF \times \frac{9}{(GPT)}$$

Where $ISF$ is the previously defined index of stomach fullness, and $GPT$ is the gut passage time. The daily ration was then converted to carbon weight by multiplying $C_w$ (as a proportion) by the carbon weight nominal size class ($CW_{Ni}$; Table 3.2-1). We assumed an assimilation efficiency of 85% for all micronekton. Therefore, to calculate the gut flux (non-digested material) for each nominal size class (mgC ind⁻¹ day⁻¹) the carbon weight nominal size class was multiplied by the carbon weight daily ration (expressed as a proportion) and 0.15 (1-assimilation efficiency). To get the total gut flux for each nominal
size class (mgC m\(^{-2}\) day\(^{-1}\)), the gut flux for each nominal size class was multiplied by the abundance of organisms in each nominal size class using Equation 2.4 with the lower and upper limits of each nominal size class present in Table 3.2-1. The total community gut flux was then calculated by adding each gut flux together. This calculation can be represented by the following equation:

Equation 3.11  \[ \hat{G} = \sum_{i=1}^{N} N_{W,ni} * G(CW,ni) \]

Where \( \hat{G} \) is the total community gut flux (mgC m\(^{-2}\) day\(^{-1}\)) and \( G(CW,ni) \) is the amount of egested/non-digested material (mgC/day). For the purposes of this study it was assumed that the total night time stomach content of micronekton was carried from the epipelagic to mesopelagic zone before being evacuated (Clarke 1980).

3.2.6 Quantification of active carbon transport

It was assumed that all micronektonic organisms present in the epipelagic during the nighttime were vertically migrating to depth during the day, and thus contributing to active carbon flux. To determine the amount of active carbon flux from the epipelagic to the mesopelagic the following equation was applied to the biomass size spectrum for the nighttime in the epipelagic:

Equation 3.12  \[ Total\ Active\ Carbon\ Transport = \bar{R} + \bar{M} + \bar{E} + \hat{G} \]

Where total community respiration (\( \bar{R} \)), mortality (\( \bar{M} \)), excretion (\( \bar{E} \)), and gut flux (\( \hat{G} \)) are all taken into consideration, and are applied according to the equations in the preceding sections (Equations 2.3, 2.6, 2.7, and 2.11; Section 3.2.1-3.2.5). A sensitivity analysis was then conducted to assess the model. Each input parameter was varied depending on the associated uncertainty, and the percent change in the final output (i.e. active carbon flux) was determined.
3.3 Results

3.3.1 Quantification of active carbon transport

In alignment with the biomass spectra theory, smaller organisms were more abundant and contributed less in terms of carbon weight than larger organisms (Table 3.3; Figure 2.8). Active carbon transport predicted for the southwest coast of Oahu using the biomass spectra theory was 105 mgC m⁻² day⁻¹ (Table 3.4). However, when calculated solely based on net catch abundance, active carbon transport amounted to 17.6 mgC m⁻² day⁻¹, accounting for only 17% of the biomass spectra theory estimate. Gut flux contributed the most (43%) to total active carbon transport, followed by respiration (31%), mortality (16%) and excretion (10%) (Table 3.4). The model was most sensitive to changes in gut passage time and carbon weight (Table 3.5), within ± 40% change affecting both model outputs by ± 29%. Under the same conditions, other parameters resulted in ≤ 17% change in final model outputs (Table 3.5).

Table 3.3. Nighttime epipelagic abundance and total migrant biomass according to nominal size class based on the biomass size spectra of micronekton.

<table>
<thead>
<tr>
<th>Nominal size class (µgC)</th>
<th>Abundance (ind. m⁻²)</th>
<th>Migrant Biomass (µgC m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>178.2</td>
<td>183.3</td>
<td>32664.1</td>
</tr>
<tr>
<td>356.3</td>
<td>120.1</td>
<td>42791.6</td>
</tr>
<tr>
<td>712.6</td>
<td>78.7</td>
<td>56081.6</td>
</tr>
<tr>
<td>1425.2</td>
<td>51.6</td>
<td>73540.3</td>
</tr>
<tr>
<td>2850.5</td>
<td>33.8</td>
<td>96346.9</td>
</tr>
<tr>
<td>5701.0</td>
<td>22.1</td>
<td>125992.1</td>
</tr>
<tr>
<td>11401.9</td>
<td>14.5</td>
<td>165327.6</td>
</tr>
<tr>
<td>22803.8</td>
<td>9.5</td>
<td>216636.1</td>
</tr>
<tr>
<td>45607.6</td>
<td>6.2</td>
<td>282767.1</td>
</tr>
<tr>
<td>91215.2</td>
<td>4.1</td>
<td>373982.3</td>
</tr>
<tr>
<td>182430.4</td>
<td>2.7</td>
<td>492562.1</td>
</tr>
<tr>
<td>364860.8</td>
<td>1.8</td>
<td>656749.4</td>
</tr>
<tr>
<td>729721.6</td>
<td>1.1</td>
<td>802693.8</td>
</tr>
<tr>
<td>1459443.1</td>
<td>0.8</td>
<td>1167554.5</td>
</tr>
<tr>
<td>2918886.3</td>
<td>0.5</td>
<td>1459443.2</td>
</tr>
<tr>
<td>5837772.5</td>
<td>0.3</td>
<td>1751331.8</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>531.1</strong></td>
<td><strong>7796464.4</strong></td>
</tr>
</tbody>
</table>
Table 3.4. Relative contribution of each nominal size class to total active carbon transport by flux (i.e., respiration, excretion, mortality, gut flux). The total flux for each is reported along with the percent contribution of each flux to total active carbon transport.

<table>
<thead>
<tr>
<th>nominal size class (µg)</th>
<th>abundance (ind. m⁻²)</th>
<th>Flux (µgC m⁻² day⁻¹)</th>
<th>Active carbon transport (µgC m⁻² day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Respiration</td>
<td>Excretion</td>
</tr>
<tr>
<td>178.15</td>
<td>183.3</td>
<td>501.0</td>
<td>155.31</td>
</tr>
<tr>
<td>356.31</td>
<td>120.1</td>
<td>585.7</td>
<td>181.58</td>
</tr>
<tr>
<td>712.62</td>
<td>78.7</td>
<td>684.9</td>
<td>212.31</td>
</tr>
<tr>
<td>1425.24</td>
<td>51.6</td>
<td>801.3</td>
<td>248.39</td>
</tr>
<tr>
<td>2850.47</td>
<td>33.8</td>
<td>936.5</td>
<td>290.32</td>
</tr>
<tr>
<td>5700.95</td>
<td>22.1</td>
<td>1092.6</td>
<td>338.72</td>
</tr>
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<td>11401.90</td>
<td>14.5</td>
<td>1279.2</td>
<td>396.54</td>
</tr>
<tr>
<td>22803.80</td>
<td>9.5</td>
<td>1495.4</td>
<td>463.58</td>
</tr>
<tr>
<td>45607.60</td>
<td>6.2</td>
<td>1741.5</td>
<td>539.85</td>
</tr>
<tr>
<td>91215.20</td>
<td>4.1</td>
<td>2054.9</td>
<td>637.01</td>
</tr>
<tr>
<td>182430.39</td>
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<td>4853.0</td>
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<td>TOTAL</td>
<td></td>
<td>531.1</td>
<td>33042.5</td>
</tr>
<tr>
<td>% of active carbon transport</td>
<td>31%</td>
<td>10%</td>
<td>16%</td>
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</table>

Table 3.5. Results of the sensitivity analysis as percentage change in active carbon flux from the epipelagic to mesopelagic for perturbation in individual parameters. Where, cw=carbon weight nominal size class, dw=dry weight nominal size class, ISF=index of stomach fullness, GPT=gut passage time, GF=gut flux, RO=respiratory oxygen equivalent, R=respiration, DM=daily mortality, M=mortality, and E=excretion.

<table>
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<tr>
<th>Parameter</th>
<th>Perturbation</th>
<th>-40%</th>
<th>-30%</th>
<th>-20%</th>
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<th>-5%</th>
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<th>10%</th>
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<td>dw</td>
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<td>0</td>
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<td>-11</td>
<td>-5</td>
<td>-2</td>
<td>2</td>
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<tr>
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<td>8</td>
<td>4</td>
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<td>2</td>
<td>1</td>
<td>-1</td>
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<td>1</td>
<td>0</td>
<td>-1</td>
<td>-2</td>
<td>-3</td>
<td>-5</td>
<td>-4</td>
</tr>
</tbody>
</table>
3.4 Discussion

3.4.1 Flux model

The model was based on the biomass spectra theory, and thus quantified active carbon transport for the whole community of organisms ranging from 20 to 100 mm in length. As previously mentioned (Section 2.1), the biomass spectra theory assumes that 1) the system is in steady state, 2) predation is the only source of mortality, 3) large organisms consume only smaller organisms, 4) there is a constant input of energy to the smallest size class, and 5) the flow of energy is unidirectional. It is recognized that no real ecosystem is in a perfect steady-state, but that at any given time all systems are approaching or have just deviated from steady state (Quiñones et al., 2003). Therefore, the theory may be applied to our system. Gaps within the micronekton size spectra were assumed to represent size intervals in which biomass exists but was not captured due to gear limitations. This assumption was met (Section 2.3.3) by plotting the size spectra for all three gears. Finally, all micronekton present in the epipelagic (0-100 m) during the nighttime were assumed to undergo diel vertical migrations to depths of at least 500 m during the daytime. Because no trawls were conducted during the day in the epipelagic zone, acoustic data were used to estimate that ~16% of micronekton remain within the epipelagic realm during the day (Domokos et al., 2010; Kwong et al., In Review). This portion of epipelagic residents were corrected for after the model was run. However, this correction doesn’t account for variability in the size of organisms that were remaining within the epipelagic zone and the acoustic measurements were targeted towards mesopelagic fishes (Section 2.3.2). Therefore, in the absence of a daytime epipelagic micronekton size spectrum, this correction may introduce some error to our model.

The sensitivity analysis suggested that estimated active carbon transport was robust against under- and overestimations of mortality, excretion and respiration, but was highly sensitive to changes in gut flux via gut passage time, as well as carbon weight.

Respiration was estimated using the empirical allometric relationship developed by Ikeda (1985). The relationship estimates respiration rate based on temperature and biomass using a variety of different zooplankton and micronekton (i.e., decapods, euphausiids, stomatopods, amphipods, mysids, fishes, copepods, chaetognaths). Ikeda (1985) found that
carbon weight and ambient temperature explained 95.5% of variation in oxygen uptake, suggesting that the uncertainty associated with this model was likely minimal.

Excretion was estimated based on excretory rates of several different taxonomic groups, including shrimp, euphausiids, copepods, amphipods and polychaetes. Steinberg et al. (2000) found that excretory flux was consistently ~31% of respiratory flux across all taxonomic groups. Similar to respiration, excretion rates were dependent on temperature and organism dry weight (Steinberg et al., 2000). The error margin associated with excretory flux was thus considered minor, and the parameter had little effect on the models final output.

Mortality was calculated using the Peterson and Wroblewski (1984) size-dependent mortality rate model for fishes ranging from 0.1 mg (eggs) to 1000 g (adults) dry weight. The empirical values deviated from the model by an order of magnitude and this deviation was greatest for the smallest and largest organisms. Our organisms ranged from 0.5 mg to 14.6 g (dry weight), and therefore included the smallest organisms in the Peterson and Wroblewski model. However, because we have applied the model to the whole community, and not just individual species, and given that the distribution of error is relatively even for the model, we consider this relationship reasonable for our calculations. Regardless, future studies should focus on refining this model to reduce the uncertainty associated with mortality.

The main source of error associated with our model was the gut passage time parameter in the gut flux portion of the model. Once literature values of gut passage time were corrected for different temperatures, using a $Q_{10}$ value of 2, carbon weight was able to explain ~ 52% of the variation in gut passage time. Past studies have found that gut passage time is strongly temperature dependent. However, none of these studies have incorporated effects of both temperature and organism size (e.g., Reeve, 1980; Atkinson et al., 1996; Pakhomov et al., 1996; Perissinotto and Pakhomov, 1996; Gurney et al. 2002). As such, this represents the first approximation of gut passage time in relation to organism size and temperature and its further refinement is strongly recommended. Index of stomach fullness (ISF) may have also introduced some error to the gut flux portion of the model. We found that carbon weight explained only 52% of the variation in ISF, and because it was not possible to determine which values in the literature represented full stomachs, our
model was run using only the maximum values for each 5 mgC size bin. We consider the relationship acceptable as no other estimates of ISF and gut flux exist in the literature, but caution using this relationship in the future studies. Overall gut flux increased from small to mid-sized micronekton and then decreased for larger micronekton. This is because the gut passage time for larger nekton is longer than 24 hours suggesting that these animals do not feed every day.

Despite the discussed shortcomings, we consider the current model to be an effective approach by which active carbon transport can be estimated. This model provides a unifying, ataxonomic, less labor intensive approach to quantifying active carbon transport.

3.4.2 Active carbon flux

Several studies have assessed active carbon transport via zooplankton and/or micronekton at various locations (Table 3.1). These studies vary substantially in terms of fluxes assessed, location, timing, depth, species/groups included, and the size range of organisms (Table 3.1), which makes global intercomparison challenging if not impossible.

Domokos et al. (2010) and Kwong et al. (In Review) estimated that ~16% of organisms present during the nighttime in the epipelagic zone were epipelagic residents. Thus, corrected active carbon transport to a minimum of ~450 m depth on the southwest coast of Oahu during the current study was approximately 88.5 mgC m⁻² day⁻¹. This is significantly higher than previous estimates of active carbon transport (Table 3.1), and comparable to total global carbon export estimates (i.e., 83 to 91 mgC m⁻² day⁻¹; Schlitzer, 2002; Falkowski et al., 2003; Usbeck et al., 2003; Davison et al., 2013). Furthermore, when looking at the contribution of single fluxes (i.e., respiration, mortality, gut flux and excretion) reported in the literature (Angel and Pugh, 2000; Longhurst et al., 1990; Hidaka et al., 2001) our model produced consistently higher values (Table 3.1). Hidaka et al. (2001) assessed micronekton mortality, respiration and gut downward flux in the western equatorial North Pacific using comparable gears to this study. Their assessment of active carbon flux was only a quarter of our model estimates. We argue that the discrepancies are likely due to undersampling as well as temporal and/or spatial variability. Using acoustics, Domokos et al. (2010) demonstrated that a considerable degree of temporal and spatial
variability in backscatter distribution was found along the southwest coast of Oahu. In addition, the decapod community composition on the southwest coast of Oahu, and at station ALOHA (Podeswa, 2012) was significantly different from that reported by Hidaka et al. (2001). Furthermore, Podeswa (2012) reported that the contribution to export production of migratory decapods alone in the North Pacific Subtropical Gyre was an order of magnitude higher than Hidaka et al. (2001) estimates, and attributed these differences to the community composition.

Our model reported values similar to Hudson et al. (2014) and Davison (2011). These two studies assessed the contribution of major micronekton groups (i.e., myctophids and mesopelagic fishes, respectively) to active carbon transport, which were comparable to fluxes mediated by similar groups in our study. For example, the excretory flux alone ranged from 0.04 to 2.78 mgC m⁻² day⁻¹ and from 2.0 to 3.3 mgC m⁻² day⁻¹ in Hudson et al. (2014) and our study, respectively. Similarly, Davison (2011) evaluated the contribution of mesopelagic fish respiration and excretion to downward carbon flux (22-24 mgC m⁻² day⁻¹) in a subtropical coastal environment, which was close to our estimate of 14.3 mgC m⁻² day⁻¹. It should, however, be noted that these inferences do not take into consideration the size of organisms, and are calculated solely based on their relative contribution to total micronekton. Furthermore, discrepancies between Hudson et al. (2014), Davison (2011) and our studies, could also be attributed to the spatial and temporal variability.

Temporal and spatial variability in micronekton abundance and biomass, may lead to substantial differences in active carbon transport estimates. This is because all ecological rates associated with the active carbon transport modelling are highly temperature dependent (Section 3.2). Thus, in regions with higher temperatures the respiration, excretion and gut flux rates are substantially higher at the surface of the ocean than at depth. Furthermore, the carbon weight of various micronekton groups varies, so in regions dominated by gonostomatids the active carbon flux may be lower than in regions dominated by myctophids. This is because gonostomatids and myctophids have fundamentally different body shapes (long slender vs deep bodied shape) significantly affecting the distribution of carbon biomass across size classes and thus the slope and intercept of the nighttime epipelagic size spectra. Differences in estimates of active carbon transport may also be attributed to gear dimensions, sampling strategy (e.g., targeted
sampling; Kwong et al., In Review), net-biased avoidance (Kaartvedt et al., 2012; Kwong et al., In Review), and volume filtered (Pearcy, 1983). For example, Clarke (1983), Pearcy (1983) and Kwong et al., (In Review) demonstrated clearly how different gears effectively capture different species and sizes of micronekton.

Fine-scale temporal changes in active carbon transport may also occur due to changes in solar (i.e., cloud cover; Pinot and Jansà, 2001) and lunar (Benoit-Bird et al., 2009; Hernández-León et al., 2010) illumination and their effect on micronekton behavior. For example, in the presence of strong lunar illumination, micronekton net avoidance may be enhanced and/or the timing and depth of vertical migrations altered (Pinot and Jansà, 2001; Benoit-Bird et al., 2009; Hernández-León et al., 2010). This makes it increasingly more difficult to compare estimates of active carbon transport across studies. Because the lunar conditions during sampling were waning from last quarter to new moon, we assumed that the effects of lunar illumination on micronekton density during our study were minimal (Benoit-Bird et al., 2009; Hernández-León et al., 2010). The effects of cloud cover were not accounted for in this study, and may indeed contribute to micronekton density underestimation. Because our estimates of active carbon transport, and in Chapter 2 micronekton migratory flux, greatly exceeded previous estimates it is possible that the use of size spectra in predicting micronekton active carbon transport reduces the bias associated with the net sampling. However, further investigation is required to test this hypothesis.

The ratio of active to passive carbon downward flux to the base of the euphotic zone ranges from 3 to 70% depending on the environment and the organisms included (Table 3.1). It appears that both zooplankton and micronekton contribute significantly to total carbon export, a contribution which has largely been neglected and underestimated in the past (Ariza et al., 2015; Bianchi et al., 2013b). We were unable to calculate this ratio for the current study, as no estimate of passive carbon transport was available. Nevertheless, it is important to note that with depth the contribution of diel vertical migrators to downward carbon transport becomes increasingly more important, as these organisms are capable of migrating to depths of 1000 m or more, while passive carbon flux strongly attenuates with depth below the euphotic zone (Karl et al., 1996; Figure 3.1). These vertical migrators transport carbon much more rapidly than sedimentary flux,
packaging particles into dense fecal pellets, which makes consumption by detritivores less likely. Thus, these organisms transport carbon to a depth below which most remineralization occurs (Buesseler and Boyd, 2009). It should be noted that this model does not account for the portion of active carbon transport which is indeed passive flux (i.e., excretion and gut flux during downward migration), and that this model suggests that this component has likely also been underestimated in the past. Our model estimate of active carbon transport is significantly higher than previous estimates. Therefore, it is likely that past estimates of active to passive carbon downward flux ratios are underestimated, and that active carbon transport may contribute equally or more to downward carbon flux than passive carbon transport. This makes it crucial that active carbon transport by micronekton be included in biogeochemical models.

### 3.4.3 Implications

The biological carbon pump sequesters atmospheric carbon to the deep ocean. Therefore, changes in oceanic conditions may affect the efficiency of the pump, impacting atmospheric carbon concentrations (Volk and Hoffert, 1985). Changes in ocean temperature, circulation and reduced mixing may lead to intensification of ocean stratification decreasing deep ocean oxygen and surface water nutrient replenishment (Roemmich and McGowan, 1995; Sarmiento et al., 1998; Matear et al., 2000; Plattner et al., 2001; Bopp et al., 2002; Keeling and Garcia, 2002). Collectively, these processes would promote changes in surface productivity and OMZ expansion. Because micronekton are aerobic organisms and their downward migration is restricted by the OMZ (Bianchi et al., 2013a,b), the above changes may have a substantial impact on carbon export to the deep ocean, reducing the oceans capacity to absorb and/or transport excess atmospheric CO₂. Bianchi et al. (2013a,b) used acoustics to demonstrate that in low-oxygen areas of the ocean, DVM accentuates oxygen depletion, as organisms will only migrate as deep as the upper extent of the OMZ. The upper extent of the OMZ provides refuge from predators which require higher oxygen concentrations (Bianchi et al., 2013a,b). Therefore, with OMZ expansion the depth of active carbon export decreases, such that the efficiency of the biological pump will be reduced. In addition, the vulnerability of micronekton and other fishes will be increased (e.g., Stramma et al., 2010) impacting food pathways resulting in
predator-prey decoupling or compression (Goodyear et al., 2008; Prince and Goodyear, 2006; Stramma et al., 2011).

Changes in ocean temperature due to climate change will also affect the efficiency of the biological carbon pump. This has been demonstrated by Irigoien et al. (2014), as the proportion of vertical migrators was reported to decrease with increasing water temperature and turbidity. Therefore, a reduction in vertical migrators paired with the temperature dependence of the ecological rates assessed in the present study (Sarmiento et al., 2004; Bopp et al., 2005; Ready et al., 2010) may alter carbon sequestration to the deep ocean.

If our model is robust, past estimates of carbon export via vertically migrating micronekton may have been substantial underestimates. It is noteworthy, that previous estimates were largely based on net sampling, and it is not uncommon that net biomass estimates are around 1/8 to 1/10 of those derived from acoustics (Koslow et al., 1997; Kloser et al., 2009; Pakhomov et al., 2010; Kaardvedt et al., 2012; Irigoien et al., 2014). Therefore, the biomass spectra approach used in our study is likely close to “real” micronekton biomass estimates worldwide. This model may therefore have important implications for assessing the global impacts of climate change on pelagic ecosystems and biogeochemical cycling. Refinement of this model could be extremely beneficial in understanding the full impacts of climate change on carbon cycling.
3.4.4 Concluding remarks

To date, few studies have quantified the contribution of micronekton to downward carbon flux. By including all organisms ranging from 20 to 100 mm in size, our study provides a more realistic estimate of micronekton contribution to active carbon flux. We produced a biomass / production size dependent model based on the biomass spectra theory. This model allowed us to estimate active carbon transport at a community level. The model predicted that active carbon transport via micronekton DVM was 88.5 mgC m\(^{-2}\) day\(^{-1}\) to \(~450\) m depth, assuming that \(~16\%\) of micronekton remained within the epipelagic zone during the day. The model suggests that the contribution of these organisms to the biological carbon cycle is substantial and has been drastically underestimated in the past.
4 Overall conclusions

This dissertation examines diel changes in micronekton species composition and size spectra in the tropical epipelagic and mesopelagic zones off the southwest coast of Oahu. A linear relationship between abundance/normalized biomass and body size of micronekton was identified, consistent with the biomass spectra theory. As hypothesized, the DVM of micronekton in the water column can be viewed as changes in the slope and elevation (y-intercept) of the size spectra. These findings were further confirmed by changes in the relative proportions of dominant micronekton taxa during the day and night in the mesopelagic realm. We estimated total migratory micronekton abundance and biomass to be ~487 ind.m$^{-2}$ and ~6,014 mgC m$^{-2}$, respectively. This equated to 30% and 18% of the total micronekton abundance and biomass, respectively.

Micronekton in the vicinity of Oahu Island, exhibited strong mesopelagic layering, extensive diel horizontal and vertical migrations from the mesopelagic and/or bathypelagic into the epipelagic zone during the night. We found that the three gears efficiently captured different sizes of organisms, and that gaps in the size spectra represented areas in which biomass existed but was not captured. Finally, we found that estimates of abundance and biomass using the biomass spectra theory were more consistent with acoustic measurements (e.g., Koslow et al., 1997; Kloser et al., 2009; Kaardvedt et al., 2012; Irigoien et al., 2014) than trawl measurements. This finding suggests that the use of size spectra may reduce net sampling bias commonly associated with larger micronekton net avoidance (Kaartvedt et al., 2012; Kwong et al., In Review).

We observed notable changes in the biomass spectra during the day and night, suggesting that active carbon flux via micronekton DVM could be inferred using the biomass spectra theory. The most important contribution of this thesis was the development of the biomass/production size dependent model based on the biomass spectra theory. Using this model, we were able to estimate active carbon transport at a community level. The model predicted that active carbon transport via micronekton DVM was 88.5 mgC m$^{-2}$ day$^{-1}$ to ~450 m depth. This estimate was substantially higher than other estimates of active carbon transport (e.g., Longhurst et al., 1990; Williams and Koslow, 1997; Hidaka et al., 2001; Schlitzer, 2002; Falkowski et al., 2003; Usbeck et al., 2003; Podeswa, 2012;
Davison et al., 2013; Ariza et al., 2015), and comparable to recent total global carbon export estimates (i.e., 83 to 91 mgC m\(^{-2}\) day\(^{-1}\); Schlitzer, 2002; Falkowski et al., 2003; Usbeck et al., 2003; Davison et al., 2013). Therefore, it is possible that the relative contribution of these organisms to carbon cycling is equal to or greater than passive transport. Our model corroborates the argument that by neglecting micronekton carbon export to the deep ocean may be drastically underestimated (Buesseler et al., 2007; Davison et al., 2013; Falkowski et al., 2003; Martz et al., 2008; Hernández-León et al., 2010; Usbeck et al., 2003; Wexels Riser et al., 2010). We also found that spatio-temporal variation in micronekton and differences in sampling techniques may lead to different estimates of active carbon transport.

This thesis represents the first attempt at modelling active carbon transport via vertically migrating micronekton using the biomass spectra theory. As such, regional and global estimates of active carbon transport using the same methodology are advisable. By streamlining the methodology used to predict active carbon flux, we can gain insight into the impacts of climate change on biogeochemical cycling. Future studies should therefore accompany this method with acoustic observations to confirm time spent at depth, relative proportion of epipelagic residents, and depth of carbon transport/migratory depth. Our model was most sensitive to changes in gut passage time. Therefore, future studies should also work on refining the uncertainty associated with this parameter in pelagic ecosystems. By combining this model with optical (e.g., laser optic particle counter and/or FlowCam) and acoustic methods, estimates of regional and global active carbon flux can be assessed. This method may prove to be less labor-intensive and time consuming than current methods and may be used to validate modelling active carbon flux calculations.
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Appendix

Table A.1. Summary of conversion factors used to convert data from length to carbon weight. In some cases, two conversions were conducted: standard length (sl) or total length to dry weight (dw), wet weight (ww), and carbon weight (cw), and then from dw or ww to cw where necessary. Measurements were made in g, mg or lbs for weights, and cm or mm for length as indicated by subscripts. Where available, sample size (N) and R² values are reported. Regressions developed in this study and provided in Figure A-1.

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<th>Species</th>
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<th>Conversion 1</th>
<th>N</th>
<th>R²</th>
<th>Conversion 2</th>
<th>References</th>
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<td>Cephalopoda</td>
<td>log_{10}w_g = 2.611 x log_{10}(tl_{mm}) – 3.5</td>
<td>209</td>
<td>0.854</td>
<td>cw=0.0554*ww</td>
<td>2,3</td>
</tr>
<tr>
<td>Amphipods</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 2.717 x log_{10}(tl_{mm}) – 1.911</td>
<td>125</td>
<td>0.884</td>
<td>cw=0.345*dw</td>
<td>4,5</td>
</tr>
<tr>
<td>Euphausiids</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 3.23 x log_{10}(tl_{mm}) - 3.261</td>
<td>245</td>
<td>0.98</td>
<td>cw=0.419*dw</td>
<td>4,5</td>
</tr>
<tr>
<td>Copepods</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 2.486 x log_{10}(tl_{mm}) – 2.021</td>
<td>524</td>
<td>0.924</td>
<td>cw=0.48*dw</td>
<td>4,5,6,7,8,9,10</td>
</tr>
<tr>
<td>Crab larvae</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 1.24 x log_{10}(tl_{mm} - 0.54) – 2.58</td>
<td>21</td>
<td>0.86</td>
<td>cw=0.435*dw</td>
<td>4,11</td>
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<tr>
<td>Decapods</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 3.787 x log_{10}(tl_{mm}) – 3.972</td>
<td>751</td>
<td>0.864</td>
<td>cw=0.435*dw</td>
<td>4,12</td>
</tr>
<tr>
<td>Isopod</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 2.732 x log_{10}(tl_{mm}) - 2.402</td>
<td>1103</td>
<td>0.86</td>
<td>cw=0.435*dw</td>
<td>4,5,6,15</td>
</tr>
<tr>
<td>Mysids</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 2.676 x log_{10}(tl_{mm}) - 2.472</td>
<td>131</td>
<td>0.949</td>
<td>cw=0.435*dw</td>
<td>4,15,16</td>
</tr>
<tr>
<td>Nauplii</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 1.9 x log_{10}(tl_{mm}) - 2.559</td>
<td>157</td>
<td>0.546</td>
<td>-</td>
<td>17,18,19,20,21,22</td>
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<tr>
<td>Ostracods</td>
<td>Crustacean</td>
<td>log_{10}dw_{mg} = 2.86 x log_{10}(tl_{mm}) - 1.599</td>
<td>-</td>
<td>-</td>
<td>cw=0.435*dw</td>
<td>4,5,23,24</td>
</tr>
<tr>
<td>Stomatopods</td>
<td>Crustacean</td>
<td>log_{10}ww_{g} = 2.788 x log_{10}(tl_{mm}) - 4.468</td>
<td>52</td>
<td>0.978</td>
<td>cw=0.435*dw</td>
<td>4,25,26</td>
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<tr>
<td>Chaetognaths</td>
<td>Gelatinous Zooplankton</td>
<td>dw_{mg} = 0.0001352*tl_{mm}^{3.1545}</td>
<td>-</td>
<td>-</td>
<td>cw=0.367*dw</td>
<td>4,27</td>
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<tr>
<td>Ctenophores</td>
<td>Gelatinous Zooplankton</td>
<td>log_{10}ww_{g} = 2.455 x log_{10}(tl_{mm}) - 3.058</td>
<td>56</td>
<td>0.815</td>
<td>-</td>
<td>28,29,30,31</td>
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<tr>
<td>Cnidarians</td>
<td>Gelatinous Zooplankton</td>
<td>log_{10}ww_{g} = 2.767 x log_{10}(tl_{mm}) - 3.643</td>
<td>161</td>
<td>0.974</td>
<td>-</td>
<td>5,32,33</td>
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<tr>
<td>Tunicates</td>
<td>Gelatinous Zooplankton</td>
<td>log_{10}ww_{g} = 1.867 x log_{10}(tl_{mm}) - 0.948</td>
<td>53</td>
<td>0.715</td>
<td>cw=0.103*dw</td>
<td>4,5,34</td>
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<tr>
<td>Polychaetes</td>
<td>Other Zooplankton</td>
<td>log_{10}ww_{g} = 1.798 x log_{10}(tl_{mm}) - 2.17</td>
<td>30</td>
<td>0.897</td>
<td>cw=0.37*dw</td>
<td>4,5,6</td>
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<tr>
<td>Echinoderm</td>
<td>Other Zooplankton</td>
<td>log_{10}ww_{g} = A x log_{10}(tl_{mm}) - B</td>
<td>-</td>
<td>-</td>
<td>cw=0.387*dw</td>
<td>4</td>
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<tr>
<td>Molluscs</td>
<td>Other Zooplankton</td>
<td>log_{10}ww_{g} = 1.646 x log_{10}(tl_{mm}) - 0.915</td>
<td>73</td>
<td>0.876</td>
<td>cw=0.289*dw</td>
<td>4</td>
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<tr>
<td>Fish</td>
<td>Fish</td>
<td>log_{10}ww_{g} = 1.279 x log_{10}(tl_{mm}) - 0.498</td>
<td>33</td>
<td>0.866</td>
<td>cw=0.5019*dw</td>
<td>35,36</td>
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<tr>
<td>Unidentified Fish</td>
<td>Fish</td>
<td>log_{10}ww_{g} = 2.729 x log_{10}(sl_{mm}) - 2.144</td>
<td>8956</td>
<td>0.945</td>
<td>cw=0.4286*dw</td>
<td>1,37,38</td>
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<tr>
<td>Acanthuridae</td>
<td>Acanthuridae</td>
<td>w_{g} = 0.0000045 x sl_{mm}^{2.849}</td>
<td>202</td>
<td>-</td>
<td>cw=0.8847*ww</td>
<td>37,40</td>
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<tr>
<td>Naso sp.</td>
<td>Acanthuridae</td>
<td>w_{g} = 0.0000845 x sl_{mm}^{2.849}</td>
<td>56</td>
<td>-</td>
<td>cw=0.0847*ww</td>
<td>37,40</td>
</tr>
<tr>
<td>Apogonidae</td>
<td>Apogonidae</td>
<td>ln(w_{g}) = ln(0.0143) + 3.143(ln(1.312*sl_{cm}))</td>
<td>1873</td>
<td>0.97</td>
<td>cw=0.362*dw</td>
<td>39,41,45</td>
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<tr>
<td>Rhinecanthus sp.</td>
<td>Balistidae</td>
<td>ln(w_{g}) = ln(0.0057) + 3.901(ln(1.111*sl_{cm}))</td>
<td>595</td>
<td>0.994</td>
<td>cw=0.0847*ww</td>
<td>37,38,45</td>
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References
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<tr>
<th>Species</th>
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<tr>
<td>Blenniidae</td>
<td>Blenniidae</td>
<td>$\ln(ww) = \ln(0.0022) + 3.143(\ln(1.13*sl_{cn}))$</td>
<td>246</td>
<td>0.86</td>
<td>$cw=0.411*dw$</td>
<td>39,41,45</td>
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<tr>
<td>Bothus sp.</td>
<td>Bothida</td>
<td>$\ln(ww) = \ln(0.0072) + 3.213(\ln(1.143*sl_{cn}))$</td>
<td>260</td>
<td>0.962</td>
<td>$cw=0.0847*ww$</td>
<td>37,39,45</td>
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<tr>
<td>Engyprosopon sp.</td>
<td>Bothida</td>
<td>$\ln(ww) = \ln(0.0168) + 2.894(\ln(1.189*sl_{cn}))$</td>
<td>108</td>
<td>0.979</td>
<td>$cw=0.0847*ww$</td>
<td>37,39,45</td>
</tr>
<tr>
<td>Bremaceros sp.</td>
<td>Bremacerotidae</td>
<td>$\ln(ww) = \ln(0.0143) + 3.143(\ln(1.312*sl_{cn}))$</td>
<td>64</td>
<td>0.945</td>
<td>$cw=0.0847*ww$</td>
<td>37,42,45</td>
</tr>
<tr>
<td>Coryphaenidae</td>
<td>Coryphaenidae</td>
<td>$\log_{10}ww= -4.1966+2.711(\log_{10}(sl_{cn}+1.73))$</td>
<td>-</td>
<td>-</td>
<td>$cw=0.0847*ww$</td>
<td>37,43,44</td>
</tr>
<tr>
<td>Istius brasiliensis</td>
<td>Dalatiidae</td>
<td>$ww_{g}=0.00363*(sl_{num}/10)^{1.1643^{1.12}}$</td>
<td>-</td>
<td>-</td>
<td>$cw=0.0847*ww$</td>
<td>37,45</td>
</tr>
<tr>
<td>Engraulidae</td>
<td>Engraulidae</td>
<td>$ww_{g}=(6.3<em>10^{-8})</em>(sl_{num}^{*1.1776})^{3.125}$</td>
<td>2550</td>
<td>0.96</td>
<td>$cw=0.0847*ww$</td>
<td>37,50</td>
</tr>
<tr>
<td>Coccorella atlantica</td>
<td>Evermannellida</td>
<td>Individual measured</td>
<td>-</td>
<td>-</td>
<td>$cw=0.091*ww$</td>
<td>37</td>
</tr>
<tr>
<td>Fistularia corneta</td>
<td>Fistulariidae</td>
<td>$ww_{g}=0.017(sl_{cm}/0.884)^{3.555}$</td>
<td>-</td>
<td>0.693</td>
<td>$cw=0.0847*ww$</td>
<td>37,47</td>
</tr>
<tr>
<td>Gymnodyctes</td>
<td>Gymnodyctidae</td>
<td>$ww_{g}=0.00073*(sl_{num}/10*1.094)^{3}$</td>
<td>-</td>
<td>-</td>
<td>$cw=0.0847*ww$</td>
<td>37,45</td>
</tr>
<tr>
<td>Gobiiidae</td>
<td>Gobiidae</td>
<td>$\ln(ww)=\ln(0.0264)+2.623(\ln(1.229*sl_{cm}))$</td>
<td>296</td>
<td>0.951</td>
<td>$cw=0.406*dw$</td>
<td>39,41,45</td>
</tr>
<tr>
<td>Gonostomatidae</td>
<td>Gonostomatidae</td>
<td>$\log_{10}(ww_{mg})=2.945(\log_{10}(sl_{num}))-5.282$</td>
<td>111</td>
<td>0.902</td>
<td>$cw=0.053*ww$</td>
<td>37,46</td>
</tr>
<tr>
<td>Howellia sp.</td>
<td>Howellidae</td>
<td>Individual measured</td>
<td>-</td>
<td>-</td>
<td>$cw=0.0847*ww$</td>
<td>37</td>
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<tr>
<td>Labridae</td>
<td>Labridae</td>
<td>$\ln(ww)=\ln(0.0107)+3.178(1.17*sl_{cm})$</td>
<td>-</td>
<td>-</td>
<td>$cw=0.0847*ww$</td>
<td>37,39</td>
</tr>
<tr>
<td>Leptocephalus</td>
<td>Leptocephalus</td>
<td>$\log_{10}(dw)=1.857(\log_{10}(sl_{num}))-1.877$</td>
<td>25</td>
<td>0.693</td>
<td>$cw=0.0847*ww$</td>
<td>1.37</td>
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<tr>
<td>Lutjanidae</td>
<td>Lutjaniidae</td>
<td>$ww_{g}=0.018(sl_{cm}/1.187)^{2.895}$</td>
<td>1359</td>
<td>0.995</td>
<td>$cw=0.0847*ww$</td>
<td>37,47</td>
</tr>
<tr>
<td>Malacosteidae</td>
<td>Malacosteida</td>
<td>$ww_{g}=0.0226*(sl_{cm}^{*1.065})^{2.58}$</td>
<td>27</td>
<td>-</td>
<td>$cw=0.036*ww$</td>
<td>37,45,48</td>
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<tr>
<td>Melamphaidae</td>
<td>Melamphaidae</td>
<td>$\log_{10}(ww_{mg})=3.259(\log_{10}(sl_{num}))-2.164$</td>
<td>55</td>
<td>0.982</td>
<td>$cw=0.039*ww$</td>
<td>37,46</td>
</tr>
<tr>
<td>Mulidae</td>
<td>Mulidae</td>
<td>$\ln(ww)=\ln(0.0114)+3.211(\ln(1.069*sl_{cm}))$</td>
<td>53</td>
<td>0.981</td>
<td>$cw=0.406*dw$</td>
<td>39,41</td>
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<tr>
<td>Myctophidae</td>
<td>Myctophidae</td>
<td>$\log_{10}(ww_{mg})=2.902x(\log_{10}(sl_{num}))-1.797$</td>
<td>506</td>
<td>0.935</td>
<td>$cw=0.092*ww$</td>
<td>37,46</td>
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<tr>
<td>Cubiceps sp.</td>
<td>Nomeida</td>
<td>$ww_{g}=0.0222*(1.186*(sl_{num}/10))^{2.949}$</td>
<td>-</td>
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<td>$cw=0.0847*ww$</td>
<td>37,45</td>
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<tr>
<td>Brotulaetaenia sp.</td>
<td>Ophidiodae</td>
<td>$ww_{g}=0.01*(sl_{num}/10)^{3.04}$</td>
<td>-</td>
<td>-</td>
<td>$cw=0.0525*ww$</td>
<td>38,45</td>
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<tr>
<td>Opisthncroctus soleatus</td>
<td>Opisthncroctidae</td>
<td>$\log_{10}(ww_{mg})=2.16(\log_{10}(sl_{num}))-0.025$</td>
<td>28</td>
<td>0.771</td>
<td>$cw=0.0525*ww$</td>
<td>1.37</td>
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<tr>
<td>Rhynchohylus natantis</td>
<td>Opisthncroctidae</td>
<td>Individual measured</td>
<td>-</td>
<td>-</td>
<td>$cw=0.0525*ww$</td>
<td>1.37</td>
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<tr>
<td>Paralepididae</td>
<td>Paralepididae</td>
<td>$\ln(ww)=\ln(2.0*10^{4})+2.824(\ln(sl_{num}^{*1.0482}))$</td>
<td>104</td>
<td>0.957</td>
<td>$cw=0.0847*ww$</td>
<td>37,42,45</td>
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<tr>
<td>Phosichthyidae</td>
<td>Phosichthyidae</td>
<td>$\log_{10}(ww_{mg})=4.036x(\log_{10}(sl_{num}))-3.418$</td>
<td>29</td>
<td>0.928</td>
<td>$cw=0.0847*ww$</td>
<td>37,46</td>
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<tr>
<td>Pomacanthidae</td>
<td>Pomacanthidae</td>
<td>$\ln(ww_{g})=0.0745+2.577(\log_{10}(sl_{num}-0.082387)-0.766))$</td>
<td>210</td>
<td>0.98</td>
<td>$cw=0.0847*ww$</td>
<td>37,39</td>
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<tr>
<td>Tuna</td>
<td>Scombridae</td>
<td>$ww_{g}=0.00179x(sl_{cm})^{3.846}$</td>
<td>89</td>
<td>0.934</td>
<td>$cw=0.0847*ww$</td>
<td>37,49</td>
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<tr>
<td>Scorpaenidae</td>
<td>Scorpaenidae</td>
<td>$\ln(ww_{g})=0.0246+2.908x(\ln(1.24xsl_{cm}))$</td>
<td>140</td>
<td>0.984</td>
<td>$cw=0.0847*ww$</td>
<td>37,39</td>
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<tr>
<td>Serriomer sp.</td>
<td>Serriomeridae</td>
<td>$ww_{g}=0.000001x(sl_{cm})^{4.45}$</td>
<td>344</td>
<td>-</td>
<td>$cw=0.4509*dw$</td>
<td>2,48</td>
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<tr>
<td>Argyropeleus spp.</td>
<td>Sternoptichys</td>
<td>$\log_{10}(ww_{mg})=2.95x(\log_{10}(sl_{num}))-1.52$</td>
<td>109</td>
<td>0.98</td>
<td>$cw=0.067*ww$</td>
<td>37,46</td>
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<tr>
<td>Danaphos spp.</td>
<td>Sternoptichys</td>
<td>$\log_{10}(ww_{mg})=3.515x(\log_{10}(sl_{num}))-2.901$</td>
<td>109</td>
<td>0.96</td>
<td>$cw=0.084*ww$</td>
<td>37,46</td>
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<td>Sternoptys sp.</td>
<td>Sternoptichys</td>
<td>$\log_{10}(ww_{mg})=2.877x(\log_{10}(sl_{num}))-1.08$</td>
<td>21</td>
<td>0.969</td>
<td>$cw=0.056*ww$</td>
<td>37,46</td>
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<td>Valenciennellus sp.</td>
<td>Sternoptichys</td>
<td>$\log_{10}(ww_{mg})=2.757x(\log_{10}(sl_{num}))-1.3$</td>
<td>109</td>
<td>0.7</td>
<td>$cw=0.067*ww$</td>
<td>37,46</td>
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<tr>
<td>Stomiidae</td>
<td>Stomiidae</td>
<td>( \log_{10}(ww_{mg}) = 2.52 \times \log_{10}(sl_{mm}) - 1.593 )</td>
<td>39</td>
<td>0.955</td>
<td>( cw=0.046 \times ww )</td>
<td>37,46</td>
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<tr>
<td>Synodontidae</td>
<td>Synodontidae</td>
<td>( \log_{10}(ww_{g}) = 0.12 \times (sl_{cm}/1.131)^{2.749} )</td>
<td>1011</td>
<td>0.977</td>
<td>( cw=0.0847 \times ww )</td>
<td>37,47</td>
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<td><em>Benthodesmus</em> sp.</td>
<td>Trichiuridae</td>
<td>( \log_{10}(ww_{g}) = 3.23 \times \log_{10}(sl_{cm}) - 2.189 )</td>
<td>82</td>
<td>0.952</td>
<td>( cw=0.0847 \times ww )</td>
<td>1,37</td>
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<tr>
<td><em>Zanclus cornutus</em></td>
<td>Zancillidae</td>
<td>( \log_{10}(ww_{g}) = \ln(0.0147) + 3.370 \times \ln(1.1795 \times sl_{cm}) )</td>
<td>11</td>
<td>0.985</td>
<td>( cw=0.0847 \times ww )</td>
<td>37,39,45</td>
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</table>

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Figure A.1. Length-weight relationship for several zooplankton and micronekton groups compiled from the literature. See Table A-1 for associated references for each regression.
Figure A.1. Continued…Length-weight relationship for several zooplankton and micronekton groups compiled from the literature. See Table A-1 for associated references for each regression.
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