Quantifying spatiotemporal variability in mesozooplankton distribution and nutritional quality around seamounts within the Canadian Offshore Pacific Bioregion

By

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We acknowledge and respect the Lək̓ʷəŋən on whose traditional territory the university stands and the Songhees, Esquimalt, and WSÁNEĆ Peoples whose historical relationships with the land continue to this day.

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Abstract:

Zooplankton are a diverse group of organisms that are the key link between primary producers and higher trophic levels in marine ecosystems. They are an important food source for many fish, marine mammal, and sea bird species, and are a major allochthonous energy source for seamounts. Therefore, zooplankton are an important indicator of ecosystem processes in the open ocean. The southern portion of the Canadian Offshore Pacific Bioregion (OPB), in the Northeast Pacific, is a seamount-rich environment that has recently been a target of conservation efforts by the Canadian Government via the proposal of the Tang.G̱wan - ḥačxʷiqak - Tsig̱is (TḥT) Marine Protected Area (MPA). Oceanographic research expeditions (Northeast Pacific Deep-sea Exploration Project; NEPDEP) from 2015 to 2022 surveyed near seamounts to inform the monitoring and management of TḥT and other MPAs in the Canadian OPB. Part of this sampling program included oceanographic and zooplankton sampling. Marine monitoring typically only accounts for variability in zooplankton biomass and/or species abundance, overlooking potential variability in zooplankton nutritional quality. This thesis uses size fractionated zooplankton biomass samples to quantify the spatiotemporal variability in zooplankton biomass and nutritional quality (*i.e.*, energy density, total lipids, and total proteins) in the Canadian OPB. The data presented in this thesis indicate that zooplankton distribution is driven primarily by mesoscale oceanographic processes and not by the presence of seamounts, *per se*. Interannual variability was the most significant driver of change in the zooplankton community, representing up to a 7-fold difference in biomass and up to a 2-fold difference in zooplankton nutritional quality, where generally warm (cool) water years had less (more) nutritious zooplankton communities. Spatially, there were distinct differences between zooplankton collected within offshore and continental slope regions, which influences the allochthonous energy provided to seamount ecosystems. This data was also used to identify key zooplankton taxa which appear to have a disproportionate effect on total zooplankton nutritional quality. Notably, *Neocalanus* spp. were associated with lipid-rich zooplankton samples, while gelatinous species (*e.g.*, doliolids and salps) were associated with lower energy density. These data and analyses have important implications for the future monitoring and conservation of the Canadian OPB and provide important baseline characterization of the spatiotemporal variability of the zooplankton community around seamounts in this region.

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Chapter 1: A brief overview of zooplankton spatiotemporal variability, nutritional quality, and seamount interactions in the Northeast Pacific

1.1 Mesozooplankton in the Northeast Pacific

Zooplankton are a key component in marine ecosystems as they are the main conduit of energy and nutrients between primary producers and larger consumers. In the Northeast Pacific (NE Pacific hereafter), these consumers include pelagic fishes (Brodeur, 1989; Foy and Norcross, 1999; Tanaka et al., 2013; Hertz et al., 2016; Contreras et al., 2020), marine mammals (Dunham and Duffus, 2001; Miller et al., 2019), and sea birds (Hipfner et al., 2020). Zooplankton contribute to the biological pump in marine systems through the production of negatively buoyant particles that sink through the water column, forming a portion of marine snow (*e.g.*, carcasses, fecal pellets, and discarded mucus nets; Alldredge and Silver 1988; Longhurst and Harrison 1989). Marine snow, in turn, feeds many mesopelagic and benthic organisms and contributes to the burial of carbon (Turner, 2002; Archer et al., 2018; Lebrato et al., 2019). Zooplankton also contribute to the biological pump through the direct export of carbon from the photic zone via the vertical migration of zooplankton, thereby directly shuttling carbon through the upper few hundred meters of the water column (Steinberg et al., 2000; Hays, 2003; Bandara et al., 2021). The trophic importance of zooplankton is clear and highlights the importance of understanding their distribution and variability as a food source.

The zooplankton community off the west coast of Canada is often dominated by highly-abundant crustacean species but is also known to have periodically high abundances of gelatinous organisms. As is generally the case in marine food webs, copepods (particularly boreal and subarctic species) are the most abundant and diverse group of crustaceans in this region, with common species including *Oithona similis*, *O. atlantica*, *Neocalanus cristatus, N. plumchrus*, *N. flemingeri*, *Metridia pacifica*, *Calanus marshallae, C. pacificus*, *Pseudocalanus mimus*, and *Acartia longiremis* (Mackas and Tsuda, 1999; Pata et al., 2022). Amphipods are also common planktonic crustaceans in this region, particularly *Themisto pacifica*, *Primno abyssalis*, and *Cyphocaris challengeri*. Among other crustacean zooplankton, euphausiid biomass can sometimes rival copepod biomass dominance in the NE Pacific (specifically *Euphausia pacifica* and *Thysanoessa inspinata*) (Mackas et al., 2004). Euphausiids are the largest of the planktonic crustaceans commonly found in this region and perform deep diel vertical migrations (DVM), often occupying waters ≥125m during daytime (De Robertis et al., 2003; DFO, 2019). Non-crustacean zooplankton commonly found in this region include chaetognaths, the pteropod *Limacina* spp., plus various ctenophores, cnidarians, and larval forms of polychaetes, mollusks, and fishes. Many gelatinous species including pyrosomes, salps, and doliolids appear only episodically in the Canadian offshore Pacific and have an extremely variable presence between years (Mackas, 1992; Archer et al., 2018; Lüskow et al., 2022).

1.1.1 Zooplankton spatial variability

The high degree of spatial variability of zooplankton has been explored by oceanographers for the past century and remains an ongoing challenge in the study of zooplankton ecology (Hardy, 1936; Greenblatt et al., 1982; Mackas, 1984; Mackas et al., 1985; Denman and Dower, 2001; Robinson et al., 2021). Typically, the similarity of zooplankton taxonomic composition decreases with the geographical distance between sampling locations. For example, Star and Mullin (1981) reported a ~20% decay of similarity across 10km in the open NE Pacific (Star and Mullin, 1981). Sample-to-sample similarity tends to decay at a faster rate across oceanographically heterogeneous regions (*i.e.*, a seaward transect from coastal to offshore regions) compared to that seen within large, relatively homogeneous, open ocean environments (Star and Mullin, 1981; Mackas, 1984). Zooplankton are often organized into discreet aggregations with gaps in between, often referred to as “patches” (Denman and Dower, 2001). Many physical processes can create or enhance zooplankton patchiness, via (for example) displacement from current-mediated flow dynamics and current-topography interactions (Genin et al., 1988; Denman and Dower, 2001; Genin and Dower, 2007; Kaiser and Williams, 2011; Chen et al., 2021). There are also patch-forming and gap-forming biological drivers, such as those created by species-specific swimming behaviours leading to differential displacement by water flow, or by predation, that can create gaps and influence species distributions (Folt and Burns, 1999; Urmy and Benoit-Bird, 2021). Although zooplankton patchiness and variability are ubiquitous in the ocean, most species do follow distinct annual/seasonal cycles and patterns of abundance and development, which allow for mathematical prediction and modelling of their biomass distribution (Mackas et al., 2004; Ratnarajah et al., 2023).

1.1.2 Zooplankton temporal variability

Pacific decadal and El Niño southern oscillations

The Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO) are examples of recurring ocean-atmosphere phenomena that oscillate at multi-year to multi-decade scales, and which contribute to transitions between warm and cool sea surface temperature (SST) "regimes" in the NE Pacific (Mantua et al., 1997; Mantua and Hare, 2002; Newman et al., 2016). During "cool" regimes (and La Niña events) there is an increase in trade wind intensity across the Pacific basin, thereby lowering sea-surface height, shallowing the thermocline and increasing upwelling in the eastern tropical Pacific. In addition, these climactic oscillations can significantly influence the transport boundaries of currents and major atmospheric circulation (Chavez et al., 2003). The shallowing of the thermocline and increased upwelling in the eastern Pacific provide higher nutrient transport, leading to enhanced primary productivity and increased zooplankton abundance (Chavez et al., 1999, 2003). "Warm" regimes (and El Niño events) weaken the trade winds, therefore having the opposite effects. In the NE Pacific, "cool" regimes relax the Aleutian low pressure system (thereby decreasing upwelling in the Alaska current system) and enhance the California current (leading to a shallowing of the thermocline and upwelling in the California current system; Chavez et al. 2003). Conditions in the Canadian Offshore Pacific Bioregion (OPB hereafter) sometimes align with the California current and with PDO effects, as is demonstrated by a general increase in large subarctic copepods during "cool" regimes and an increase in smaller southern and boreal copepod species in "warm" regimes (Mackas et al., 2001; Keister et al., 2011; Hipfner et al., 2020). Alternatively, there is a positive correlation between euphausiid biomass and “warm” SST events within the Canadian OPB that does not match what is observed in the California current euphausiid biomass (Tanasichuk, 1998; Evans et al., 2023).

Both ENSO and PDO can have similar effects on zooplankton but on different timescales, whereby ENSO occurs over 3-7 year while PDO is a decadal shift. Generally, during the positive phase of ENSO (El Niño) there is a decrease in zooplankton biomass in the NE Pacific (Fisher et al., 2015), the offshore central and eastern equatorial Pacific Ocean (White et al., 1995; Chavez et al., 1999), the Californian current (Bograd and Lynn, 2001), and coastal British Columbia (Mackas and Galbraith, 2002a). In contrast, La Niña events usually have the opposite effect, resulting in increased zooplankton biomass (Bograd and Lynn, 2001). During some ENSO events, there is little to no significant influence on open ocean zooplankton biomass beyond the tropical Pacific (Mackas and Galbraith, 2002a; Hipfner et al., 2020). Both PDO and other SST anomalies have also been observed to correlate with zooplankton biomass anomalies, disproportionally affecting different functional zooplankton (Venello et al., 2021), which can in turn change the overall community composition.

Seasonal cycles of zooplankton in the subarctic Northeast Pacific

Timing and intensity of seasonal changes vary as a function of latitude, but generally zooplankton biomass in the NE Pacific fluctuates significantly (Bertram et al., 2001), peaking in late spring (May/June), a few weeks after the spring phytoplankton bloom (Goldblatt et al., 1999). From spring (May/June) to summer (August) researchers have observed a 3-5 fold decrease in zooplankton biomass at open ocean and coastal stations, with little to no seasonal change at sites nearer the shelf break (Mackas, 1992; Goldblatt et al., 1999). The zooplankton species that displays the largest annual change in biomass is the large subarctic copepod *Neocalanus plumchrus*, which peaks in near-surface biomass in the spring (May/June; Goldblatt et al., 1999). The timing of the *Neocalanus* peak biomass is variable and past research has reported earlier peaks with warming, possibly disrupting synchrony between zooplankton peak biomass, spring phytoplankton blooms, and predator reproduction and migration (Mackas et al., 2007). In the fall, decreasing temperatures and increased wind-driven mixing can initiate a second (but smaller) phytoplankton bloom, resulting in a second, though less intense, increase in zooplankton biomass (Smetacek and Passow, 1990). Winter months typically have the lowest levels of zooplankton biomass and abundance in the NE Pacific (Goldblatt et al., 1999). Interannual variability in the timing and magnitude of the basic seasonal cycle can be considerable; however, both are highly dependent on regional and annual climate conditions (Mackas, 1992; Bertram et al., 2001).

Vertical migration of zooplankton species

Species-specific vertical migration drives a large amount of variation in the vertical distribution of zooplankton, ontogenetically (OVM), seasonally (SVM), and daily (DVM) (Roe, 1984; Goldblatt et al., 1999; Sogawa et al., 2016; Bandara et al., 2021). OVM is the migration of species to different depths as determined by their development and reproduction cycles, which can often be correlated with the seasonal cycle. In the subarctic NE Pacific, the most important long-term OVMs are completed by calanoid copepods of the genus *Neocalanus*, which begin development in productive surface waters in the spring before migrating to depth (often between 250-1000 m) in early summer and diapausing, where they remain for the fall and winter (Miller et al., 1984; De Leo et al., 2018).

DVM is primarily a form of predator avoidance, whereby zooplankton spend daylight hours at depth (where it is darker) to avoid visual predators and ascend to the phytoplankton-rich surface waters to feed at night (Huntley and Brooks, 1982; Ohman et al., 1983; Urmy and Benoit-Bird, 2021). The depth and timing of DVM is species-specific, ranging from non-migrating species to species that migrate up to 800 m depth daily (Brinton, 1967; Pearcy et al., 1977; Wiebe et al., 1979; Hays et al., 2001; Sogawa et al., 2016). Additionally, some zooplankton species perform reverse DVM, in which they inhabit surface waters by day and deep waters at night to avoid invertebrate predators who themselves are performing a typical DVM (Ohman et al., 1983). Zooplankton vertical migrations cause substantial displacement of biomass in the oceans and are thus a major consideration in marine ecology (Hays, 2003; Bandara et al., 2021).

1.1.4 Zooplankton sampling methodologies

Much of our understanding of zooplankton ecology comes from the direct collection of zooplankton samples using a wide variety of specialized nets (Wiebe and Benfield, 2003). Despite their well-known shortcomings and biases (Wiebe et al., 1982; Banse, 1962), nets still remain the most widely used method of zooplankton collection as they provide a cheap, internally consistent, and relatively straightforward approach to sampling (Sameoto et al., 2000). Once collected, there are many ways to analyze zooplankton samples, but among the most basic objectives is to quantify biomass (the other being to quantify/identify abundance). Typically, zooplankton biomass is determined either gravimetrically (*i.e.*, wet weight, dry weight, ash-free dry weight) or volumetrically (*i.e.*, displacement volume) using either fresh or frozen samples (Postel et al., 2000; Yebra et al., 2017b). Alternatively, biomass can also be calculated from abundance data using established length-weight relationships for each species/taxon (Mackas, 1992). Each method has its advantages and drawbacks (see section 3.4), but all are well established in the literature (Mackas, 1992; Postel et al., 2000; Watkins et al., 2011).

1.2 Determination of zooplankton nutritional quality

In the NE Pacific and elsewhere, ecosystem modelling has generally used zooplankton abundance to estimate food availability to higher trophic levels. However, spatiotemporal variability in zooplankton community composition can also lead to variations in the quality (*i.e.*, as opposed to quantity) of prey available to higher trophic levels (Österblom et al., 2008; Weil et al., 2020; Stevens et al., 2022). Having long been ignored, the importance of food quality is increasingly being included in ecosystem modeling and management exercises (Österblom et al., 2008; Spitz and Jouma'a, 2013). Prey quality can be characterized variously as the total energy content of zooplankton, or the relative composition of lipids, proteins, and other vital dietary components (Cumminns and Wuycheck, 1971; Spitz et al., 2010; Taipale et al., 2018; Harmelin-Vivien et al., 2019; Weil et al., 2020). Many researchers have worked to establish a simple means to quantify prey quality in order to better inform marine ecosystem modelling and management (Cumminns and Wuycheck, 1971; Spitz and Jouma'a, 2013; Surma et al., 2018; Weil et al., 2019). Fine-scale determinations of zooplankton nutritional quality may be particularly helpful in species-specific research into individual energetic food web connections, such as the feeding ecology of juvenile salmon (Weil et al., 2020). Alternatively, the broad nutrient composition of different zooplankton groups (which is rarely measured) may be more suitable to address questions about total energy supply and nutrient flow through ecosystems.

1.2.1 The energy density of zooplankton

Zooplankton energy density (ED) is the amount of energy (Joules) stored in a given quantity of biological material. The most direct and widely accepted method to determine ED is via bomb calorimetry (Cumminns and Wuycheck, 1971), although this process has monetary, time, and sample size limitations.

Alternatively, estimation models based on the relationship between ED and other easily measured biological compounds have also been developed (Weil et al., 2019). ED is often used as a currency to quantify energy sources (*e.g.*, allochthonous prey) within ecosystem modelling to quantify energy flux through trophic levels (Benoit-Bird, 2004; Deslauriers et al., 2016; Surma et al., 2018). In addition, it has frequently been used to determine nutritional quality in prey organisms (Cumminns and Wuycheck, 1971; Weil et al., 2020). Within zooplankton, ED varies among different taxonomic groups, particularly when comparing gelatinous and non-gelatinous taxa (Schaafsma et al., 2018; Weil et al., 2020; Lüskow et al., 2021). In addition, species-specific zooplankton ED has been shown to change seasonally (Weil et al., 2020) and over ontogenetic cycles (Schaafsma et al., 2018). When used on bulk zooplankton samples ED represents a measure of all organic material. Consequently, although it may fail to detect fine-scale differences in somatic composition within a bulk sample, it remains a useful way to quantify broad changes in the nutritional quality of zooplankton communities (Schaafsma et al., 2018).

1.2.2 Zooplankton total lipids and fatty acids

Lipids are a vital component of all heterotrophic and mixotrophic diets and are a crucial form of long-term energy storage in many species (Lee et al., 2006). Most consumers, including zooplankton and their predators, have a limited ability to create fatty acids *de novo*, relying instead on altering fatty acids gained from their diet (Dalsgaard et al., 2003). Consequently, the lipid composition of a prey field (*i.e.*, DHA:EPA, PUFA content) can be predictive of predator growth, survival, and development (Rainuzzo et al., 1997; Copeman et al., 2002; Copeman and Laurel, 2010; Xu et al., 2016). Additionally, being the most energy dense of the macromolecular components in zooplankton (Cumminns and Wuycheck, 1971; Beukema, 1997; Postel et al., 2000), lipids are also ideal for energy storage (Lee et al., 2006). Migrating and diapausing species across a broad range of taxa use lipids (*i.e.*, wax esters and triacylglycerols) as long-term energy storage during periods of low food availability (Lee et al., 1971; Lee and Hirota, 1973; Sargent and Lee, 1975; Kattner et al., 1998; Dalsgaard et al., 2003; Lee et al., 2006; Murphy, 2012). Locally, this is observed in the subarctic copepod genus *Neocalanus*, which store large amounts of lipids in advance of overwintering, and which enables them to reproduce at depth in a low-food environment (Miller et al., 1984; Lee et al., 2006; Evanson et al., 2000).

Within zooplankton, total lipid content is highly variable between species (Lee et al., 1971; Larson and Harbison, 1989), regions, and seasons (Evanson et al., 2000; Tsuda et al., 2001; Perumal et al., 2009; Stevens et al., 2022). One major difference is that observed between gelatinous and crustacean species, in which gelatinous zooplankton tend to have a much lower lipid content than crustacean taxa (Lee et al., 2006; Nelson et al., 2000; Ju et al., 2004). A large difference in lipid content has also been observed between boreal/polar (lipid-rich) and subtropical/tropical species (lipid-poor; Kattner and Hagen, 2009). The relatively low lipid content in tropical species is a result of more consistent seasonal (and relatively low) primary productivity and fast generation time (*i.e.*, multiple generations per year), which limits the opportunity and the need for the accumulation of large lipid stores (Lee and Hirota, 1973; Lee et al., 2006). In temperate regions, the highest lipid content in most zooplankton tends to occur following the spring phytoplankton bloom, when large quantities of food allow for the conversion of excess fatty acids into neutral storage lipids across several weeks (Graeve et al., 1994; Stevens et al., 2004; Lee et al., 2006). Understanding this variability and distribution of lipid content can give insight into the dietary quality and growth/survival outcomes for many marine predators, thus making lipids a good indicator of nutritional quality.

1.2.3 Zooplankton total proteins

Proteins are vital dietary compounds needed by higher trophic levels for somatic growth and maintenance, and are often the most prevalent macromolecules in zooplankton, accounting for the largest proportion of zooplankton dry weight (Postel et al., 2000; Wang and Jeffs, 2014; Teles et al., 2020). Within zooplankton, although less energy dense than lipids the large proportion of proteins results in similar quantities of absolute energy as lipids in many zooplankton taxa (Cummins and Wuycheck, 1971; Postel et al., 2000; Harmelin-Vivien et al., 2019). Most fish require high protein diets (and specific essential amino acids in proteins) to attain a large enough size to survive, as some juvenile fish are believed to have a threshold size in order to survive food-limited conditions of some seasons (Beamish and Mahnken, 2001). Protein content has also been found to be a good indicator of the nutritive state of organisms, indicating whether the species (zooplankton or otherwise) is currently food limited in its environment (Guisande, 2006). Proteins have been used as an important metric in diet quality for aquaculture and fish rearing, but to date they have not received the same attention as other metrics of nutritional quality in oceanographic research (Postel et al., 2000; Teles et al., 2020).

1.3 Zooplankton size spectrum

Zooplankton are often grouped based on size, and the distribution within these size groups can be used to understand prey distribution for higher trophic levels. This thesis focuses on mesozooplankton, which range from 0.2 – 20 mm in length (Sieburth et al., 1978; Harris et al., 2000) and can be effectively sampled using nets. In contrast, viro-, nano-, and micro-zooplankton (<0.2 mm) are poorly sampled with nets because of the rapid clogging of very fine mesh sizes and have therefore been widely excluded from many analyses, while macrozooplankton (>20 mm) usually have stronger swimming abilities, allowing many of them to avoid slow moving nets (Wiebe et al., 1982; Sameoto et al., 2000). It is important to consider zooplankton size classes when investigating prey available to zooplanktivorous species, as most marine predators swallow their prey whole, being described as gape-limited predators (Harris et al., 2000).

One method that researchers have used to investigate the structure and function of zooplankton communities is through the use of normalized biomass size-spectra (NBSS), which produces a linear representation of the relative contribution of zooplankton size-classes to total zooplankton biomass (Zhou and Huntley, 1997). NBSS is preferably calculated using a high-resolution (and number) of size bins and measurements of each species (Platt and Denman, 1977). From a more practical perspective, recent studies have used a model developed by Rykaczewski and Checkley (2008), which uses just 5 biomass size fractions to approximate NBSS but which still tends to reach similar conclusions as the high resolution method (Rykaczewski, 2019). Features of NBSS (*i.e.*, slope and intercept) can be used to investigate zooplankton community features. NBSS slopes are determined by the ratio between smaller and larger organisms (increasing small:large organisms creates a steeper slope), and can be interpreted in terms of biomass assimilation efficiency, community structure, and trophic steps, while the slope intercept is indicative of the abundance of small zooplankton (Zhou, 2006; Décima, 2022).

1.4 Physical and biological processes of submarine mountains (seamounts) pertaining to zooplankton distribution in the Canadian Offshore Pacific Bioregion

The Canadian OPB is a topographically complex environment which contains many large extinct volcanoes, known as seamounts, that can represent biomass hot-spots and which can often host large aggregations of nektonic and benthic organisms (Boehlert and Genin, 1987; Rogers, 2018). A seamount is a submarine mountain that exceeds 1000m in elevation above the seafloor, and which is roughly circular or elliptical in basal shape (United States Board of Geographic Names 1981).

1.4.1 Zone of influence

Seamounts are often massive structures that have significant physical, chemical, and biological impacts on the surrounding ocean (Boehlert and Genin, 1987; White et al., 2007). The "zone of influence" around a given seamount is a useful indicator of what surrounding/overlying area might be expected to be influenced by the presence of the seamount and to help understand the broader oceanographic effects that seamounts may cause. In the NE Pacific, Dower et al. (1992) and Dower and Mackas (1996) determined a 30 km radius as the zone of oceanographic influence of Cobb Seamount, based on its topographic footprint and the apparent limit of detected biological and physical effects on the overlying water column. Since then, a 30 km radius has become the common boundary used by Fisheries and Oceans Canada (DFO) researchers to designate the oceanographic boundaries of seamounts in the OPB for policy and remote sensing research (Ban et al., 2016; Du Preez and Norgard, 2022). Since this estimation was based on a single very shallow seamount, however, it is likely inaccurate for all seamounts in this region which vary widely in size, depth, and shape. Consequently, zones of influence (if present) should ideally be determined on a case-by-case basis.

1.4.2 Physical processes and current dynamics around seamounts

The physical structure of seamounts can lead to upwelling of deep ocean water, changes in current flow dynamics, the retention of overlying water masses, and the enhancement of water column mixing (Roden, 1991; Mackas and Galbraith, 2002a; Genin, 2004). In idealized conditions seamounts have been theorized to have many persistent effects on the surrounding hydrographic structure, generally as a result of current-topography interactions deflecting and otherwise influencing the flow of water currents (White et al., 2007; Dai et al., 2022). There have also been occasional observations of anti-cyclonic flow patterns of limited height above seamounts summits (also known as Taylor cones) and the formation of eddies, both of which are capable of retaining water above a seamount summit to varying degrees (Roden, 1991; Dower et al., 1992; White et al., 2007; Guo et al., 2020). There have also been observations of enhanced near-bottom ocean currents near seamounts (Roden, 1991). Taken together, these mechanisms (and interactions among them) may contribute to the bottom-up enhancement of local biological productivity via the influx and retention of nutrient-rich water in the nutrient depleted photic zones, thereby enhancing primary productivity (Boehlert and Genin, 1987; Rogers, 2018). On the other hand, the enhancement of near bottom currents can lead to increased horizontal particle flux, lowering settling rates but allowing benthic organisms (*e.g.*, corals and sponges) to take advantage of this potentially valuable food source (Genin and Dower, 2007).

1.4.3 Evidence of enhanced primary productivity in the water overlying seamounts

Widespread enhancement of local primary production has been detected via remote sensing at many seamounts globally, with at least 17% of Pacific seamounts showing some level of persistent chlorophyll-a enhancement (Leitner et al., 2020), and generally attributed to the aforementioned current-topography interactions (White et al., 2007). Enhancement of primary production has also been detected *in-situ* at seamounts of varying summit depths (Genin and Boehlert, 1985; Dower et al., 1992; Dai et al., 2020, 2022).

However, despite widespread occurrence, localized increases in primary production are unlikely to propagate to higher trophic levels at seamounts, as this would require retention of high-productivity waters on a scale of weeks to months (Boehlert and Genin, 1987; Genin, 2004; Rowden et al., 2010), and for which little evidence exists. This is especially unlikely over deep seamounts where the summits are too deep (>400 m) to retain water in the euphotic zone, thereby not retaining any enhancements in primary productivity and more likely shedding it downstream (Demarcq et al., 2020; Dai et al., 2022).

1.4.4 Zooplankton-seamount interactions

The trophic focusing (Genin, 2004) of advected zooplankton may provide a large input of energy to seamount ecosystems, thereby contributing to the establishment and maintenance of dense aggregations of nektonic and benthic organisms (Boehlert and Genin, 1987). Trophic focusing occurs when zooplankton are advected and/or accumulated in an area where they can be consumed at higher rates by zooplanktivorous organisms (Genin and Dower, 2007). This increases the rate and/or efficiency of many zooplanktivorous hunting strategies, thereby enhancing the energy transferred to higher trophic levels (Isaacs and Schwartzlose, 1965; Genin and Dower, 2007). For example, topographic blockage (or bottom trapping) of zooplankton is the blocking of the full descent of vertically migrating species (*e.g.*, euphausiids) by the benthic topography, trapping them in well-lit areas near-surface waters where they are vulnerable to higher rates of predation (Isaacs and Schwartzlose, 1965; Genin et al., 1988; Aarflot et al., 2019). Evidence of bottom trapping via increased predation (*i.e.*, resulting in locally reduced zooplankton biomass) above seamounts summits and other abrupt topographic features have been observed at the Great Meteor Seamount (Fock et al., 2002; Martin and Nellen, 2004), Southeast Hancock Seamount (Seki and Somerton, 1994), Nidever Bank (Genin et al., 1988), and above shallow banks in the Barents Sea (Aarflot et al., 2019).

Bottom trapping can only occur at seamounts which are within the depth range of zooplankton DVM, which typically spans the top few 100m of the water column. This process is thus unlikely to occur above seamounts with deeper (>400m) summits (Genin, 2004; Genin and Dower, 2007). Regardless of depth, however, seamounts can still have enhanced near-bottom currents and complex topographies, allowing nektonic zooplanktivores to employ highly efficient feed-rest cycles, as described in Genin (2004) and observed in Lorance et al. (2002) and Brodeur (2001). These enhanced currents can also increase the flux of particles to benthic suspension feeders, resulting in rich benthic communities which add to the structure and complexity of seamount communities (Genin et al., 1986).

1.5 Structure of this thesis

As discussed above, zooplankton distribution, taxonomic composition, nutritional quality, and productivity can be useful tools to investigate environmental and topographical features (such as seamounts) and their influence on pelagic ecosystems. Zooplankton are recognized as useful indicators of marine ecosystem state in a changing ocean because their distribution, phenology, and community structure are highly reflective of their physical environment, while at the same time less likely to be confounded by anthropogenic exploitation through fishery activities, as zooplankton fisheries are uncommon (Richardson, 2008). The study of zooplankton dynamics can thus be used as an important monitoring tool of ecosystem function in the face of environmental change, be it from climate perturbations (*e.g.*, marine heat waves) or regional features (*e.g.*, seamounts).

This thesis will demonstrate one approach using these tools to investigate zooplankton communities in the NE Pacific, and specifically those within the seamount-rich Canadian OPB. This work was conducted under the aegis of the Deep-Sea Ecology Program, and aims to contribute to DFO's efforts to develop effective conservation and monitoring programs for these valuable ecosystems in Canadian oceans. Working towards these conservation goals, this thesis attempts to quantify the main energy source for higher trophic levels (*i.e.*, zooplankton) in the OPB.

In Chapter 2, zooplankton biomass and nutritional quality are used to quantify the energy availability to 13 seamounts in the OPB. The results are used to make suggestions on the monitoring of pelagic systems in the OPB and possible avenues to directly address the energy source supporting these seamounts in future research.

In Chapter 3, zooplankton biomass samples are used for a variety of analyses to quantify spatiotemporal variability in zooplankton nutritional quality in the OPB. This chapter exemplified a procedure to perform seven analyses on frozen biomass samples, which are a commonly collected but often under-utilized zooplankton sample.

Finally, Chapter 4 summarizes the major findings of previous chapters. Using the previous chapter conclusions, clear next steps are proposed to further our knowledge on the topic of zooplankton as an energy source to seamounts and to establish long-term monitoring of zooplankton nutritional quality.

Chapters 2 and 3 are structured as individual articles, therefore some themes may be repeated throughout, apart from the methods (Sections 2.2 and 3.2), which are detailed in Chapter 2 but are not covered in detail in Chapter 3. Instead, Chapter 3 refers back to Chapter 2 for the sake of brevity.

Chapter 2: Zooplankton biomass and nutritional variability near seamounts within the Canadian Offshore Pacific Bioregion

2.1 Introduction

The Canadian Offshore Pacific Bioregion (OPB) is a seamount-rich region, with 62 known or predicted seamounts (Du Preez and Norgard, 2022). The OPB is one of four biogeographic units in Canada's Pacific Exclusive Economic Zone (EEZ) and was designated by the government of Canada to be used as a management region (DFO 2009). The OPB includes Canada's Pacific continental slope and offshore regions, stretching from the shelf break to the edge of the Canadian EEZ. The boundaries of the OPB were designated using geographic and political boundaries and therefore do not necessarily represent ecologically or oceanographically significant boundaries. As of 2022, seamounts accounted for 20,430 km^2 or 6.5% of the Canadian OPB (Du Preez and Norgard, 2022). Seamounts in this region are often arranged in chains, and if not, they tend to be in close proximity (≤ 100km) to other seamounts or the continental shelf (Du Preez and Norgard, 2022). Most Canadian seamounts have summit depths that are considered deep (≥ 800m) with only five intermediate depth seamounts (200-800 m) and one shallow seamount (≤ 200 m, SG̲áan K̲ínghlas-Bowie Seamount; Genin and Dower, 2007; Clark et al., 2011; Du Preez and Norgard, 2022). The extent of interactions between these NE Pacific seamounts and zooplankton are currently unknown, but if present, such interactions are likely not driven by topographical interactions because most summits are deeper than the vertical migration depth of most zooplankton species (Genin, 2004; Genin and Dower, 2007). Seamounts within the Canadian OPB have been identified as ecologically or biologically significant areas (EBSAs), as per the Fisheries and Oceans Canada (DFO) guidelines (DFO, 2004).

In recent years the Canadian government has pledged to protect 30% of its land and oceans by 2030. As a part of this program the Tang.G̲wan - ḥačxʷiqak - Tsig̲is (TḥT) and the SG̲áan K̲ínghlas-Bowie Seamount Marine Protected Areas (SK̲-B MPA) were created to protect deep-sea features in the Canadian OPB. Currently the TḥT MPA and SK̲-B MPA encompass, respectively, 76% and 5% of seamounts within the Canadian OPB, and include many more undersea hills and knolls (Du Preez and Norgard, 2022). The MPA co-managing partners (the Nuu-chah-nulth Tribal Council, the Council of the Haida Nation, Pacheedaht First Nation, Quatsino First Nation, and DFO) require understanding of key seamount ecosystem processes and functions to effectively protect and monitor these MPAs. One area requiring research is the spatiotemporal variability of allochthonous energy input (zooplankton biomass) to these regions. Currently, there is no direct measurements of allochthonous food input, which likely helps support the diverse and dense organisms that reside on these seamounts (Boehlert and Genin, 1987; Rogers, 2018; Du Preez and Norgard, 2022).

There has been limited research into the interactions between plankton and the Canadian OPB seamounts (*e.g.*, bottom trapping of zooplankton, phytoplankton enhancement), therefore the energy source which supports high benthic and nektonic biomass remains unclear (Genin and Dower, 2007; Rowden et al., 2010; Du Preez and Norgard, 2022). The only research into energy flow at these seamounts has been completed in Du Preez and Norgard (2022), where the export productivity to each seamount was estimated using remote-sensing of sea surface temperature (SST) and chlorophyll-a (SSC). However, these estimates did not specifically address the source of energy provided to these seamounts. Existing literature provides insight to energy sources within the region. In particular, past monitoring programs and research projects have identified common zooplankton species and the spatiotemporal variability of zooplankton biomass and taxonomic composition in the Canadian OPB (Mackas and Galbraith, 2002a; Pata et al., 2022). Using these data, one can approximate zooplankton standing stock in the region, in turn, using species-specific energy densities and macromolecular composition to estimate energy and dietary nutrients (*i.e.*, lipids and proteins) available to these seamounts (Rogers, 2018). Estimates of zooplankton standing stock are helpful in determining the energy availability to higher trophic levels, but zooplankton-seamount interactions must also be considered because they can have significant influence on energy flow to seamounts (Boehlert and Genin, 1987; White et al., 2007). In one case, Isaacs and Schwartzlose (1965) estimated up to a 40-fold increase in energy input because of the topographic blockage of vertically migrating zooplankton.

This chapter poses three questions to help further our understanding of energy and nutrient supply to Canadian OPB seamounts:

1) Does the spatiotemporal variability of zooplankton biomass, abundance, and/or taxonomic composition around seamounts in the Canadian OPB differ from the background levels of mesoscale variability in the region?

2) Does mesoscale variability within the Canadian OPB result in differences in the availability of zooplankton biomass, species, energy, lipid, and protein at different Canadian OPB seamounts?

3) What are the implications of these results for future conservation, management, and monitoring strategies within the Canadian OPB?

2.2 Methods

2.2.1 Sampling location

Oceanographic and zooplankton samples were collected within the Canadian OPB from July 10th-15th July 22nd-29th 2017, July 20th-27th 2019, and June 18th-26th 2021 (DFO-IOS cruises 2015-048, 2017-036, 2019-014, and 2021-036, respectively) onboard the CCGS *John P. Tully*. The sampling dates largely corresponded to seasonal maxima of zooplankton for this latitudinal range and are therefore representative comparisons of biomass and taxonomic diversity of zooplankton in the region. Sampling was conducted at 13 of these seamounts, the majority being situated within the Ṯ͟hT MPA (Fig. 2.1). Seamounts were not sampled evenly; four (SK̲-B, Union, NEPDEP 54 [formally known as Dellwood], and Explorer) were considered 'well sampled' with >6 sampling events each, three seamounts were 'moderately sampled' with 3-5 sampling events, and eight seamounts were 'poorly sampled' with <3 sampling events (Table 2.1). Additionally, the Du Preez and Norgard (2022) seamount classification system was used, which is grouped as per their modelled export productivity (indicated by letter) and the combination categories of summit depth and summit dissolved oxygen content (indicated by number). When possible, sampling occurred at sites both above the seamount and from the surrounding ocean (designated "ON" and "OFF" hereafter) to facilitate the comparison of zooplankton biomass and taxonomic composition inside and outside the "presumed seamount zones of influence", as described in section 1.4. Seamount boundaries were defined by Du Preez and Norgard (2022) as the depth of the first topographic contour with a 3° upward slope. Sites were designated ON if they were within these seamount boundaries, while OFF sites were located outside the seamount boundaries. Seamounts in the Canadian OPB have a variety of sizes and geographical features, and therefore have variable areas of influence, likely being elongated downstream as seen with island wake effects (Doty and Oguri, 1956; Barton, 2001; Perfect et al., 2020). Therefore, it is plausible some of the sites designated as OFF were actually within the zone of influence of a given seamount.

2.2.2 Oceanographic sampling and setting

Oceanographic sampling was conducted at each site to provide an environmental context at the time of zooplankton sampling. Fluorescence, salinity, temperature, and oxygen were measured with a Sea-Bird SBE-911plus CTD. Water property values recorded in this study were determined from the upper 250 m of the water column to match the environment sampled with zooplankton nets. The mixed layer depth was determined as the depth at which the maximum Brunt-Vaisälä frequency (Wahl and Teague, 1983) occurred, which was calculated with the *oce* package (Kelley et al. 2023) in RStudio. Using a rosette bottle-sampling system, water samples were also collected at a subset of sites for later lab analysis of chlorophyll, inorganic nutrients (*i.e.*, NO_{3-} and NO_{2-}), and salinity, all of which were performed at the Institute of Ocean Sciences, Fisheries and Oceans Canada (IOS, Sidney, BC, Canada).

The TḥT MPA is situated at the bifurcation of the North Pacific current, creating a region of weak but variable surface currents. Due to logistical constraints, current velocities were not measured *in-situ*. Instead, surface velocities were estimated using modelled current velocities using data from CMEMS multi-model reanalysis currents from the NE Pacific (NEP; https://doi.org/10.48670/moi-00024). This model was calculated from monthly mean current velocities over a span of 29 years (1992-2021). Northing and easting current velocities were used to determine current velocity and direction above each seamount at the time sampled.

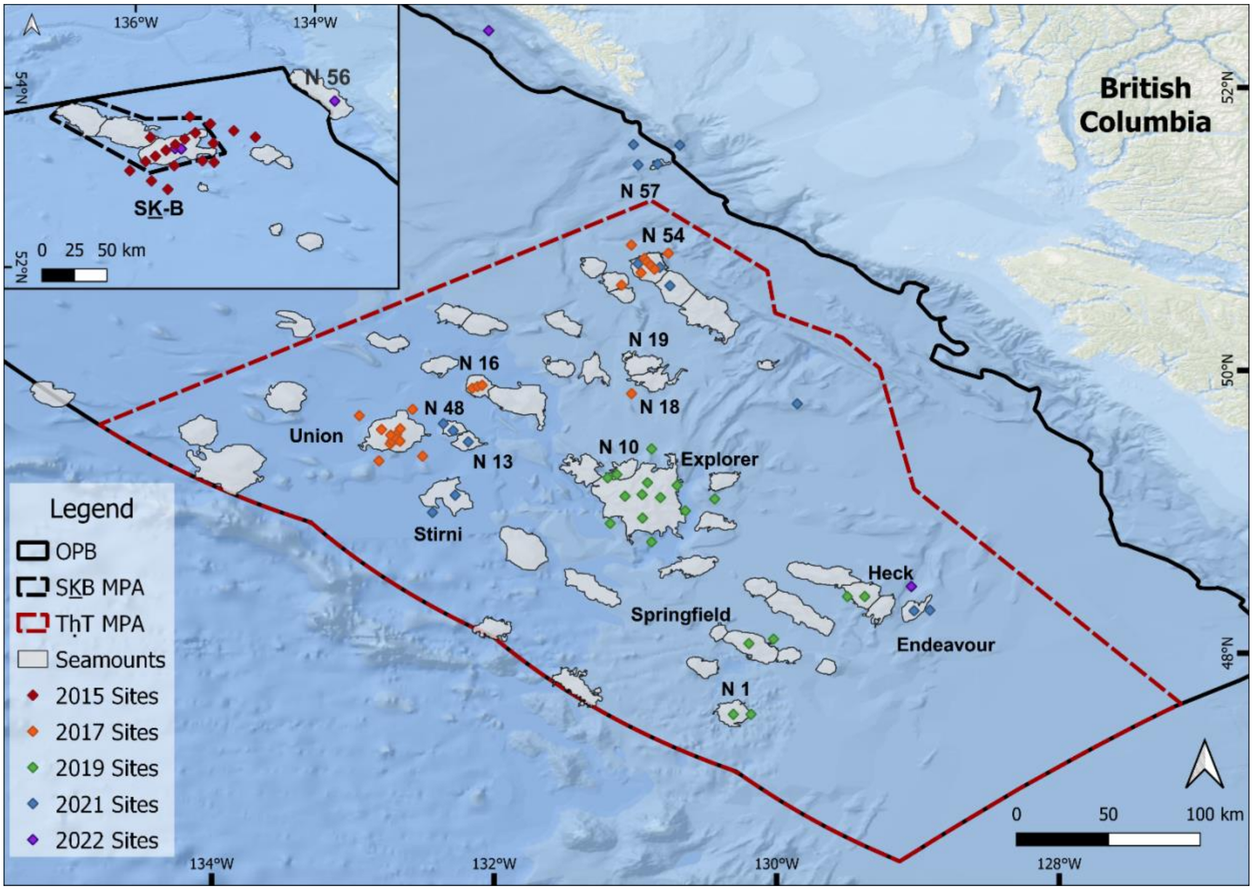


Figure 2.1. A map of the Canadian Offshore Pacific Bioregion (OPB) and Tang.G̱wan - ḥačxʷiqak - Tsig̱is (TḥT) and the SG̱áan Ḵínghlas-Bowie Seamount(SḴ-B) Marine Protected Areas (MPAs) with the location of seamounts and zooplankton sampling sites. Unnamed seamounts have the place holder name NEPDEP #, which is abbreviated as N #. Seamount boundaries collected from Du Preez and Norgard (2022). Base map: ESRI Ocean by wms (https://services.arcgisonline.com/ArcGIS/rest/services/Ocean/World_Ocean_Base/MapServer/tile/{z}/{y}/{x}).

2.2.3 Zooplankton sampling

Mesozooplankton were collected along transects across the well-sampled seamounts, or above the summit and in the surrounding ocean for the poorly sampled seamounts. Vertical bongo nets (mouth diameter 0.56 m; mesh size 236 µm, equipped with a T.S.K flowmeter) were towed from a depth of 250 m at an ascent rate of 1 m s^{-1}. The contents of one side of the bongo net were fixed in 10% buffered formalin for taxonomic identification. Organisms were later identified to species level when possible, following the IOS identification key. Contents of the other side of the net were flash frozen at -80ºC then stored at -20ºC for subsequent biomass and macromolecular analyses.

Post-cruise, frozen zooplankton samples were thawed and passed through a sieve stack (4 mm, 2 mm, 1 mm, and 250 µm meshes) to separate the samples into four discrete size fractions. Distilled water was used to create a positive flow through the sieves and to allow the organisms to sort into each size fraction. The use of distilled water can have an immediate deleterious effect of up to 30% of biological material due to the lysis of cells (Omori, 1978). The percent of dry weight lost for each sample was calculated following Postel et al. (2000) as:

$$y = 4.3329\ln(x) + 12.32$$

where y = loss of dry mass (%) and x = milliliter (ml) of distilled water per milligram (mg) of dry mass. The dry mass lost was then added to the dry weight measured for each sample to account for the loss of material during sieving. As per this equation, samples lost 20-40% (mean = 26%) of dry weight as a result of prolonged rinsing with distilled water.

Following sieving, each size fraction was placed on a Whatman 1 filter paper (Qualitative) and filtered using vacuum suction to remove interstitial water before being placed in pre-weighed vials. Samples were weighed to determine the wet weight (WW) of each size fraction, then freeze-dried for 24 hours or until constant mass was reached. Dried samples were then re-weighed to determine dry weight (DW). The sum of the four size fraction DWs was used as the total DW for each station. Dried samples were then pulverized to a homogeneous powder using a mortar and pestle and stored in a desiccator until used for energy density, lipid, and protein analyses.

Zooplankton collected in 2015 at SK-B seamount were fixed in 10% buffered formalin for use in taxonomic identification. Biomass for these samples was back-calculated at IOS using stage-specific length-DW relationships derived from the literature or from locally measured relationships to convert abundance to total biomass (mg m^{-3}; Mackas 1992).

Table 2.1: Summary information on the 13 seamounts sampled and one non-seamount site. All are located within the Canadian Pacific Exclusive Economic zone (EEZ), with the majority in the Tang.G̱wan - ḥačxʷiqak - Tsig̱is MPA, except for SG̱áan Ḵínghlas-Bowie (SḴ-B) which is within the SḴ-B Marine Protected Area (MPA) and NEPDEP 57 which is located outside of conservation zones in the Haida Gwaii basin. Seamounts are listed in order of year sampled and the number of zooplankton sampling events. Seamounts were classified as per Du Preez and Norgard (2022)[1] and distance from slope was collected from DFO (2019)[2].

Seamount	Year sampled	Zooplankton sampling events	Summit depth (m)[1]	Summit Latitude[1]	Summit Longitude[1]	Seamount classification[1]	Distance from continental slope (km)[2]	Surface current velocity ($m\ s^{-1}$) and direction
SḴ-B	2015	16	25	53.299792	-135.65106	H5	125.33	0.062 E
Union	2017	12	271	49.546481	-132.70242	H4	128	0.115 SSE
NEPDEP 54	2017 / 2021	8 / 4	535	50.748881	-130.89797	H3	On slope	0.046 E / 0.12893 SSE
NEPDEP 16	2017	3	1097	49.88355	-132.11363	M2	95.28	0.027 WSW
Explorer	2019	12	795	49.058736	-130.94218	H3	17	0.080 NNE
Heck	2019	2	1015	48.400701	-129.37674	H2	On slope	0.177 S
Springfield	2019	2	922	48.06795	-130.19647	H2	33	0.087 NE
NEPDEP 1	2019	2	895	47.567004	-130.30425	H2	58	0.070 NNE
NEPDEP 10	2019	1	1124	49.2627	-131.131	H2	27.69	0.009 WSW
NEPDEP 57	2021	4	1388	51.458095	-130.84638	H2	On slope	0.10828 S
NEPDEP 13/48	2021	3	2035/2057	49.49516 / 49.573221	-132.18185 / -132.2902	L1 / L1	102.42 / -	0.059 NE
Stirni	2021	2	1710	49.130001	-132.30000	M1	125	0.133 S
Endeavour	2021	2	1583	48.299028	-129.04386	M2	On slope	0.136 S
None	2021	1	-	49.763	-129.854	-	On slope	-

2.2.4 Zooplankton energy density determination using ash-free dry weight

Energy density (ED) is the amount of joules of energy per gram of sample, and can be used to estimate the amount of energy stored in an organism (or in bulk zooplankton samples in this case) and to help determine the upper range of energy available to higher trophic levels. ED was determined via the estimation model of Weil et al. (2019) which uses ash-free dry weight (AFDW) to estimate the ED of aquatic organisms, and which was developed using data collected from the literature for broad taxonomic groups including aquatic invertebrates. The model created for aquatic invertebrates was deemed suitable here as the majority of bulk zooplankton samples were composed of invertebrate species. Although some samples contained vertebrates (*i.e.*, larval fish) this was likely insignificant given their low abundance (<0.1% of the total counts).

Sub-samples (≥10mg) of dried zooplankton from each size fraction were collected and weighed before being placed in a muffle furnace at 550ºC for 4 hours. The remaining ash was weighed and subtracted from the initial DW, then divided by WW in order to determine the percent AFDW (%WW). ED (KJ per gram WW) was then calculated following Weil et al. (2019) as:

$$\log10(ED) = 1.08 * \log10(AFDW) - 0.77 + 0.05$$

2.2.5 Lipid and protein quantification

If enough material remained after ED analysis, sub-samples (≥10mg) of dried zooplankton from each size fraction were collected and weighed prior to lipid extraction. If insufficient amounts of dried zooplankton remained following ED analysis, lipids and proteins were not measured. Lipids were extracted following Parrish (1999), as modified from Folch et al. (1957). Extracted lipids were weighed and divided by dry weight to determine the total lipid (TL) content as %DW.

If enough material remained after ED and TL analyses, sub-samples (≥5 mg) of dried zooplankton were analyzed for total protein concentration (TP) using the Bicinchoninic Acid (BCA) spectrophotometric protocol using commercial BCA protein Assay Kits (Sigma-Aldrich BCA1 and B9643). If insufficient amounts of dried zooplankton remained following ED and TL analyses, TP was not measured. Each sub-sample was processed in triplicate and diluted with Tris-HCL buffer (pH = ~7.8) to a protein concentration between 200-1000 μg ml^{-1}, the desired range for BCA analysis. For this procedure, BSA protein standard was used to establish a linear standard curve with which a 562nm absorbance was fitted for each replicate to determine protein content. Replicates were divided by DW and the average value was used as the TP content as %DW.

2.2.6 Normalized biomass size-spectra approximation

Normalized biomass size-spectra (NBSS) were calculated using the four biomass size fractions following Rykaczewski and Checkley (2008). Log(biomass Δx^{-1}) was plotted against Log(x), where biomass represents zooplankton DW (mg m^{-3}), Δx represents the size interval for each size fraction (0.25-1 mm, 1-2 mm, 2-4 mm, and 4-20 mm), and x represents the corresponding sieve mesh size (250 μm, 1 mm, 2 mm, and 4 mm). The 20 mm upper limit was chosen based on estimates of the largest organisms to be reliably caught in the bongo nets used. Linear spectral slopes were then calculated by fitting the least-squares regression of the following equation:

$$\mathrm{Log}(\mathrm{biomass}/\Delta x) = m(\mathrm{Log}(x)) + b$$

2.2.7 Statistical analysis

All statistical analyses were completed using RStudio, version 4.1.3 (R core team 2022). When assumptions for normality and homoscedasticity were met, ANOVA with post-hoc Tukey HSD tests ($\alpha = 0.95$) were used to compare zooplankton biomass, abundance, NBSS, richness, diversity, energy, TL content and TP content between different seamounts, across annual surveys, and time of day. T-tests were used to compare ON and OFF seamount sites. When data did not meet assumptions and could not be transformed to fit the assumptions, the non-parametric Kruskal-Wallace test with Pairwise Wilcox Post-hoc test were used, as it is more robust to deviations from normality and equal variance.

All multivariate and taxonomic composition analyses were completed using the *vegan* package (version 2.6-4; Oksanen et al. 2022) in R (version 2.6-4). Taxonomic composition among zooplankton samples was compared using non-metric multidimensional scaling (NMDS) plots and dendrograms, wherein increased distance between points and nodes represents the dissimilarity between sites. 95% confidence ellipsoids were fitted on the NMDS for survey year and seamount groupings, and PERMANOVA tests were performed to test for significant differences between these groupings. Additionally, ANOSIM tests were performed to test whether between-grouping variability was greater than within-grouping variability, thereby indicating significant difference between clustered groups. When significant differences ($p < 0.05$) were detected between species assemblages SIMPER tests were performed to determine which taxonomic groups drove taxonomic composition differences between seamounts and across years.

When investigating zooplankton distribution at well-sampled seamounts, Spearman rank correlations calculated with the *corrplot* package (version 0.92; Wei et al. 2021) were used to quantify correlations between relative site location (*i.e.*, distance from seamount summit, longitude, and latitude), zooplankton community features (*i.e.*, biomass, abundance, and NBSS), and oceanographic properties (*i.e.*, temperature, salinity, nutrients, and chlorophyll-a). Where significant correlations were identified, relationships were further investigated using linear regressions. In addition, the relative abundance of vertically migrating (*e.g.*, *Metridia* spp., euphausiids, and *Neocalanus* spp.) and non-migratory zooplankton (*e.g.*, chaetognaths and larvaceans) species were compared across sites to investigate the possibility of enhanced predation on vertical migrators around seamount summits as per Genin et al. (1994).

Spatial dissimilarity in zooplankton taxonomic composition was investigated to determine the existence of "seamount effects" (Genin and Dower, 2007). Similar methods were used at Cobb seamount by Dower and Mackas (1996), whereby sample-to-sample dissimilarity was plotted as a function of both straight-line geographic separation between samples (SEP) and the relative radial difference in distance from the seamount summit (DELRAD). If seamounts cause significant changes in zooplankton taxonomic composition, there would be a more significant decay of between-sample dissimilarity with an increasing DELRAD in comparison to increasing SEP. A LOWESS model was used to determine the effect size of both distance measures.

2.3 Results

2.3.1 Sampling site grouping and classification

For simplicity's sake this study will continue to refer to individual sites by referencing the seamount at which the samples were collected (for example, sites collected within 30km of the Union Seamount summit are considered "Union Seamount sites" and/or "zooplankton collected at Union Seamount"). Thus, when differences between seamounts are mentioned, this is not attributing any causal relationship with the associated seamount but merely as a way to identify the region and timing in which the sampling occurred.

2.3.2 Zooplankton biomass

Zooplankton biomass data are summarized in Figures 2.2 and Table 2.2. As tests for day/night differences in zooplankton biomass were all non-significant, time of day was not factored into any subsequent analyses. Zooplankton biomass was highly variable between annual surveys in the OPB. Total zooplankton DW ranged from 0.45 mg m^{-3} to 53.47 mg m^{-3} with a mean of 7.73 ± 9.32 mg m^{-3}. Between the three surveys there was a threefold variation in average DW, 10.8 ± 8.9 mg m^{-3}, 5.72 ± 11.5 mg m^{-3}, and 19.32 ± 9.84 mg m^{-3}, from 2017, 2019, and 2021, respectively. Total DW was largely driven by interannual variability, as seen in the near 2-fold increase in zooplankton DW from the 2017 and 2019 surveys relative to the 2021 survey (with similar standard deviations in each year).

Total zooplankton biomass (sum of all size fractions) was not statistically different between most seamounts when sampled within any given survey (Fig. 2.2; Table 2.2). During the 2017 and 2019 survey total zooplankton DW was not significantly different across seamounts ($p > 0.05$). However, during the 2019 survey zooplankton DW was marginally lower ($p=0.06$, $df=3$, F-stat=3.5) at NEPDEP 1 than at Explorer. During the 2021 survey, zooplankton DW collected at Endeavour Seamount was lower than at NEPDEP 13 ($p=0.029$) and NEPDEP 54 ($p=0.032$), however no statistical differences in zooplankton DW were found between the rest of the seamounts ($p > 0.05$).

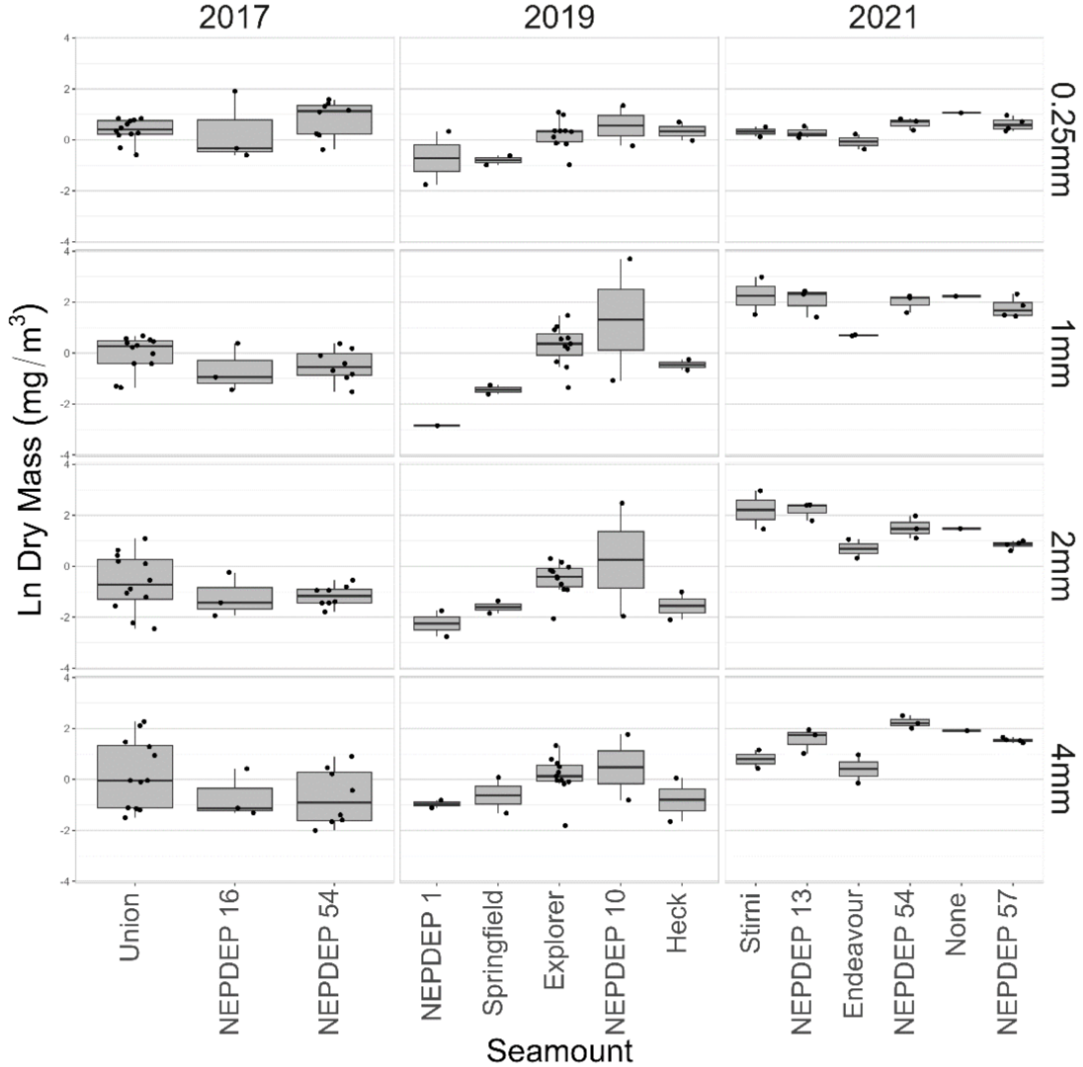


Figure 2.2: The natural log of zooplankton dry weight (mg m^{-3}) at each seamount ordered from offshore towards the continental shelf (left to right), subdivided into size fractions (rows) and years (columns). Black dots represent the dry weight of each sample size fraction. Significant differences ($p < 0.05$) are indicated with an asterisk (*). SK-B (2015) zooplankton biomass data was not included because size fractionated dry weights were not collected.

Table 2.2: Summary of ecological and macromolecular composition of zooplankton community collected at each seamount. Values were calculated as stated in the methods (section 2.2). Where each value is the calculate mean (± standard deviation) between all sites at each seamount and n = sample number.

Seamount	Year	Sites	Dry weight (mg m^{-3} ± SD)	Abundance (#ind m^{-3} ± SD)	Evenness	Diversity	Richness (#spp)	Energy density (J g^{-1}WW^{n} ± SD)	Lipid content (% DW^{n}± SD)	Protein content (% DW^{n}± SD)
SK-B	2015	16	32.33* ± 17.26	395.28 ± 326.86	0.64 ± 0.083	2.71 ± 0.40	69 ± 8.92	-	-	-
Union	2017	12	5.49 ± 3.84	802.72 ± 884.3	0.59 ± 0.068	2.49 ± 0.2	67 ± 7.82	1190.71^{6} ± 442.15	15.63^{5} ± 3.75	6.71^{3} ± 1.73
NEPDEP 54	2017	8	4.11 ± 1.88	2053.85 ± 764.01	0.49 ± 0.036	2.10 ± 0.13	70.13 ± 9.64	1848.24^{5} ± 210.39	15.54^{3} ± 1.1	-
NEPDEP 16	2017	3	3.78 ± 4.06	565.99 ± 409	0.54 ± 0.12	2.23 ± 0.48	62.67 ± 13.05	1719.59^{2} ± 73.89	19.37^{1}	-
Explorer	2019	11	5.18 ± 2.88	415.52 ± 282.32	0.66 ± 0.052	2.91 ± 0.22	82.64 ± 7.45	1549.43^{9} ± 399.39	13.84^{10} ± 2.3	6.86^{9} ± 0.99
Heck	2019	2	3.01 ± 1.71	413.2 ± 201.57	0.73 ± 0	3.2 ± 0.078	77.5 ± 7.78	1626.25^{2} ± 7.1	19.46^{1}	7.53^{1}
Springfield	2019	2	1.58 ± 0.33	107.28 ± 44.75	0.75 ± 0	3.21 ± 0.16	75 ± 19.8	1665.79^{2} ± 669.26	-	-
NEPDEP 1	2019	2	1.32 ± 0.99	119.45 ± 133	0.59 ± 0.26	2.39 ± 1.05	59 ± 1.41	2011.73^{2} ± 429.37	-	-
NEPDEP 10	2019	1	1.28	-	-	-	-	1646.684^{1}	18^{1}	6.14^{1}
NEPDEP 57	2021	4	15.26 ± 2.80	145.39 ± 37.89	0.68 ± 0.049	2.97 ± 0.29	77.5 ± 13.72	1843.69^{4} ± 243.81	26.35^{4} ± 3.95	6.91^{4} ± 1.02
NEPDEP 54	2021	3	24.07 ± 6.16	121.89 ± 19.25	0.70 ± 0.057	2.97 ± 0.32	67 ± 7.55	1707.93^{3} ± 138.05	26.55^{3} ± 1.43	5.7^{3} ± 0.55
NEPDEP 13/48	2021	3	24.45 ± 5.43	127.17 ± 55.72	0.73 ± 0.046	3.08 ± 0.23	67 ± 3.46	1626.62^{3} ± 236.92	28.33^{3} ± 3.08	7.13^{3} ± 0.38
Stirni	2021	2	27.73 ± 22.93	176.03 ± 59.23	0.71 ± 0.11	2.97 ± 0.37	67.5 ± 7.78	3221.37^{2} ± 1605.96	31.3^{2} ± 3.86	7.6^{2} ± 1.45
Endeavour	2021	2	6.85 ± 0.27	178.34 ± 99.06	0.68 ± 0.15	2.89 ± 0.65	71 ± 1.41	1018.32^{2} ± 370.32	26.03^{2} ± 1.87	7.39^{2} ± 1.9
None	2021	1	23.34	262.98	0.52	2.18	69	1144.33^{1}	21.76^{1}	6.79^{1}

*Biomass calculated using length weight relationships established by IOS Plankton program

2.3.3 Spatiotemporal variability in nutritional composition of zooplankton

The OPB zooplankton community was quite variable in terms of ED, TL, and TP content (Fig. 2.3), as summarized in Table 2.2. Interannual variability resulted in significant differences in TL content between surveys ($p < 0.001$), but in neither TP content nor ED.

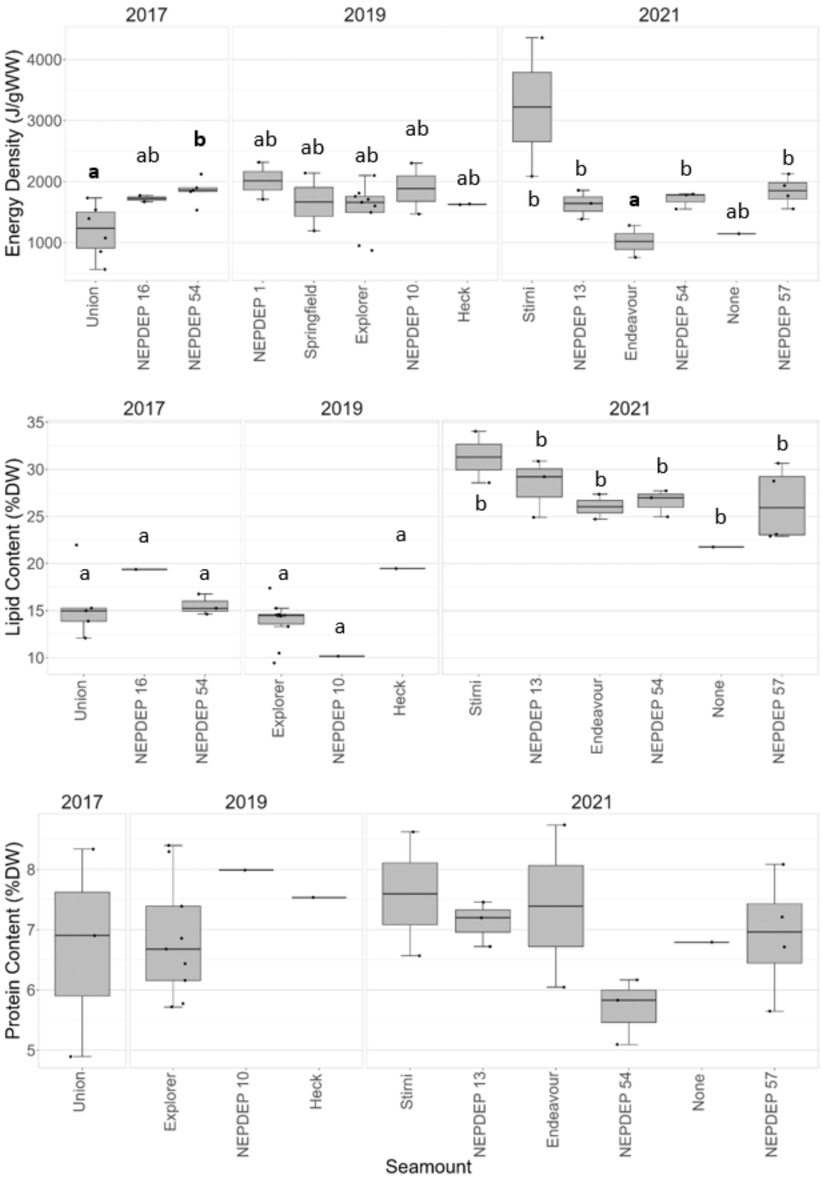


Figure 2.3: The mean energy density (J gWW^{-1}), total lipids (%DW), and total protein (%DW) of bulk zooplankton caught at each seamount sampled. Black dots represent the mean ED, TL, or TP of all size fractions of the sample. Different letters indicate significant differences ($p < 0.05$).

Bulk zooplankton ED differed significantly between some seamounts during the 2017 and 2021 surveys ($p < 0.05$), but not during the 2019 survey ($p=0.59$; Fig. 2.3). During the 2017 survey, zooplankton collected at NEPDEP 54 had higher ED than at Union Seamount (1848.24 ± 210.39 vs 1190.71 ± 442.15 J gWW^{-1}; $p=0.025$). During the 2021 survey, the ED of zooplankton collected at Endeavour Seamount was ~50% of that of zooplankton collected at the other seamounts during the same survey.

Zooplankton TL content (%DW) was not statistically different between zooplankton collected at different seamounts within any given survey ($p > 0.05$), but was significantly different between the surveys (Fig. 2.3). The average TL content of zooplankton communities during the 2017 and 2019 surveys was 17.9 ± 6.4 %DW and 15.7 ± 6.7 %DW respectively, whereas samples collected during the 2021 survey had significantly higher mean values at 26.6 ± 3.9 %DW.

TP content (%DW) did not differ significantly between zooplankton collected at different seamounts during the 2021 survey ($p = 0.316$) or interannually (Fig. 2.3). There were too few zooplankton samples with sufficient biomass to conduct TP analysis from the 2017 and 2019 surveys to adequately compare TP content spatially. The zooplankton community across this study was on average composed of 7.7 ± 2.4 % TP.

2.3.4 Variability in water properties

Mean mixed layer temperature (MLT) during the 2021 survey was relatively cooler (12.8 ± 0.83°C) than the 2015, 2017, and 2019 surveys (15.22 ± 0.24ºC, 14.4 ± 1.6ºC, and 15.9 ± 0.7ºC respectively).

With a few exceptions, water properties at seamounts within the OPB were similar when sampled within the same survey (Table 2.3). For example, the concentration of chlorophyll-a (Chl-a) in the water column surrounding Union Seamount appeared to be higher at all sampling depths (5, 10, and 20 m) than at other seamounts, however, the difference was not statistically significant ($p > 0.05$), except between the Chl-a measured at Union and Explorer Seamounts ($p=0.007$). During the 2017 survey, the water column near Union Seamount had a shallower chlorophyll max depth ($p=0.036$) and lower mixed layer oxygen concentrations ($p <0 .01$), while the water column near NEPDEP 54 Seamount had a warmer MLT ($p < 0.04$) than at other seamounts. During the 2021 survey, the water column near Endeavour and NEPDEP 13 Seamounts had a shallower mixed layer ($p < 0.05$) and samples collected at NEPDEP 54 Seamount had lower inorganic nutrient (NO_{3-} and NO_{2-}) concentrations than found at other seamounts ($p < 0.05$).

Table 2.3: Summary of water column properties at each seamount at the time of sampling. CTD profiles and water sampling was completed to compliment the zooplankton net tows at each site when possible. All values are means calculated from all stations at the seamount indicated ± standard deviation. Mixed layer, chlorophyll max depth, temperature, oxygen, and salinity measurements were taken using a seabird CTD. Chlorophyll and nutrients (NO_{-3} + NO_{-2}) were measured from water samples processed at the institute of ocean sciences (IOS). *Mixed layer depth for SG̲áan K̲ínghlas-Bowie (SK̲-B) was calculated using pressure.

Seamount	Year	Mixed Layer Depth (m)	Chlorophyll Max Depth (m)	Chlorophyll 5m (ug L^{-1})	Chlorophyll *20m* (50m for 2019; ug L^{-1})	Nitrate + Nitrite	Mixed layer temp (^{o}C)	Mean Temp (^{o}C)	Mixed layer Oxygen (mL L^{-1})	Mean Oxygen (mL L^{-1})	Mixed layer salinity	Mean Salinity
SK̲-B*	2015	**17.21** ± 5.15	**39.82** ± 7.07	-	-	**24.98** ± 8.94	**15.22** ± 0.24	8.46 ± 0.45	6 ± 0.07	4.68 ± 0.36	31.99 ± 0.06	32.9 ± 0.24
Union	2017	**13.23** ± 3.32	**18.93** ± 6.02	**0.60** ± 0.19	**1.4** ± 0.52	**25.98** ± 1.57	**14.27** ± 0.24	7.65 ± 0.13	6.32 ± 0.06	4.77 ± 0.08	32.24 ± 0.12	33.27 ± 0.02
NEPDEP54	2017	**13.48** ± 3.77	**25.29** ± 3.49	**0.33** ± 0.04	**0.54** ± 0.26	**26.31** ± 1.96	**15.19** ± 0.16	8.56 ± 0.14	6.03 ± 0.06	4.03 ± 0.08	31.16 ± 0.17	33.11 ± 0.08
NEPDEP 16	2017	**13.57** ± 1.53	**25.77** ± 5.17	**0.21**	**1.12**	**27.13**	**12.39** ± 4.37	7.81 ± 0.16	5.52 ± 0.91	4.64 ± 0.1	32.46 ± 0.75	33.25 ± 0.02
NEPDEP 18/19	2017	**24.8**	**43.6**	-	-	-	**15.3**	**8.36**	**5.96**	**4.74**	**32.42**	**33.22**
Explorer	2019	**16.25** ± 5.5	**34.6** ± 4.49	**0.19** ± 0.03	**0.26** ± 0.10 (**0.38** ± 0.07)	**32.81** ± 2.48	**15.4** ± 0.16	**8.49** ± 0.18	**5.98** ± 0.043	**4.33** ± 0.29	**32.23** ± 0.09	**33.20** ± 0.06
Heck	2019	**19.35** ± 2.19	**40.7** ± 1.41	**0.19** ± 0.01	**0.23** ± 0.0 (**0.64** ± 0.014)	**31.73** ± 1.98	**16.35** ± 0.009	**8.86** ± 0.04	**5.83** ± 0.07	**4.91** ± 0.076	**32.32** ± 0.01	**33.12** ± 0.02
Springfield	2019	**18.8** ± 2.83	**54.55** ± 2.76	**0.15** ± 0.03	**0.15** ± 0.04 (**0.42** ± 0.09)	**29.43** ± 4.15	**16.9** ± 0.06	**9.25** ± 0.13	**5.81** ± 0.01	**4.93** ± 0.07	**32.32** ± 0.003	**33.08** ± 0.01
NEPDEP 1	2019	**14.4** ± 0.71	**44.6** ± 4.24	**0.23** ± 0.07	**0.17** ± 0.04 (**0.36** ± 0.06)	**29.85** ± 3.29	**17.05** ± 0.08	**8.84** ± 0.13	**5.82** ± 0.02	**5.29** ± 0.08	**32.32** ± 0.006	**33.05** ± 0.02
NEPDED 10	2019	**7.9**	**34.7**	**0.18**	**0.36** (0.37)	**35.89**	**15.52**	**8.07**	**6.0**	**4.26**	**32.24**	**33.24**
NEPDEP 57	2021	**18.15** ± 6.17	**50.1** ± 37.17	-	-	**39.42** ± 0.53	**12.3** ± 0.26	**7.48** ± 0.13	**6.44** ± 0.03	**4.45** ± 0.31	**31.83** ± 0.03	**33.14** ± 0.1
NEPDEP 54	2021	**15.93** ± 5.8	**34** ± 6.34	-	-	**33.46**	**12.36** ± 0.16	**7.48** ± 0.12	**6.44** ± 0.01	**4.56** ± 0.14	**31.89** ± 0.06	**33.11** ± 0.04
NEPDEP 13/48	2021	**9.37** ± 2.8	**58** ± 6.46	-	-	**40.05**	**13.33** ± 0.12	**7.44** ± 0.12	**6.24** ± 0.04	**5.06** ± 0.09	**32.24** ± 0.003	**33** ± 0.04
Stirni	2021	**14.65** ± 4.17	**44.95** ± 9.12	-	-	**40.03** ± 0.04	**12.4** ± 0.23	**7.4** ± 0.22	**6.34** ± 0.01	**5** ± 0.04	**32.27** ± 0.0001	**33.02** ± 0.004
Endeavour	2021	**9.7** ± 1.4	**35.95** ± 10.54	-	-	**39.67** ± 0.26	**14.67** ± 0.11	**8.34** ± 0.3	**6.1** ± 0.07	**4.56** ± 0.02	**32.05** ± 0.08	**33.11** ± 0.02
None	2021	**21.6**	**55.3**	-	-	**39.59**	**12.68**	**7.98**	**6.25**	**5.33**	**32.29**	**32.98**

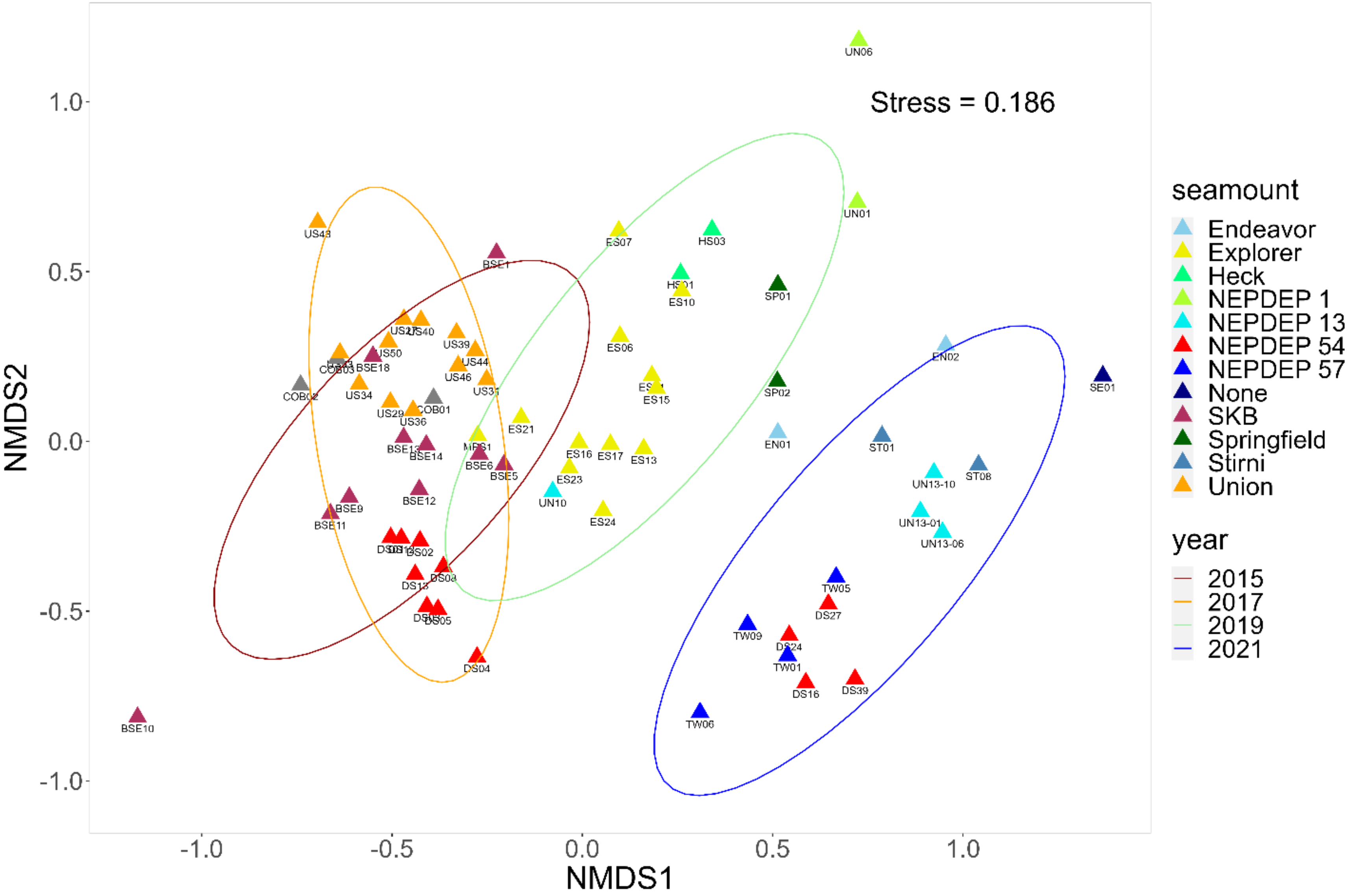


Figure 2.4. NMDS ordination of zooplankton species composition from seamounts in the Canadian Offshore Pacific Bioregion. Sampling years are grouped with ellipses (95% confidence level).

2.3.5 Zooplankton taxonomic composition

NMDS cluster analysis indicated differences in zooplankton taxonomic composition between surveys (Fig. 2.4). There were no significant day/night differences in zooplankton abundance and taxonomic composition, therefore time of day was not factored into any subsequent analyses. Site dissimilarity was primarily driven by interannual changes in community composition ($p < 0.001$, ANOSIM stat = 0.67). SIMPER analysis indicated that differences in zooplankton taxonomic composition between surveys with warm MLT (2017/2019) and cold MLT (2021) were primarily driven by a lower relative abundance of small-bodied copepod species (*Oithona similis*, *Mesocalanus tenuicornis*, and *Clausocalanus arcuicornis*), plus euphausiids and doliolids, and a higher relative abundance of larger-bodied copepods (*N. plumchrus* and *Metridia* spp.) and *Pseudocalanus mimus* in cold MLT years. Interannual changes in taxonomic composition are discussed in further detail in Chapter 3.

NMDS clustering also suggested differences between the zooplankton taxonomic composition at seamounts within each survey (Fig. 2.4; stress value = 0.18). Zooplankton taxonomic data are summarized in Figure 2.5. The greatest between-seamount differences in taxonomic composition were observed during the 2017 survey ($p < 0.001$, ANOSIM stat = 0.75), when samples from Union and NEPDEP 16 Seamounts were dominated by a variety of small calanoid copepods (primarily *Oithona* spp.), doliolids, juvenile euphausiids, and larvaceans while the NEPDEP 54 Seamount assemblage was dominated by various small copepods (*Oithona* spp., *Pseudocalanus* spp., *Acartia longiremis*, *etc*.). Overall, zooplankton samples collected at Union and NEPDEP 16 Seamounts had a taxonomic composition with a higher proportion of gelatinous species while zooplankton samples from NEPDEP 54 Seamount were dominated by copepod species, with relatively fewer gelatinous zooplankton.

In 2021, there were significant differences in taxonomic composition between zooplankton samples collected at different seamounts ($p < 0.001$, ANOSIM stat = 0.68). Zooplankton samples collected at NEPDEP 57 and NEPDEP 54 Seamounts were dominated by various calanoid copepods (*Pseudocalanus mimus*, *Neocalanus* spp., *Metridia* spp., *Oithona* spp., *etc*) and the pteropod *Limacina helicina* while samples collected at Endeavour and Stirni Seamounts were dominated by doliolids and various copepods (*Neocalanus* spp., *Oithona* spp., *etc*.), and NEPDEP 13/48 samples were dominated by *Neocalanus* spp. and other copepods species, plus some doliolids.

Coastal zooplankton species were found at SK-B Seamount which is located roughly 180 km offshore of the Canadian west coast. The most notable (*i.e.*, not typically found offshore) nearshore species *Pseudocalanus newmani* (19.6 ± 28.7 indv m^{-3}), *Gaetanus minutus* (1.7 ± 1.2 indv m^{-3}), and *Cancer productus* (0.075 ± 0.056 indv m^{-3}) occurred in samples from SK-B. These species are not commonly found offshore, particularly in these abundances.

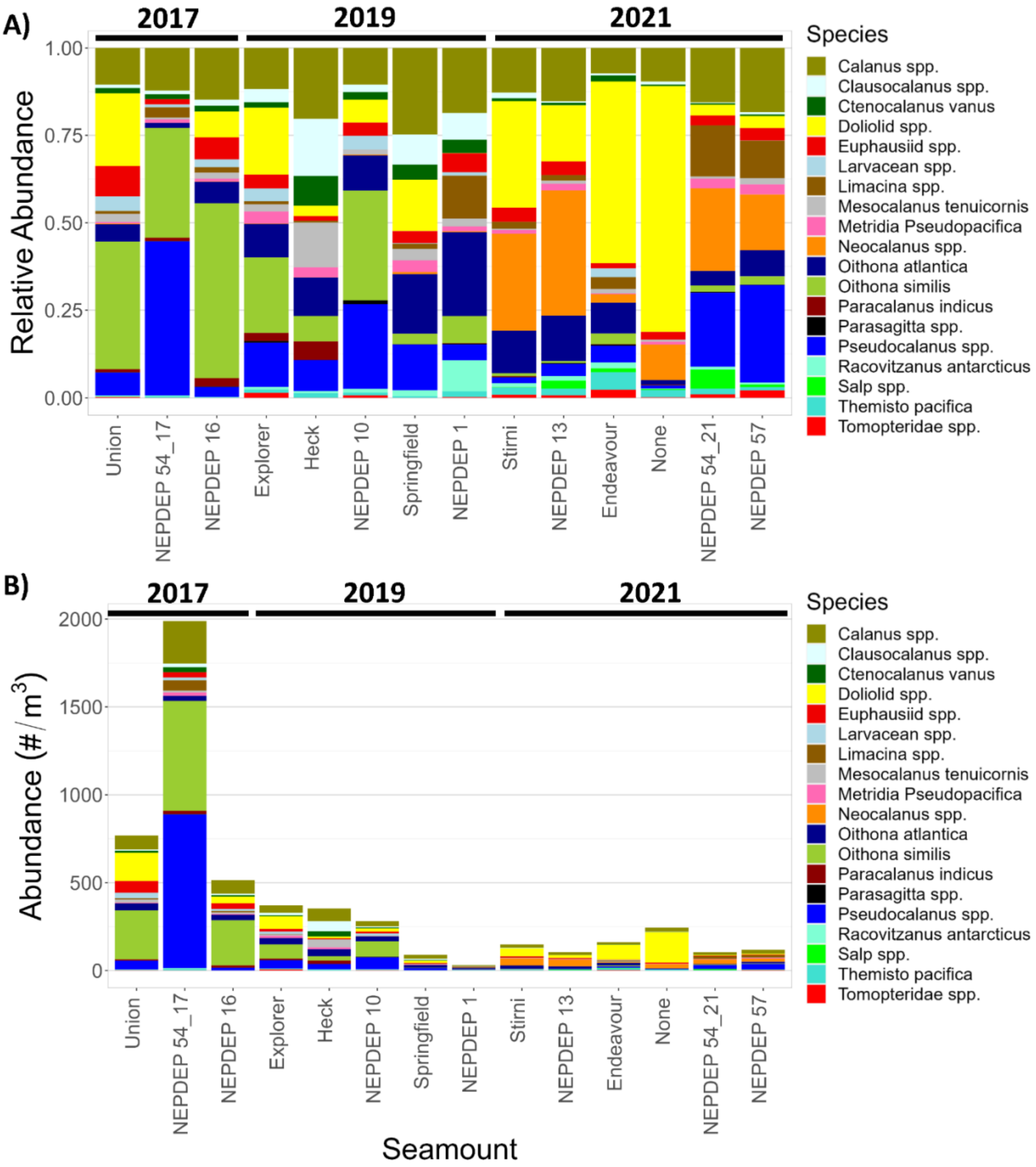


Figure 2.5. The (A) relative and (B) absolute abundance of numerically dominant species and taxa at each seamount. Species which were present in low quantities (<5% at all sites) were excluded for the ease of visualization significant differences. Complete abundance graphs are provided in Appendix 6 (Phyla), 7 (Arthropod orders), and 8 (Calanoid and Cyclopoid families).

2.3.6 Seamount effects on zooplankton in the Canadian Offshore Pacific Bioregion

Within the OPB, zooplankton biomass was not significantly different between ON and OFF seamount sites for any size fractions and across the three surveys (Fig. 2.6). This trend extended across all seamounts. There were also no significant differences between upstream and downstream zooplankton DW ($p > 0.05$). Similarly, zooplankton community size composition and NBSS were not correlated with site location around seamounts ($p > 0.05$). Furthermore, the rate at which sample-to-sample dissimilarity decays at 'well-sampled' seamounts did not significantly differ between increases in DELRAD or SEP (Fig. 2.7), indicating that proximity to a given seamount summit did not have a greater effect on zooplankton taxonomic composition than background mesoscale variability.

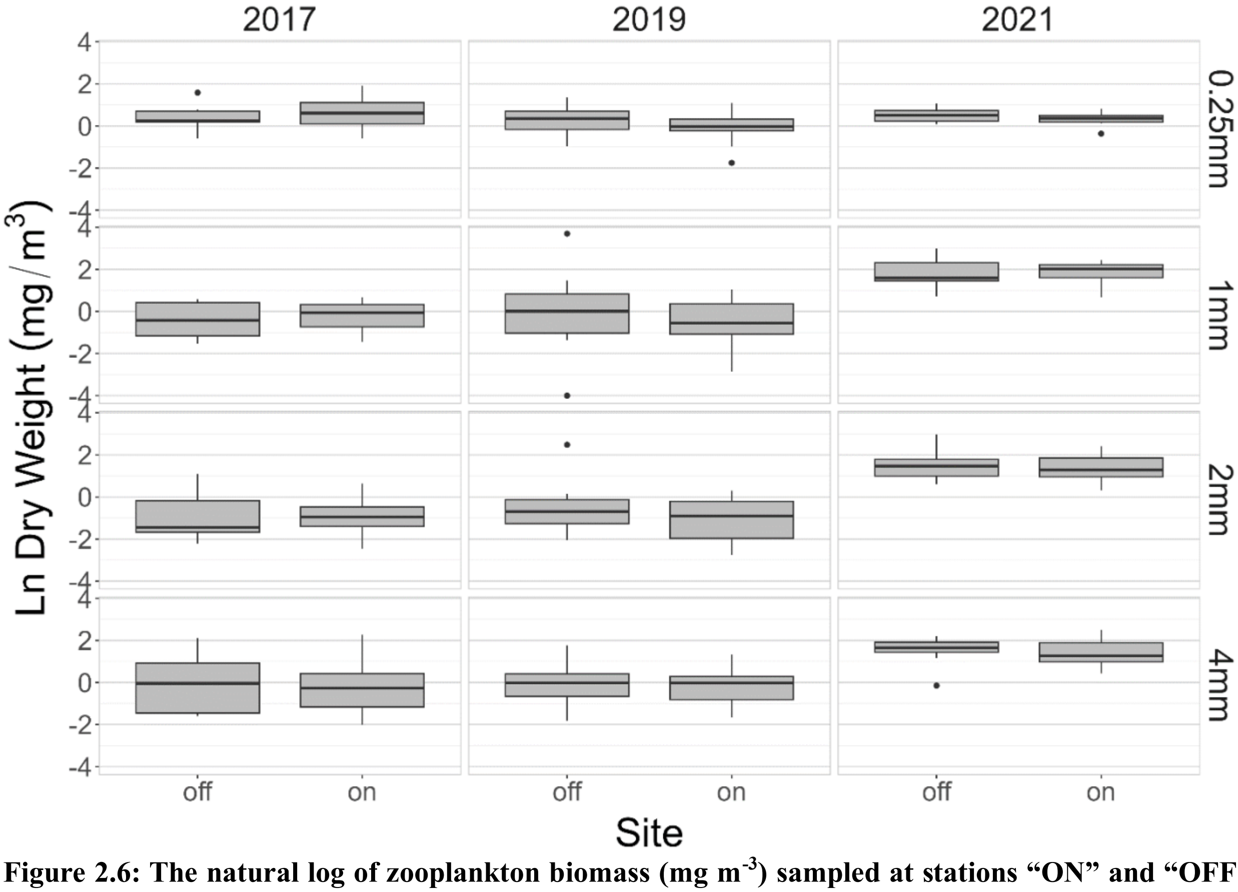


Figure 2.6: The natural log of zooplankton biomass (mg m^{-3}) sampled at stations "ON" and "OFF" seamounts in the Canadian Offshore Pacific Bioregion, subdivided into size fractions (rows) and the years sampled (columns). Black dots represent outliers in the data.

During the 2017 survey at Union Seamount, zooplankton biomass was positively correlated with site latitude. Total zooplankton DW increased with latitude ($p=0.0163$, $R^2 = 0.399$); however, total zooplankton abundance was not correlated with ON/OFF site position at Union Seamount ($p > 0.6$). Total DW ranged from 12.9 mg m^{-3} at the northern-most site decreasing to 1.14 mg m^{-3} in the southern sites (Fig. 2.8). The magnitude of variation in total DW was comparable to observations elsewhere in the region in the same year (NEPDEP 54 Seamount and unpublished data from the Line P and La Perouse monitoring programs).

Zooplankton species richness (# of species) was significantly different between ON and OFF seamount sites at NEPDEP 54 (2017), Explorer (2019), and SKB Seamounts (2015). At NEPDEP 54 Seamount during the 2017 survey, species richness decreased with distance from the summit (p=0.012, R^2=0.63) and ON sites had higher species richness in comparison to OFF sites (75.6 ± 6.04 vs 61 ± 5.33 spp; p=0.029). At Explorer Seamount during the 2019 survey, ON sites had significantly higher species richness than OFF sites (88.8 ± 3.6 vs 77.5 ± 5.1 spp; p=0.003). At SK̲-B Seamount during the 2015 survey, species richness was lower at ON sites than at OFF sites (78 ± 4.6 vs 66.5 ± 6.2 spp; p=0.018).

At poorly-sampled seamounts (≤ 2 sampling locations at each of 5 seamounts), OFF seamount sites frequently appeared to have higher zooplankton biomass and abundance than ON seamount sites, but there were too few sites per seamount to establish statistical significance. At 4 seamounts, the OFF sites had higher total zooplankton DW for most size fractions, while at all 5 seamounts there was a greater total zooplankton abundance at OFF sites. NEPDEP 13 was the only poorly-sampled seamount to have higher total zooplankton DW at the ON seamount site.

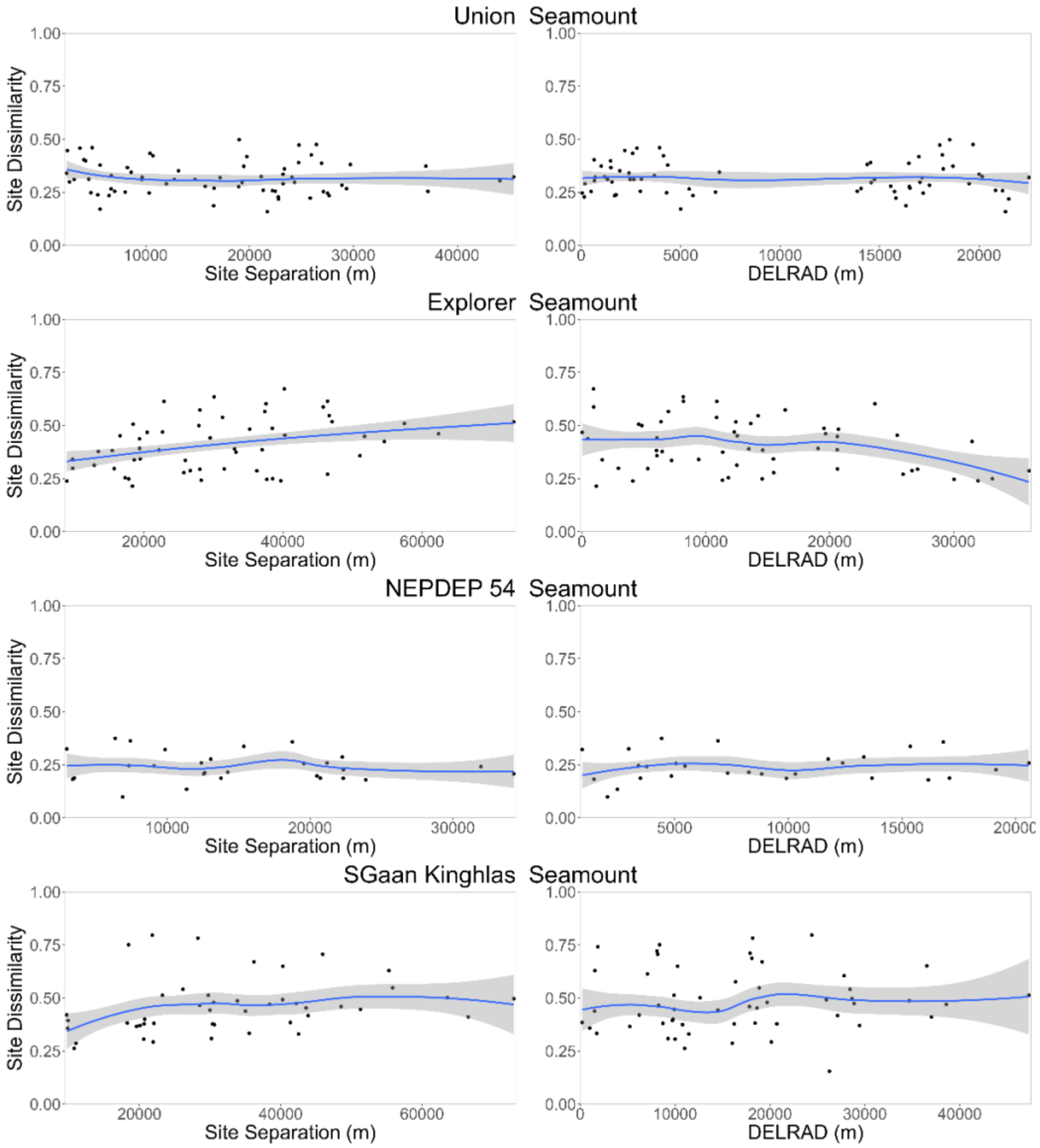


Figure 2.7: Scatterplots with LOWESS regressions (±SE) of between-sample percent dissimilarity in zooplankton community composition as a function of distance between sites (SEP; m) and DELRAD (m) for NEPDEP 54 2017, Explorer, Union and SK̲-B Seamounts.

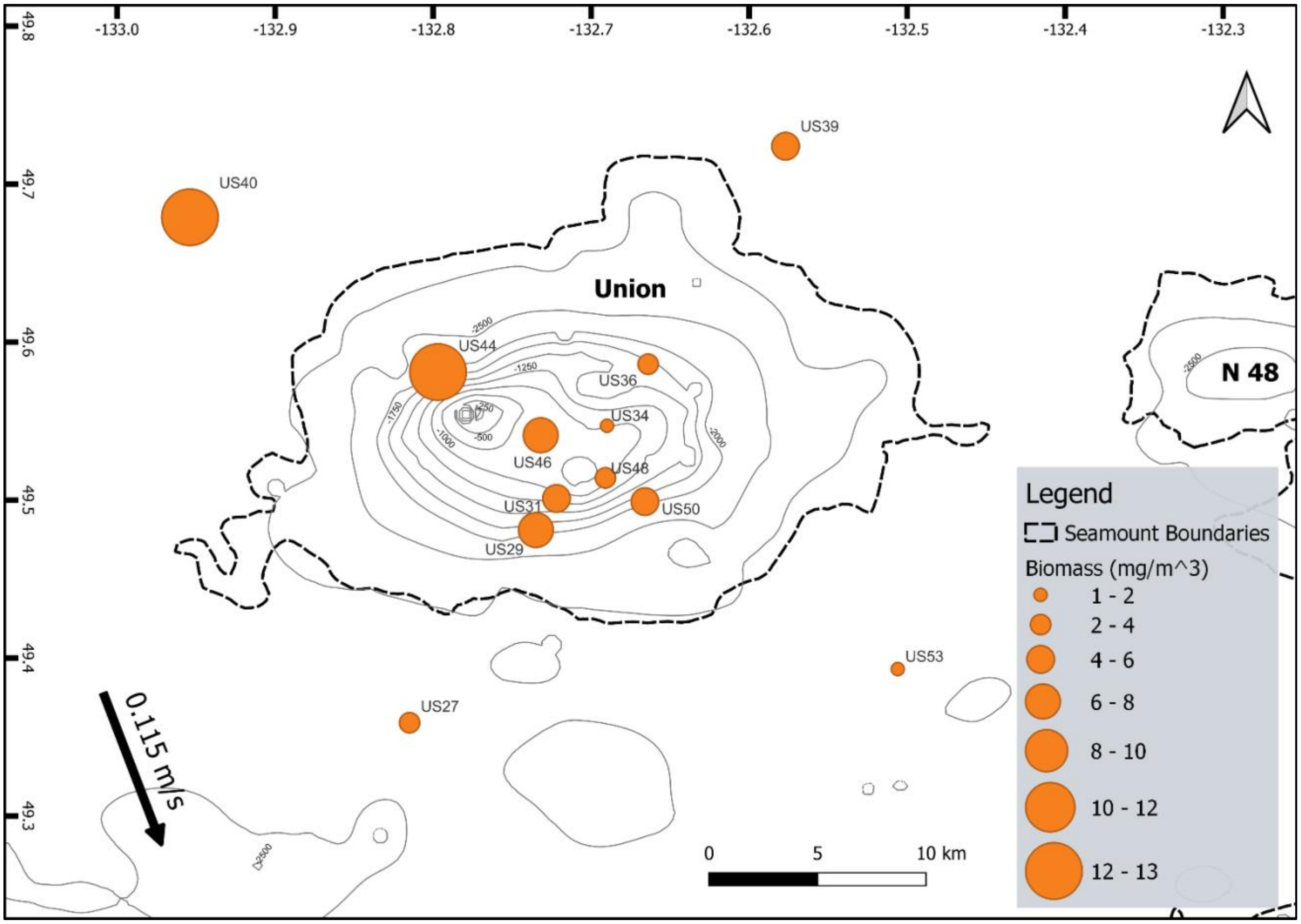


Fig 2.8. Total zooplankton biomass distribution around Union Seamount during the 2017 survey. Site numbers are included, and surface current direction and speed are indicated using an arrow in the bottom left of the map. Seamount boundaries collected from Du Preez and Norgard (2022). The GEBCO (2021) contours (https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2021/) were used were used to delineate demonstrate the topography of the region. Surface current direction and velocity were estimated using data from CMEMS multi-model reanalysis currents from the NE Pacific (NEP; https://doi.org/10.48670/moi-00024).

2.4 Discussion

This study provides the first measurements and analyses of zooplankton community composition, nutritional composition, and energy density from 13 seamounts in the Canadian OPB. Among the seamounts sampled, patterns of spatial variability in zooplankton biomass, abundance, and taxonomic assemblage did not exceed what would be expected from typical levels of mesoscale variability in offshore regions (Star and Mullin 1981; Mackas et al. 2001; and unpublished data from Line P and La Perouse monitoring programs). Putative "seamount effects" on species richness were detected at SK̲-B, Explorer, and NEPDEP 54 Seamounts. Confirmation of other such effects would require further investigation due to the low sample size (*i.e.*, resulting in weak statistical power), such as with the comparison of ON/OFF sites at poorly-sampled seamounts and the high Chl-a measured at Union Seamount in 2017. In addition, although zooplankton community and ED values did differ between some seamounts, this was also more likely due to background spatial variability than from seamount effects, *per se*.

2.4.1 Seamount effects on zooplankton distribution

The results of this study did not indicate the existence of any definitive seamount effects on zooplankton distribution at the time of sampling. Spatial variability of zooplankton sampled around OPB seamounts was within the bounds of expected zooplankton variability at this scale (Mackas et al., 2001; Mackas and Beaugrand, 2010; Noyon et al., 2020). The variability and patchiness of the OPB samples therefore indicate little potential for significant seamounts effects on zooplankton in the OPB.

Zooplankton species richness

Three of the four well-sampled seamounts displayed ON/OFF differences in species richness. At NEPDEP 54 and Explorer Seamounts there was higher species richness above the seamount, while at SK̲-B Seamount we observe the inverse with species richness being higher in the surrounding ocean. Although one might expect an increased richness above seamounts due to stronger larval contribution from resident benthic species (Schlacher et al., 2010; Crochelet et al., 2020), an increase in larval organisms was not observed above NEPDEP 54 and Explorer Seamounts. At SK̲-B Seamount, the observed reduction in species richness may have been from the displacement/enhanced patchiness of species near the summit (Chen et al., 2021), however it was more likely the result of low sample size and high mesoscale variability/patchiness of zooplankton species in the region.

Lack of strong evidence for zooplankton topographical interactions at Canadian Offshore Pacific Bioregion seamounts

Of the seamounts included in this research (Table 2.1), three (SK̲-B, Union, and NEPDEP 54) had summits that lie within the expected depth range to directly interact with vertically migrating zooplankton (Genin, 2004). Bottom trapping at these seamounts would be evidenced by (i) a reduced zooplankton biomass and (ii) a disproportionate decrease in the biomass of vertical migrators. Past studies have observed reduced zooplankton biomass above abrupt topographical features of similar depths (Martin and Nellen, 2004; Martin and Christiansen, 2009; Christiansen et al., 2009; Hirch and Christiansen, 2010; Aarflot et al., 2019), however, there was no evidence of this occurring at SK̲-B or NEPDEP 54 Seamounts in this study. The NEPDEP 54 and SK̲-B Seamount summits are both outside the depths where we would predict effective bottom trapping, thereby limiting the expected effects on zooplankton biomass. Bottom trapping is expected to be optimal near the lower boundary of the euphotic zone (200 m in the OPB; (Genin, 2004; Du Preez and Norgard, 2022). NEPDEP 54 Seamount (summit = 535 m) would therefore only impact the deepest vertical migrators, while SK̲-B Seamount (summit 24 m) may be too shallow for migrators which, in turn, may be displaced horizontally along the slope at night (Genin, 2004).

Samples collected at Union Seamount demonstrated a decline of zooplankton biomass with a decrease in latitude (upstream to downstream) during the 2017 survey (Fig. 2.8). Although this could indicate increased predation of zooplankton at depth by bentho-pelagic fish over the Union Seamount (DFO, 2019), this seems unlikely as we did not see differences in the relative abundance of vertically migratory and non-migratory zooplankton species. More likely, this change results from natural variability in zooplankton biomass, as similar biomass variability has previously been measured along transects of other monitoring programs within the NE Pacific (Mackas et al. (2001) and unpublished data from the Line P and La Perouse monitoring programs).

SG̲áan K̲ínghlas-Bowie Seamount

Although no substantial seamount effects were detected at SK̲-B Seamount in the present study this seamount still warrants additional investigation. SK̲-B Seamount is the shallowest and one of the largest seamounts within the OPB, and therefore most likely to exhibit biologically significant seamount effects (Clark et al., 2011; Du Preez and Norgard, 2022). Previous research has found that mesoscale Haida eddies occasionally stall near SK̲-B Seamount for several months, suggesting that SK̲-B may trap or slow the advection of passing eddies (Mackas and Galbraith, 2002b; Canessa et al., 2003). Eddies themselves have been found to create mesopelagic hotspots and the accumulation of zooplankton communities (Saito et al., 2014; Wang et al., 2023). In addition, eddies within this region have been shown to advect coastal zooplankton species off the continental shelf, past SK̲-B Seamount, before continuing into the open North

Pacific (Mackas and Galbraith, 2002b). This represents a plausible source of the coastal zooplankton species observed above SK̲-B Seamount in this study. SK̲-B Seamount would be a potential candidate for future research on the connectivity between seamounts and coastal ecosystems, and the ability of seamounts to act as a refugia for advected species during future and past climate perturbations (Hubbs, 1959; Rowden et al., 2010).

Between-sample taxonomic dissimilarity of zooplankton in the Canadian Offshore Pacific Bioregion

Sample-to-sample dissimilarity was used to investigate variations in zooplankton taxonomic composition. No seamount effects were found to disrupt the increase of dissimilarity among samples beyond that expected from simple geographic separation. Overall, the measured dissimilarity values had a larger range (~10 to 70%) but comparable mean (~40%) as those reported elsewhere (Haury, 1976; Star and Mullin, 1981; Dower and Mackas, 1996). The large range of sample-to-sample dissimilarity may have been due to the differences in seamount size. Larger seamounts (greater distance between sites) had higher mean between-sample dissimilarity in comparison to smaller seamounts (Fig. 2.7). The lack of increasing dissimilarity with sample-to-sample separation at any given seamount could have been an indication of relatively low sample size or of sampling sites being too sparse. Dower and Mackas (1996) found a marginal decrease in similarity with a total of 28 sites at Cobb Seamount, whereas in this study no more than 16 sites at any given seamount (Table 2.1).

2.4.2 Seamount effects on primary productivity and water properties

Among the 13 seamounts sampled during this program, the water column surrounding Union Seamount had the highest concentration of Chl-a at every depth sampled but this was not statistically significant. Although it is plausible that localized up-welling led to enhanced phytoplankton biomass, as of yet there is no strong evidence of this occurring at Union Seamount or other OPB seamounts. Persistent locally enhanced phytoplankton abundance (usually inferred via high [Chl-a]) has been observed at Cobb Seamount (summit 25 m; NE Pacific), Kocebu Seamount (summit 1198 m; West Pacific), and various other seamounts of varying depths (Dower et al., 1992; Dai et al., 2022; Leitner et al., 2020). However, additional sampling will be required to determine whether any OPB seamounts locally enhance phytoplankton biomass. All other oceanographic conditions were within the expected ranges for this area and time of year; therefore, the data reported in this study indicated no widespread biologically significant seamount effects on the surrounding water column.

2.4.3 Methodological limitations in the identification of seamount effects

Indications of seamount effects include the locally enhanced [Chl-a] or inorganic nutrients (NO_{-2} and NO_{-3}) that remains persistent near seamount summits (Leitner et al., 2020), the lifting/doming of isopycnals (*i.e.*, cold domes) over the seamount summit can indicate the formation of Taylor cones (Brechner Owens and Hogg, 1980; White et al., 2007), and the disruption or interaction of shallow and deep back scattering layers can indicate ecosystem coupling or bottom trapping (Isaacs and Schwartzlose, 1965; Fock et al., 2002).

Although no conclusive seamount effects were identified in this study, it remains possible that seamounts may influence physical and biological processes in the OPB since seamount effects are often relatively ephemeral (Genin and Boehlert, 1985; Leitner et al., 2020). The short-lived nature of these effects would only be more variable and likely shorter in the Canadian OPB, because it is situated within the bifurcation of the North Pacific current, which gradually shifts across multiple months, resulting in annual difference in bifurcation latitude (Batten and Freeland, 2007; DFO, 2019). This region is also characterized by weak and variable mesoscale currents, meaning it is unlikely these seamounts experience consistent impinging flow, therefore limiting Taylor cone/cap formation or other features which result from similarly consistent flow regimes (DFO, 2019; Guo et al., 2020; Perfect et al., 2020). In the future, a broader perspective on the occurrence of seamount effects in the region could be gained via the use of remote sensing of primary productivity, acoustic moorings (*e.g.*, equipped with current meters or Acoustic Doppler Current Profilers) or autonomous gliders to provide spatiotemporal coverage not possible with infrequent ship-based observations (Zhang et al., 2021; Leitner et al., 2020; Freeland and Cummins, 2005).

2.4.4 Regional differences within the Canadian Offshore Pacific Bioregion zooplankton community

Differences in zooplankton taxonomic composition between seamounts were likely caused by regional variability and proximity to the continental slope, with species identified being typical of the summer conditions in the NE Pacific (Batten and Freeland, 2007; Mackas and Galbraith, 2002a). Pata et al. (2022) defined two distinct zooplankton bioregions in the Canadian OPB (*i.e.*, offshore and deep shelf), the offshore zooplankton bioregion being characterized by low species abundance and high diversity, and the deep shelf bioregion having higher overall abundance but lower diversity. The zooplankton assemblages sampled in 2017 near Union Seamount exemplified many features of Pata et al.'s (2022) offshore bioregion while those near NEPDEP 54 Seamount were more similar to Pata's deep shelf bioregion. Near Union Seamount there were relatively low abundances but more diverse zooplankton taxonomic composition -

and with a relatively larger proportion of doliolids than in samples collected near NEPDEP 54 Seamount. Samples from NEPDEP 54 Seamount were dominated by very abundant small copepods and very few doliolids. While this difference in taxonomic composition could be attributed to distances between seamounts and their relative proximity to the continental slope (*i.e.*, Union Seamount is 128 km west of the slope whereas NEPDEP 54 Seamount is situated on the slope), it could also have been due to background zooplankton mesoscale variability in this region (Kaiser and Williams, 2011).

The zooplankton near Union and Endeavour Seamounts were less energy dense than those from other seamounts sampled during the same surveys. This lower ED was likely due to the higher proportion of gelatinous species (specifically doliolids) that occurred at these two seamounts, since gelatinous species tend to be less energy dense than copepods and other arthropods (Hays et al., 2018; Lüskow et al., 2021). Since total zooplankton biomass was not significantly different at these seamounts, the lower ED equated to less absolute energy (Joules) of zooplankton available for zooplanktivorous predators.

Differences in the taxonomic composition of zooplankton near OPB seamounts did not mirror differences in bulk zooplankton TL or TP content. Zooplankton TL content was not statistically different between seamounts within any given survey, but was (on average) twice as high during the 2021 survey compared to other surveys. In contrast, TP remained consistent across zooplankton sampled at most seamounts and all surveys with an average of 6.9 ±1.06 % of total dry weight. It should be noted that these TP values were lower than many of those reported the existing literature (~20 – 30 %; Harmelin-Vivien et al. 2019; Lobus et al. 2020; Martínez et al. 2020; Zaguri et al. 2021), therefore caution is advised for between-study comparisons (Further discussed in section 3.4.2). Although there were no statistically significant differences in zooplankton TP content between zooplankton collected at different seamounts, visualization of the data (Fig. 2.3) hints at lower TP levels in zooplankton at NEPDEP 54 Seamount during the 2021 survey. Lack of statistical power between TP content in some regions was a result of an overall low number of TP samples.

Past research has found allochthonous prey (*e.g.*, plankton) to be the main energy input to most seamount ecosystems (Denda et al., 2017), and some studies have used ED and/or quantity of TL and TP to determine prey "quality" (Wang and Jeffs, 2014; Schaafsma et al., 2018; Weil et al., 2020). However, no single metric has been proven to be of paramount importance to the diet of the consumers, although lipids and proteins do provide specific compounds that cannot be substituted – as many predators lack the ability to synthesize lipids and proteins *de novo* (Dalsgaard et al., 2003; Teles et al. 2020). Therefore, the present data suggest that interannual variability is likely to cause the largest impact on the supply of allochthonous food quality to OPB seamount ecosystems in comparison to the more subtle changes observed in prey ED.

2.4.5 Implications for conservation and monitoring of Tang.G̱wan- ḥačxʷiqak- Tsig̱is Marine Protected Area

The absence of any demonstrable "seamount effects" on zooplankton detected during this study suggests that future monitoring of the TḥT MPA need not be seamount-specific in design. Regional sampling may therefore provide an adequate representation of the interannual variability in offshore OPB zooplankton biomass, community, and nutritional content available to seamount ecosystems. Distinct differences in zooplankton taxonomic composition were observed between offshore and deep shelf bioregions and should therefore be considered when selecting future monitoring site locations in the OPB, (*i.e.*, since the two regions would have different baseline expectations). Otherwise, there was no evidence that spatial factors significantly change zooplankton assemblages, beyond normal levels of variability in the TḥT MPA. Knowing this, other long-term monitoring programs undertaken by DFO can therefore be used to form seasonal and annual timelines of protein, lipid, and energy supply to OPB seamounts. For example, the longstanding "Line P" monitoring program (which samples from the Strait of Juan de Fuca to Ocean Station Papa in the open NE Pacific three times per year) includes two stations within the TḥT MPA which would be good regional representations of the offshore bioregion. Similarly, the twice-yearly "La Perouse" program covers much of region off the west coast of Vancouver Island adjacent to the Canadian OPB. The western-most stations of La Perouse are near the eastern edge of the TḥT MPA and NEPDEP 57 Seamount, which could potentially provide a good representation of the deep shelf bioregion (Pata et al., 2022). The zooplankton data collected from these monitoring programs are synthesized into annual reports and made publicly available as a part of the State of the Pacific Ocean reports (SOPO; https://www.dfo-mpo.gc.ca/oceans/publications/index-eng.html#state-ocean).

To accurately translate changes of zooplankton quantity (*i.e.*, biomass and abundance) and quality (*i.e.*, TL, TP, and ED) in the overlaying water column into energy that is potentially transferred to organisms that reside on OPB seamounts, food web connections between zooplankton and animals that live above and on seamounts must be established. Stable isotopes ($\delta^{15}N$, $\delta^{13}C$), fatty acids, and gut content analysis can all be used to investigate these connections between zooplankton and nektonic/benthic predators, similar to Hirch and Christiansen (2010). Both stable isotopes and fatty acids are acquired through a predator's diet and incorporated predictably into body tissue, allowing the determination of food sources (Lee et al. 1971; Post et al. 2004). These analyses have been used to investigate pelagic-benthic trophic connections (Parzanini et al., 2019), and are further discussed in section 4.1. Once food web connections have been established, a trophic transfer efficiency (TTE) can be determined to contribute to the creation of a regional food-web model, which can be used to address the question of energy flux to seamounts from allochthonous prey sources.

Canadian OPB seamounts host large aggregations of benthic species (*e.g.*, brittle stars, cold water corals) which most likely receive nutrients and energy from advected zooplankton either directly, or through falling carcasses or fecal pellets, which make up a portion of marine snow (Turner, 2002; DFO, 2019). To quantify the nutritional quality of particles which reach the benthos, settling plates could be used to determine the rate and quantity at which marine snow accumulates in the benthos while sediment traps can be used to gather the material for laboratory analysis of energy and macromolecule content. In addition, vertically stratified net sampling or *in-situ* optical sensors could help determine the vertical extent of zooplankton and marine snow into the mesopelagic and benthopelagic environments above Canadian OPB seamounts (Picheral et al., 2021), all of which would require continuing annual oceanographic sampling expeditions to the region.

2.4.6 Conclusion

This study concludes that zooplankton distribution in the Canadian OPB was not significantly influenced by seamounts during the time of sampling and that, instead, zooplankton variability was most likely driven by other mesoscale processes. Longer-term observations would be needed to conclusively determine the energy input to Canadian OPB seamount from advected zooplankton. This could conceivably be accomplished remotely via autonomous gliders and/or moorings with acoustics capabilities (Burd and Thomson, 2019; Howatt et al., 2022). Such deployments could be used to more definitively determine the variability in zooplankton distributions in the Canadian OPB.

Overall, zooplankton ED, TL, and TP content were not broadly spatiotemporally correlated in this study. Zooplankton ED displayed significant spatial variability during surveys but was not significantly different between surveys. On the other hand, the TL content of zooplankton changed significantly between surveys but there was little spatial variability during any given survey. The results in this study indicate that the most substantial change in nutritional composition during this study resulted from the large amount of lipids in "cool" SST zooplankton assemblages, thereby likely making zooplanktonic prey during these years more nutritious for predators. The degree to which (or even whether) this affects the energy flux to seamount benthic communities is currently unknown.

This study provides important baseline information and insight regarding Canadian OPB zooplankton, which can be used to effectively monitor offshore MPAs in the region. In addition, multiple avenues of future research are provided to better understand the energy flow from zooplankton to seamounts in the Canadian OPB. In conclusion, this study demonstrates the high degree of variability in the NE Pacific zooplankton community and highlights the variability of allochthonous prey quantity and quality being provided to seamounts in the Canadian OPB.

Chapter 3: Using bongo nets to quantify size fractionated zooplankton nutritional quality in the Canadian Offshore Pacific Bioregion

3.1 Introduction

Zooplankton are a major food source to many pelagic animals, being a key link from primary producers to consumers, and therefore a common indicator of energy availability to higher trophic levels (Brodeur, 1989; Dunham and Duffus, 2001; Hertz et al., 2016; Miller et al., 2019; Hipfner et al., 2020). Oceanographic sampling programs typically prioritize estimating zooplankton biomass and/or species abundances, as it is a straightforward process that is the baseline measurement for most analyses (Postel et al., 2000). Although prey quantity (*i.e.*, biomass/abundance) is a good indicator of energy available to higher trophic levels, prey quality also has significant influence on energy availability to consumers, as well as their growth, maintenance, and survival (Rainuzzo et al., 1997; Dessier et al., 2018; Teles et al., 2020). Therefore, many sampling programs could be overlooking this aspect of spatiotemporal variability of zooplankton communities, which may have significant impact on the health and survival of zooplanktivorous species.

Due largely to logistical constraints imposed by the high cost of ship-time, researchers usually collect only one (at most a few) zooplankton samples per station. Therefore, there is large incentive to learn as much as possible from each sample collected. With the proper procedures, researchers can utilize biomass samples to perform multiple analyses which allow a more complete understanding of the spatiotemporal variability of zooplankton as an energy source for higher trophic levels.

3.1.1 Methods for estimating zooplankton biomass using bongo nets

One of the nets commonly used by oceanographers to sample zooplankton is a side-by-side paired setup, colloquially referred to as a "bongo net" (Posgay and Marak, 1980; Sameoto et al., 2000; Wiebe and Benfield, 2003). Bongo nets (bongos, hereafter) are particularly useful because they provide the simultaneous collection of two replicate samples, and are a routine sampling tool used by international and Canadian monitoring programs (Mackas et al. 2004; Mackas and Beaugrand 2010; https://www.dfo-mpo.gc.ca/science/oceanography-oceanographie/activities/index-eng.html). Although no single net type can accurately sample the whole range of mesozooplankton, mesh-, mouth size, and towing method can be used to target specific groups. For example, using a relatively coarse mesh size (*i.e.*, 0.333 vs 0.253 mm) and fast towing (*i.e.*, 3.5 vs 1.5 knots) will improve catches of large, mobile animals like krill, but will also miss and extrude smaller animals such as larval stages of copepods (Colton Jr et al., 1980; Skjoldal et al., 2013). Bongos are best suited to sample mesozooplankton within the 0.2 - 20mm size-range (Sieburth et al., 1978; Harris et al., 2000).

Standard practices for DFO monitoring on the west coast of Canada has been to fix contents from one side of the bongos for taxonomic analysis while the contents of the other side are frozen for biomass measurement. Buffered formalin is used to fix organisms with minimal morphological deformation until animals can be identified under a microscope (Thavarajah et al., 2012). In some cases, samples are instead preserved in 95% ethanol to protect fragile carbonate structures (*e.g.*, larval fish otoliths and pteropods) or for molecular analyses. Preserved zooplankton samples are also often used to calculate total zooplankton biomass using pre-determined length-weight relationships (Mackas, 1992; Runge and Roff, 2000). The frozen contents of the other half of the bongo net are often dried and weighed for direct biomass determination (Mackas, 1992; Postel et al., 2000). Wet weight, biovolume, and ash-free dry weight (AFDW), or elemental equivalents are also used as proxies for zooplankton biomass (Postel et al., 2000; Yebra et al., 2017b). Zooplankton dry weight can be determined with a scale following oven drying or freeze-drying (lyophilization), the latter of which reduces damage to biochemical components of the organisms (Fudge, 1968). Freeze-drying zooplankton samples thus allows for a variety of different analyses used to determine macromolecular composition on zooplankton samples (Postel et al., 2000).

3.1.2 Quantifying the nutritional quality of zooplankton

Energy density (ED), total lipid (TL), and total protein (TP) content can be used to estimate zooplankton nutritional value and the energy available to higher trophic levels. Consumers of zooplankton (*i.e.*, fish, whales, sea birds) have specific dietary energy requirements and ED can indicate how much prey biomass must be consumed to meet a predator's energy requirement (Cruz-Rivera and Hay, 2000). In addition, predators must meet an optimal balance of dietary macromolecules (*i.e.*, proteins and lipids) to maintain body size and support adequate growth, both of which can be strongly associated with survival rates in some fish species (Beamish and Mahnken, 2001). Higher quantities of macromolecules (within the optimal ratio) and increased ED would therefore indicate a more nutritious prey organism because less total prey would have to be consumed in order to meet the same dietary requirements.

ED, TL, and TP can be used separately and in combination to characterize the nutritional quality of zooplankton. For example, ED has frequently been used as a proxy for nutritional quality and often serving as a good energetic currency for quantifying energy flow through ecosystems (Cumminns and Wuycheck, 1971; Schaafsma et al., 2018; Weil et al., 2020). Fatty acid composition and TL content have also been used to indicate nutritional quality (Copeman et al., 2002; Copeman and Laurel, 2010; Taipale et al., 2018; Costalago et al., 2020), in part because lipids are the most energy dense macromolecule and typically used for energy storage, and therefore an efficient long-term energy reserve (Cumminns and Wuycheck, 1971; Beukema, 1997; Postel et al., 2000; Lee et al., 2006). TL is a useful indicator of nutritional quality and also quite variable (5-70% of an organisms dry weight; Kattner and Hagen 1998; Lee et al. 2006; Jo et al. 2017) and therefore warranting increased attention as not all zooplankton communities have similar TL contents. Finally, proteins are often the first macromolecule to be considered in determining fish diet composition for aquaculture (Teles et al., 2020). However, zooplankton TP in natural ecosystems has received less attention, even though they are an important dietary component required for many vital biological processes (Postel et al., 2000; Yebra et al., 2017a; Teles et al., 2020).

3.1.3 Grouping zooplankton by size

The high diversity and complexity of zooplankton assemblages underscores the need to avoid treating them as a functionally homogeneous group. Typically, zooplankton are grouped taxonomically (*e.g.*, doliolids, calanoids, and euphausiids), but this grouping can sometimes miss large differences in ecosystem function. Alternatively, zooplankton can be grouped strictly based on organism size (Harris et al., 2000; Gilljam et al., 2011; Harmelin-Vivien et al., 2019), which can be deferentially affected by environmental changes (Li et al., 2022), potentially leading to bottom-up changes to higher trophic levels (Hébert et al., 2016; Décima, 2022). For this reason, size grouping of zooplankton can be a useful tool in monitoring programs and ecosystem models which incorporate zooplankton standing stock. Understanding the spatiotemporal variability of zooplankton groups (taxonomic and size) is crucial when trying to monitor environmental change effects on ecosystem functions.

Zooplankton size distribution can also provide insight into ecosystem functioning with less time intensive methods than required for taxonomic grouping. Many researchers have investigated the use of normalized biomass size-spectra (NBSS), which is a linear relationship of the relative contribution of each size class to the total zooplankton biomass (Zhou and Huntley, 1997). NBSS has been used to estimate zooplankton productivity, energy flow, and community structure (Zhou, 2006; De Souza et al., 2020). NBSS slopes can be indicative of energy transfer in an ecosystem, whereby a steep slope can indicate a less efficient ecosystem characterized by small-bodied zooplankton and a greater number of trophic levels, and the opposite indicated by shallow slopes (*i.e.,* higher efficiency, larger body size, and fewer trophic levels). NBSS is thus another useful tool for the monitoring of ocean ecosystems.

3.1.4 Research motivation and objectives

The main objective of this chapter was to characterize the nutritional quality of bulk zooplankton samples collected during the DFO Northeast Pacific Deep-sea Exploration Program (NEPDEP) surveys in 2017, 2019, 2021, and 2022 via the quantification of total energy density, lipid content, and protein content. This chapter also explores differences in nutritional content across different zooplankton size classes and estimates the NBSS of zooplankton communities in order to provide insight on zooplankton size-distribution. More specifically, this chapter addresses three questions:

1) In addition to traditional measures of total biomass and abundance/taxonomy. What else can we learn from a single bongo net biomass sample?

2) What is the temporal and spatial variability in zooplankton biomass, taxonomic composition, and nutritional quality in the Canadian OPB?

3) To what extent are patterns of zooplankton taxonomic composition correlated with size fractionated energy content, lipid content, and protein content?

3.2 Methods

3.2.1 Sampling location

Zooplankton samples were collected within Canada's Offshore Pacific Bioregion (OPB) from July 22nd-29th 2017, July 20th-27th 2019, June 18th-26th 2021, and June 18th-24th 2022 during surveys onboard the *CCGS John P. Tully* (DFO-IOS cruises 2017-036, 2019-014, 2021-036, and 2022-035, respectively). The majority of sampling sites were located within the TḥT MPA in the proximity of numerous seamounts (Fig 2.1) and are likely indicative of summer zooplankton communities in the region. These sampling sites lie within the bifurcation of the north Pacific current which is a region of weak but variable currents. The north Pacific current flows eastward before bifurcating into the Alaska current (northward) and California current (southward). The location of the bifurcation streamline varies between years which can influence zooplankton taxonomic composition due to differential contributions from southern and northern communities (Batten and Freeland, 2007). Spatially, the sampling region can be divided into two geographic regions, the continental slope and offshore NE Pacific (Fig. 2.1). The base of the continental slope for this region is inferred at ~2500 m depth, as per Ban et al. 2016, whereby any region deeper is considered offshore. The sampling region can broadly be split into two persistent zooplankton bioregions: offshore and deep shelf (Pata et al. 2022).

3.2.2 Oceanographic sampling and water properties

Details on oceanographic sampling procedures are provided in Section 2.2.2.

3.2.3 Zooplankton sampling

Zooplankton sampling methods are detailed in Section 2.2.3.

During the 2022 survey, zooplankton were sieved using seawater at sea then stored at -80ºC until sample processing. In the lab, samples were thawed and rinsed in 3.35% ammonium formate to avoid the lysis of cells, therefore the correction in Postel et al. (2000) was not used.

3.2.4 Zooplankton biomass determination

Two methods were utilized to estimate zooplankton biomass. Whereas the first method (indirect) used pre-determined species-specific length-weight relationships to calculate biomass, the second method measured size fractionated zooplankton biomass directly. Using length-weight relationships to estimate zooplankton biomass is common practice (*e.g.*, Mackas 1992; Watkins et al. 2011; Rykaczewski 2019; Venello et al. 2021). Briefly, species-specific biomass estimates were summed to determine total bulk dry weight (hereafter, "calculated biomass"). In the direct approach, each size fraction is weighed on a microbalance and summed to estimate bulk dry weight (hereafter, "weighed biomass"). Although, calculated and weighed biomass are commonly assumed to have a near 1:1 relationship, this has yet to be thoroughly examined in the literature.

3.2.5 Zooplankton energy density determination using ash-free dry weight

Procedures for ash-free dry weight (AFDW) and energy density (ED) are detailed in Section 2.2.4.

3.2.6 Lipid and protein quantification

Procedures for total lipid (TL) and total protein (TP) are detailed in Section 2.2.5.

3.2.7 Normalized biomass size-spectra approximation

Procedures for normalized biomass size-spectra (NBSS) are detailed in Section 2.2.6.

3.2.8 Statistical analysis

All statistical analysis was completed in RStudio (Posit), using R version 4.1.3 (R core team 2022). When assumptions for normality and homoscedasticity were met, ANOVA with post-hoc HSD tests ($\alpha = 0.95$) were used to compare biomass, abundance, NBSS, richness, diversity (Shannon-Wiener Index - SWI), ED, TL, and TP between different surveys. T-tests were used to compare offshore and slope sites, and night and day tow. When data could not meet assumptions and could not be transformed to fit the assumptions, the non-parametric Kruskal-Wallace test with a Pairwise Wilcox Post-hoc test was used, as it is more robust to deviations from normality and heteroscedasticity.

All multivariate and taxonomic composition analysis was completed using the *vegan* package (version 2.6-4; Oksanen et al. 2022). The variation of taxonomic composition among zooplankton samples was visualized and compared using an NMDS plot, where distance between points represents between site dissimilarity. Ellipsoids with a 95% confidence were fitted on the NMDS for year and regional groupings, and PERMANOVA tests were performed to determine significant differences between these groupings. Additionally, ANOSIM tests were performed to determine whether between grouping variability was greater than within grouping variability. A SIMPER test was preformed when significant differences ($p < 0.05$) were detected between sites to determine which taxonomic groups drove the dissimilarity between groups.

Spearman rank correlations were calculated using the *corrplot* package (version 0.92; Wei et al. 2021) and used to determine statistical significance of monotonic correlations between zooplankton taxonomic composition and zooplankton community features for each size fraction (biomass, abundance, NBSS, ED, lipid content, protein content). Significant correlations were then investigated using linear regressions.

3.3 Results

3.3.1 Interannual variability in water properties

Water properties measured during the surveys are summarized in Table 3.1. One notable difference was that mixed layer temperatures (MLT) during the 2021 and 2022 surveys were 2-3ºC cooler than MLTs measured during the 2017 and 2019 surveys.

Table 3.1: Summary of water column properties to a depth of 250m across the four sampling years. CTD profiles and water sampling was completed to compliment zooplankton net tows at each site when possible. All values are means calculated from all stations ± standard error.

	2017	**2019**	**2021**	**2022**
Mixed Layer Depth (m)	20.73 ± 1.62	25.2 ± 1.36	28.73 ± 5.08	25 ± 6.40
Chlorophyll Max Depth (m)	22.03 ± 1.24	39.11 ± 1.99	45.61 ± 5.30	28.34 ± 2.28
Chlorophyll 5m (mg m^{-3})	0.51 ± 0.065	0.18 0.008	-	-
Chlorophyll 10m (mg m^{-3})	0.61 ± 0.11	-	-	-
Chlorophyll 20m (mg m^{-3})	1.22 ± 0.17	0.25 ± 0.025	-	-
Chlorophyll 50m (mg m^{-3})	-	0.42 ± 0.030	-	-
Nitrate + Nitrite (µmol L^{-1})	26.15 ± 0.45	32.08 ± 0.78	39.08 ± 0.63	35.54 ± 1.35
Mean temp (°C)	7.99 ± 0.094	8.65 ± 0.079	7.65 ± 0.12	6.96 ± 0.26
Mixed Layer temp (°C)	14.30 ± 0.14	15.40 ± 0.20	12.27 ± 0.29	10.99 ± 0.45
Mean Oxygen (mL L^{-1})	4.49 ± 0.075	4.61 ± 0.097	4.67 ± 0.10	4.55 ± 0.12
Mixed Layer Oxygen (mL L^{-1})	6.29 ± 0.041	6.05 ± 0.030	6.38 ± 0.031	6.99 ± 0.28
Mean Salinity (PSS-78)	33.21 ± 0.018	33.16 ± 0.017	33.10 ± 0.025	33.11 ± 0.024
Mixed Layer Salinity (PSS-78)	31.91 ± 0.10	32.27 ± 0.017	32.07 ± 0.046	31.66 ± 0.51

3.3.2 Spatiotemporal variability of zooplankton taxonomic composition in the Canadian Offshore Pacific Bioregion

Zooplankton taxonomic composition was significantly different between surveys (Fig. 3.1 & 3.2; PERMANOVA $p = 0.0026$). In general, between survey variation was greater than within survey ($p = 0.015$), but the dissimilarity between groups was only marginally higher than within groups (ANOSIM stat = 0.08). All species identified as drivers of interannual variability by the SIMPER analysis and their relative abundances have been summarized in Table 3.2. The largest difference in composition was observed between the 2019 and 2021 surveys ($p < 0.001$, ANOSIM stat = 0.59), which had the most species contributing to >1% of between-sample dissimilarity (13 species). In comparison, between 2017 and 2019 surveys the taxonomic compositions were not as dissimilar (ANOSIM stat = 0.47), but still statistically different ($p < 0.001$), and had 9 species driving >1% of the dissimilarity. Finally, the taxonomic composition of the 2021 and 2022 surveys were not significantly different ($p = 0.17$). There were no significant day/night differences in zooplankton abundance and taxonomic composition, therefore time of day was not factored into any subsequent analyses.

Zooplankton taxonomic composition was also different between continental slope and offshore sites during both 2017 and 2021 surveys (Fig. 3.1 & 3.2). During the 2017 survey ($p = 0.024$, ANOSIM stat = 0.19), the primary driver of dissimilarity between slope and offshore sites was *Pseudocalanus* spp. (12%), which were more abundant at slope sites. In addition, offshore sites had significantly higher diversity than slope sites (2.4 ± 0.04 vs 2.1 ± 0.02 Shannon Wiener Index, p <0.001) and significantly lower species richness (66.1 ± 1.1 vs 70.1 ± 1.6 species, p <0.001). During the 2021 survey, there were minor differences in zooplankton taxonomic composition between regions (p = 0.058, ANOSIM stat = 0.22, PERMANOVA p = 0.017). Differences were driven by a higher relative abundance of *Neocalanus cristatus* (4%), *Oithona setigera* (2%), and *Eukrohnia hamata* (1%) at offshore sites in comparison to continental slope sites. In addition, offshore sites had a lower species richness compared to slope sites (67.2 ± 0.94 vs 72.2 ± 1.5 species, p = 0.03).

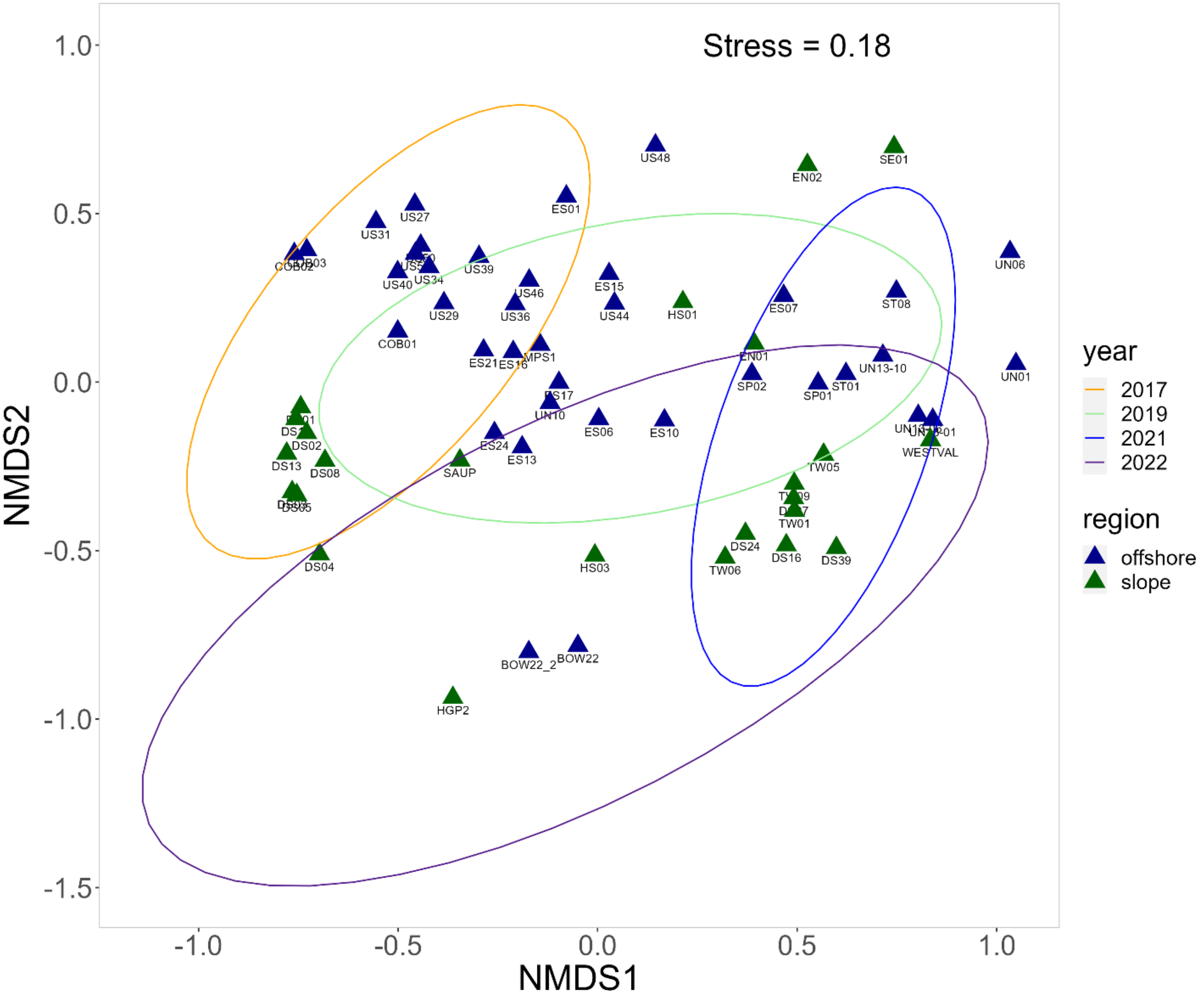


Figure 3.1: NMDS ordination of zooplankton species composition data from sites collected across 4 years in the Canadian Offshore Pacific Bioregion. Sampling years are grouped with ellipses (95% confidence level).

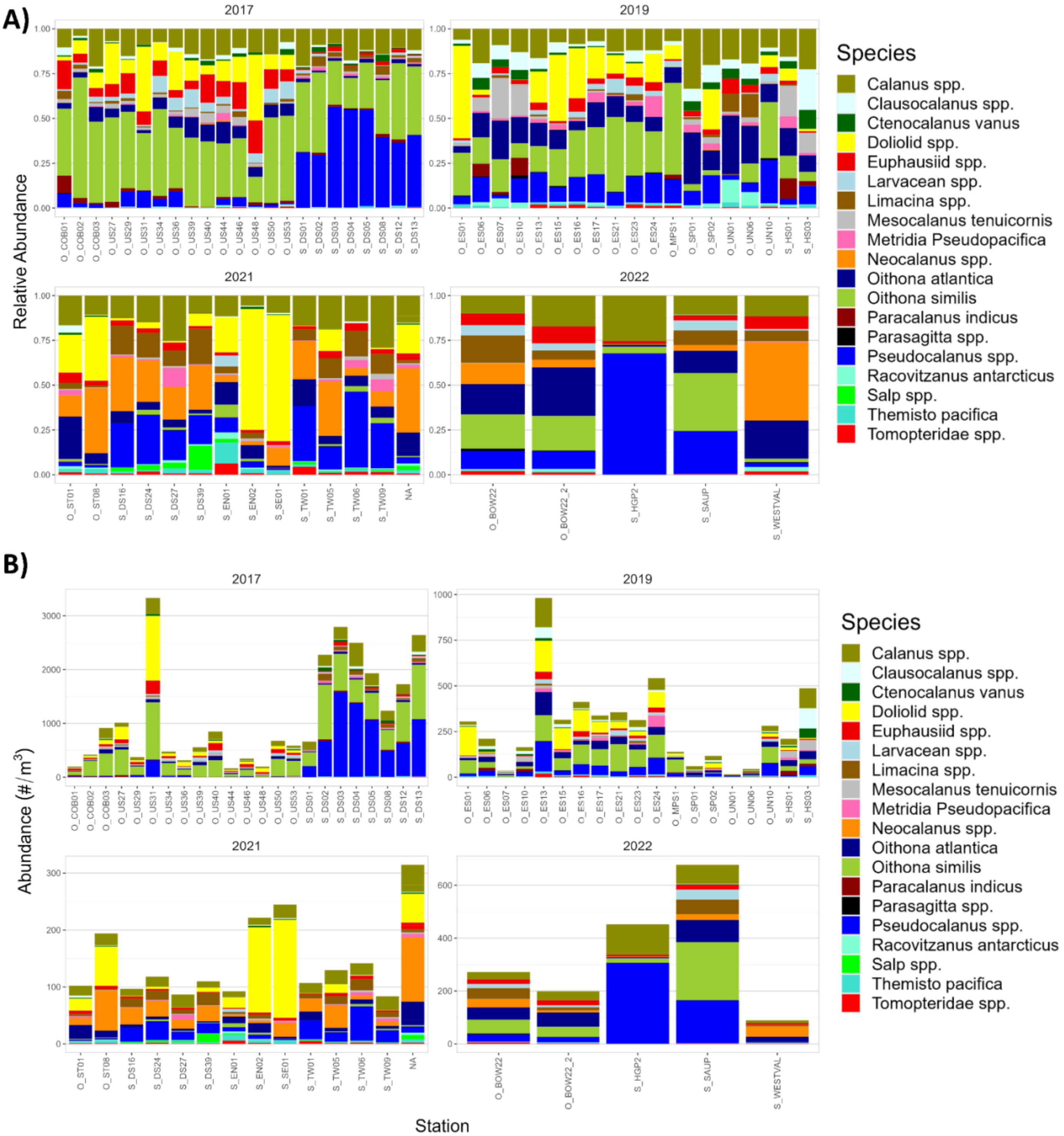


Figure 3.2: The (A) relative and (B) absolute abundance (# m^{-3}) of numerically dominant species and taxa at each station. Ecologically significant taxa which were present in very low quantities (<5% at all sites) were excluded. Complete abundance graphs are provided in Appendix 6 (Phyla), 7 (Arthropod orders), and 8 (Calanoid and Cyclopoid families). Stations are organized along the x-axis from offshore to slope sites, where station names preceded by O were offshore and by S were on the continental slope. Note the difference in the y-axis scales between (B) graphs.

Table 3.2: Summary table of species with significant ($p < 0.05$) contributions to dissimilarity between years, as calculated using SIMPER analysis in the *vegan* R package (version 2.6-4). ANOSIM (p = 0.015) and PERMANOVA (p=0.0026) analysis indicates significant differences in taxonomic composition between years, but there were similar amounts of variation within years as observed between years (ANOSIM Stat = 0.08). Species with less than 1% contribution to dissimilarity were excluded.

	Dissimilarity Contribution (%)	Relative abundance (%)	
		2017	**2019**
Oithona similis	10.6	34.4	15.7
Oithona atlantica	3.1	3.8	9.4
Heteropoda sp.	2.8	0.008	5.6
Euphausiidae sp.	2.4	5.7	1.4
Mesocalanus tenuicornis	2.0	1.5	4.1
Metridia sp.	1.8	4.1	4.7
Eucalanus sp.	1.5	3.3	0.93
Paracalanus indicus	1.1	1.3	1.6
Ctenocalanus vanus	1.0	1.2	2.5
		2019	**2021**
Doliolid sp.	6.26	8.2	12.0
Neocalanus plumchrus	5.6	0.01	11.3
Neocalanus cristatus	3.3	0.15	6.8
Oithona atlantica	3.0	9.4	4.0
Heteropoda sp.	2.8	5.6	0
Limacina helicina	2.8	0.96	6.1
Dolioletta gegenbauri form tritonis	2.3	2.8	3.1
Metridia pacifica	2.2	1.6	5.0
Mesocalanus tenuicornis	1.9	4.1	0.80
Oithona setigera	1.3	1.3	3.2
Ctenocalanus vanus	1.1	2.5	0.35
Metridia aff lucens	1.1	2.0	1.8
Calanus pacificus	1.0	0.88	2.3
		2021	**2022**
Pseudocalanus mimus	8.9	11.0	19.2
Globigerinidae sp.	5.8	0	11.7
Neocalanus plumchrus	5.3	11.3	7.1
Neocalanus cristatus	2.9	6.8	2.4
Acartia longiremis	2.0	1.4	4.8

3.3.3 Zooplankton biomass, abundance, and size distribution in the Canadian Offshore Pacific Bioregion

The calculated (*i.e.,* indirect) and weighed (*i.e.,* direct) biomass methods demonstrated a positive linear correlation between DW values ($R^2 = 0.53$; Fig. 3.3), although the calculated DW typically estimated greater zooplankton biomass relative to the weighed DW (slope = 0.28). Henceforth when discussing zooplankton DW or biomass the weighed values will be used, unless otherwise indicated.

Size fractionated zooplankton DW and total zooplankton abundance were significantly different between surveys (Fig. 3.4), although this was not consistent across every size fraction (Fig. 3.5), the exception being the smallest size fraction DW (0.25 – 1 mm) which was not statistically different between surveys ($p = 0.23$). Zooplankton in the other size fractions (1-2, 2-4, and >4 mm) tended to have similar DW during the 2017 and 2019 surveys, but significantly higher DW during the 2021 and 2022 surveys. Total zooplankton abundance was significantly different between surveys, whereby zooplankton abundance was highest during the 2017 survey and lowest during the 2021 survey, with intermediate levels during the 2019 and 2022 surveys.

The mean NBSS slope and rank order of size fractions changed between surveys (Table 3.3. and Fig. 3.4). The NBSS slopes trended upwards from -1.34 ± 0.43 during the 2017 survey to -0.64 ± 0.19 during the 2021 survey ($p < 0.001$), before declining to a moderate value of -1.08 ± 0.72 during the 2022 survey, which was not statistically different from any other survey ($p > 0.05$). The rank order of size fractionated zooplankton DW was inverted between the 2017 and 2021 cruises, whereby during the 2017 cruise the smallest size fraction (0.25-1 mm) had the highest DW and the intermediate size fractions (1-2 and 2-4 mm) had the lowest DWs and vice versa during the 2021 survey. No strong patterns in zooplankton size distribution were observed during the 2019 and 2022 surveys and most size fractions did not significantly differ in DW ($p > 0.05$).

Total and size fractionated zooplankton DW was correlated with the abundance of select taxonomic groups, but not consistently across surveys or size fractions. Linear correlation coefficients between zooplankton DW and species abundance are summarized in Table 3.4. Notably, during both the 2017 and 2021 surveys there were positive correlations between total DW and *Neocalanus* spp. abundance ($R^2 = 0.20$ and 0.53 respectively). During the 2022 survey there was a strong negative correlation between total zooplankton DW and euphausiid abundance ($R^2 = 0.58$).

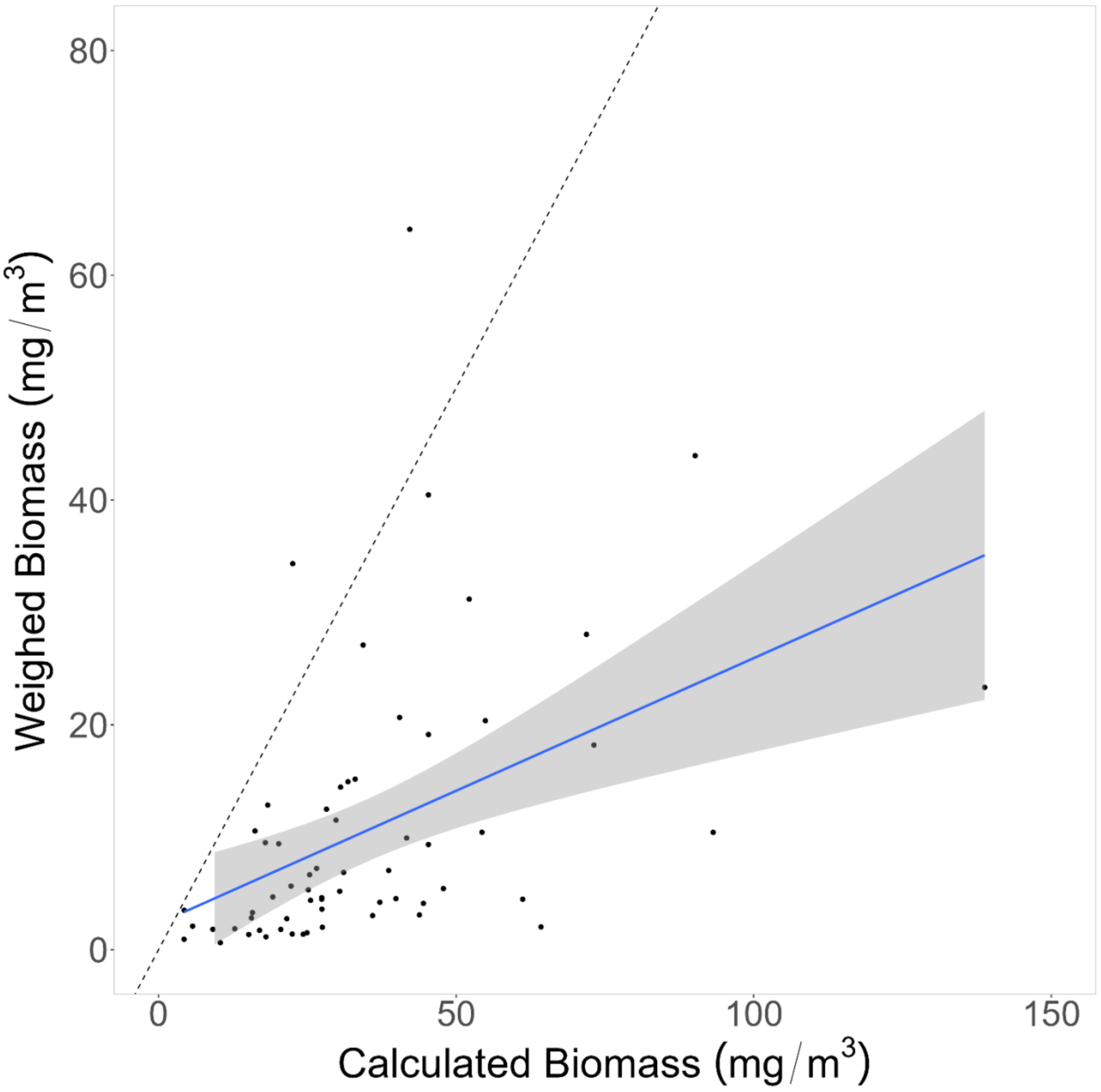


Figure 3.3. Comparison of directly weighed biomass values (*i.e.*, using a microbalance) and calculated biomass values (*i.e.*, using species-specific length-weight values). A dotted line is used to denote a 1:1 relationship. A linear model (blue line; $p < 0.001$; slope = 0.28; $R^2 = 0.53$) with standard error (gray) was used to fit the data.

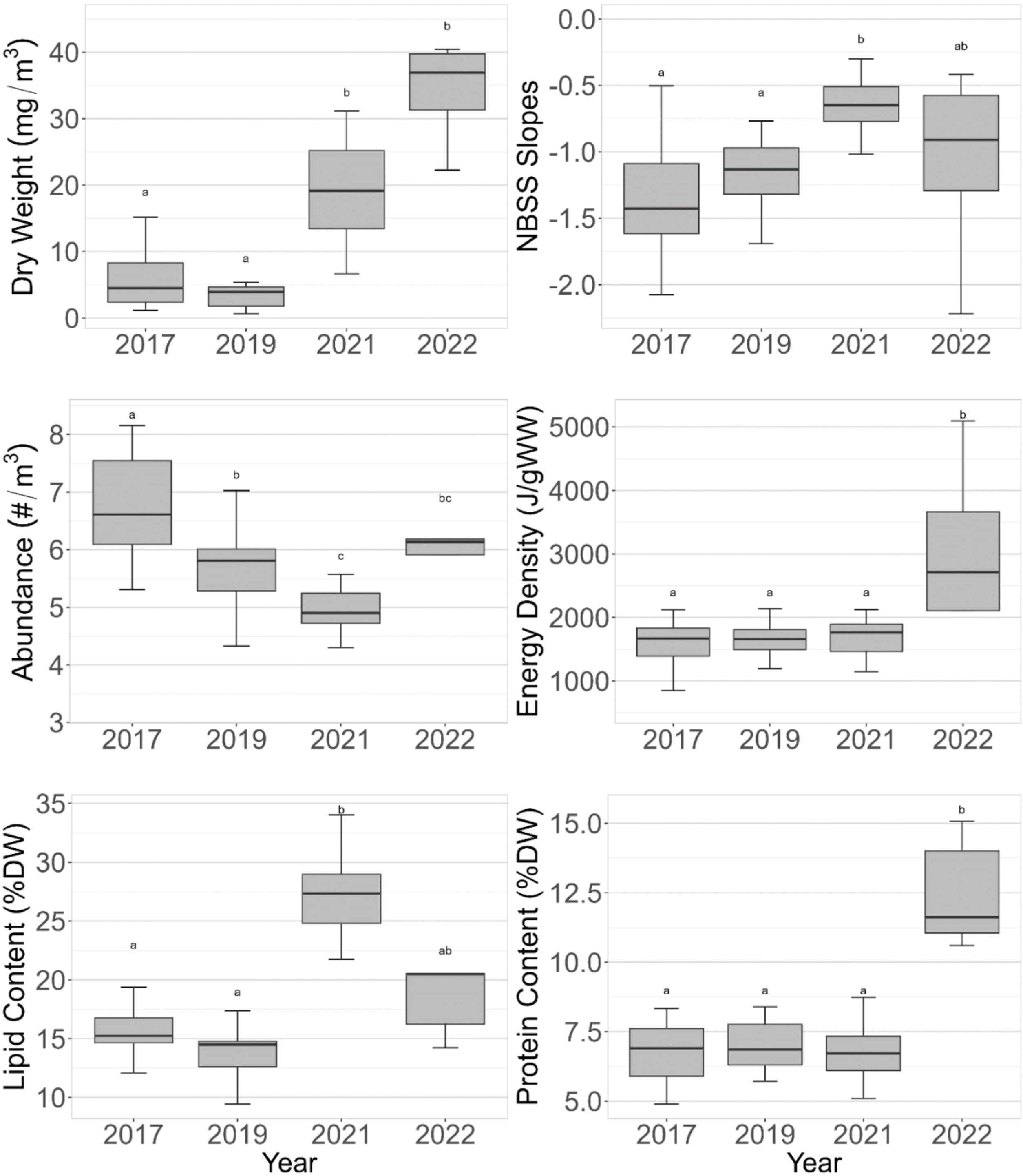


Figure 3.4: Boxplots comparing mean zooplankton dry weight, abundance, energy density, total lipid content, and total protein content across all sampling years. Dry weight and abundance were the combined sum of all the size fractions measured, while the energy density, lipid content, and protein content were the mean quantity per size fraction. Bars showing the same letter are not significantly different.

Table 3.3: A summary table of zooplankton community somatic composition, as both relative and absolute values (± Standard Error) for each size fraction across sampling years. Samples were collected during interdisciplinary expeditions across the Canadian offshore pacific.

	2017				2019				2021				2022			
Size Fraction (mm)	**0.25 – 1**	**1 – 2**	**2 – 4**	**>4**	**0.25 – 1**	**1 – 2**	**2 – 4**	**>4**	**0.25 – 1**	**1 – 2**	**2 – 4**	**>4**	**0.25 – 1**	**1 – 2**	**2 – 4**	**>4**
Dry Mass (mg/m^3)	2.13 ±0.33	0.96 ±0.12	0.63 ±0.14	1.79 ±0.53	1.37 ±0.23	3.22 ±2.08	1.11 ±0.61	1.34 ±0.32	1.68 ±0.16	7.44 ±1.19	5.62 ±1.26	5.20 ±0.78	9.59 ±5.39	14.97 ±4.81	12.81 ±4.63	2.77 ±0.99
Energy Density (kJ/g)	1.90 ±0.13	1.27 ±0.13	1.59 ±0.13	1.73 ±0.18	1.68 ±0.10	1.21 ±0.15	1.80 ±0.15	2.09 ±0.14	1.58 ±0.17	2.31 ±0.23	2.05 ±0.21	1.27 ±0.08	3.15 ±0.63	3.53 ±0.69	2.59 ±0.49	1.63 ±0.19
Energy Content (kJ/m^3)	16.47 ±3.04	6.12 ±0.88	3.33 ±0.43	14.78 ±8.37	17.30 ±3.22	52.99 ±37.40	17.44 ±10.24	19.60 ±4.92	21.23 ±2.05	133.18 ±32.18	121.88 ±50.68	69.72 ±10.51	181.68 ±10.17	329.64 ±119.45	263.98 ±105.82	48.05 ±16.67
Total Lipid content (%DW)	22.42 ±1.30	13.88 ±1.56	13.17 ±2.24	11.29 ±1.54	18.02 ±1.27	15.44 ±2.30	15.50 ±0.96	11.05 ±1.23	19.32 ±0.63	40.14 ±2.25	31.36 ±1.1	16.88 ±1.07	13.56 ±0.93	29.80 ±6.10	23.96 ±5.49	16.22 ±1.78
Total Lipids (mg/m^3)	0.36 ±0.08	0.10 ±0.02	0.05 ±0.008	0.20 ±0.11	0.24 ±0.03	0.36 ±0.18	0.28 ±0.16	0.18 ±0.03	0.32 ±0.03	3.27 ±0.68	1.83 ±0.45	0.89 ±0.12	1.28 ±0.65	5.63 ±3.02	3.98 ±2.29	0.44 ±0.17
Total Proteins content (%DW)	6.21 ±0.37	6.12 ±1.02	-	9.53 ±1.32	5.97 ±0.47	5.67 ±0.30	8.97 ±1.13	7.45 ±0.57	6.92 ±0.55	5.86 ±0.21	6.97 ±0.41	7.69 ±0.43	13.29 ±1.93	12.13 ±1.84	13.61 ±0.54	10.84 ±0.71
Total Proteins (mg/m^3)	0.09 ±0.01	0.05 ±0.008	-	0.28 ±0.17	0.94 ±0.02	0.21 ±0.12	0.35 ±0.27	0.15 ±0.5	0.12 ±0.01	0.42 ±0.06	0.39 ±0.09	0.38 ±0.05	1.30 ±0.64	1.60 ±0.37	1.70 ±0.55	0.30 ±0.11

Table 3.4: Summary tables for the R^2 values for significant ($p < 0.05$) linear correlations between relative abundance of taxonomic groups and size fractioned and total dry weight. Bold values are considered strong correlations with $R^2 > 0.5$. *Due to low sample sizes in 2022 (n = 5), there is high risk of Type 1 and 2 errors.

	R^2 values	Direction of Correlation	Year
		0.25 – 1mm	
Copepod nauplii/eggs	0.35	-	2017
Ostracods	0.22	-	2017
Ostracods	0.29	+	2019
Annelids	0.24	+	2019
Chaetognaths	0.19	-	2019
***Oithona* spp**.	**0.51**	**-**	**2021**
		1 – 2mm	
Decapods	0.28	-	2017
Euphausiids	0.26	+	2017
Euphausiids	0.24	+	2019
Cyclopoids	0.38	+	2019
Annelids	0.24	+	2019
Doliolids	0.2	+	2019
Ostracods	0.2	-	2019
Chaetognaths	0.23	-	2019
***Neocalanus* spp.**	**0.5**	**+**	**2021**
		2 – 4mm	
Decapods	0.31	+	2017
Euphausiids	0.33	+	2017
Euphausiids	0.21	+	2019
Annelids	0.19	+	2019
Doliolids	0.23	+	2019
Ostracods	0.31	-	2019
Chaetognaths	0.27	-	2019
Neocalanus spp.	0.45	+	2021

	R^2 values	Direction of Correlation	Year
		>4mm	
***Neocalanus* spp.**	**0.5**	**+**	**2017**
Cyclopoids	0.39	+	2017
Euphausiids	0.17	+	2019
Annelids	0.18	+	2019
Annelids*	**0.62**	**-**	**2022**
Oithona spp.	0.23	-	2021
Cnidaria	0.33	-	2021
Chaetognaths*	**0.65**	**-**	**2022**
		Total	
Neocalanus spp.	0.2	+	2017
***Neocalanus* spp.**	**0.53**	+	**2021**
Cyclopoids	0.24	+	2019
Annelids	0.31	+	2019
Ostracods	0.21	-	2019
Chaetognaths	0.19	-	2019
Euphausiids	0.28	+	2019
Euphausiids*	**0.58**	-	**2022**

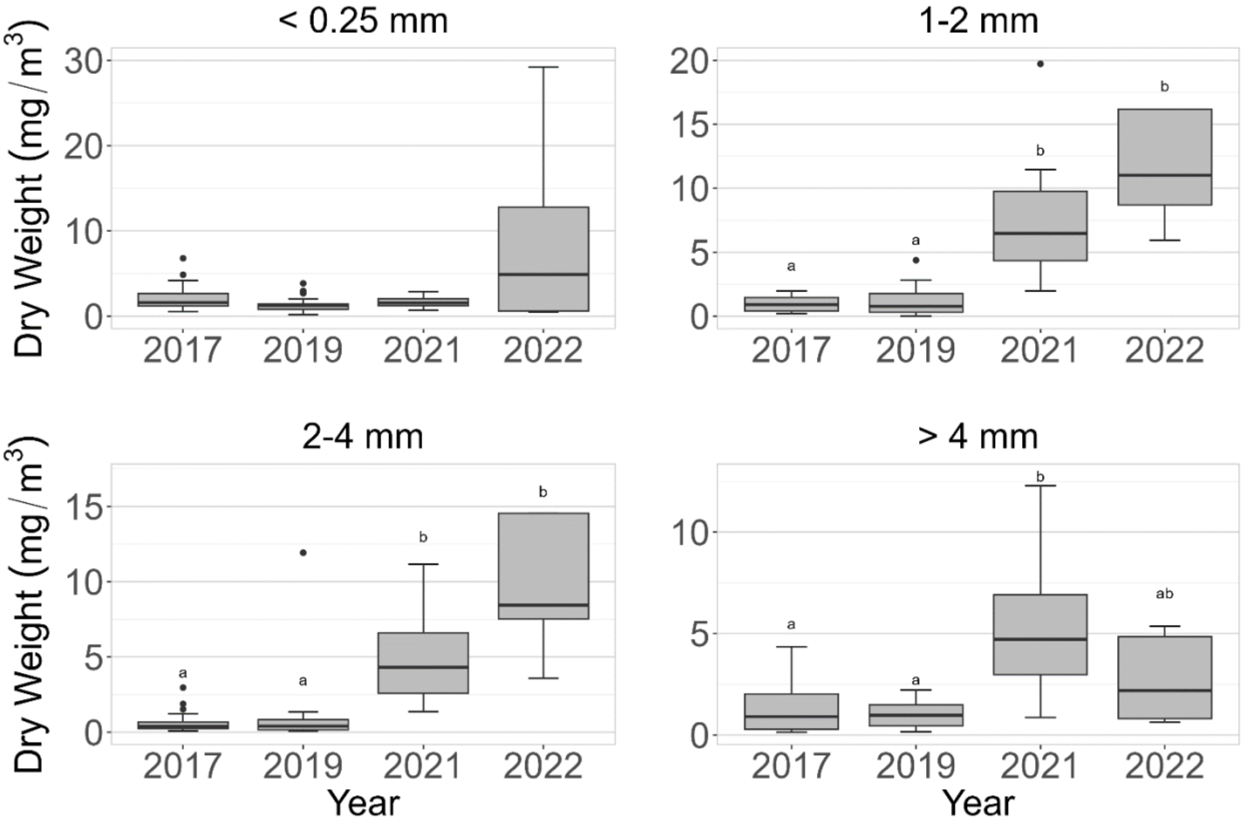


Figure 3.5: Interannual variability of size fractionated dry weight (mg m^{-3}) for bulk size fractionated zooplankton. Black dots represent outliers in the data. Insignificant differences ($p > 0.05$) are denoted by matching letters.

Total zooplankton abundance and NBSS were significantly different between regions across the 2017 survey ($p < 0.05$), but otherwise there were no significant differences between sampling regions ($p > 0.05$; Fig. 3.6). Total zooplankton abundance was significantly higher at slope sites than offshore sites across the 2017 survey, whereby offshore sites averaged less than 50% of the number of individual organisms than at slope sites ($p < 0.05$). NBSS spectral slopes were significantly shallower at offshore sites in comparison to slope sites (-1.2 ± 0.38 vs -1.6 ± 0.4, $p < 0.05$).

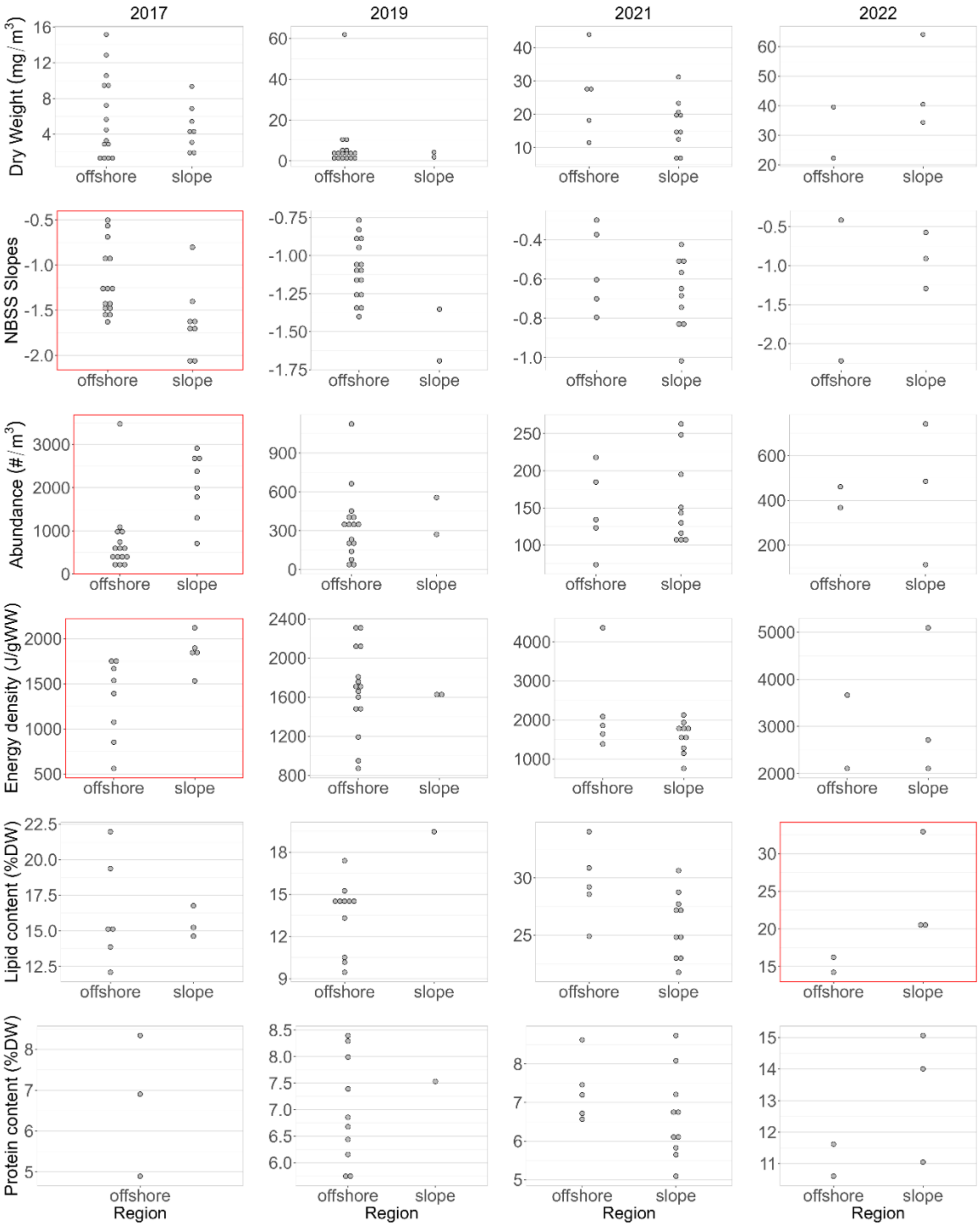


Figure 3.6: Dotplots comparing mean zooplankton dry weight, NBSS slope, abundance, energy density, total lipid content, and total protein content between offshore and slope sites in each year sampled. Each point represents the total (dry weight and abundance) or mean (energy density, lipids, and proteins) value from all size fractions from a given site. Y-axis scales are different between graphs to improve data visualization. Boxes outlined in red indicate a significant difference between offshore and slope sites.

3.3.4 Zooplankton energy density

The mean ED of bulk zooplankton was not statistically different between the 2017, 2019, and 2021 surveys, but was significantly higher during the 2022 survey (Fig. 3.4). Bulk zooplankton collected during the 2022 survey were nearly twice as energy dense as in other years (2984 J gWW^{-1} vs 1525-1800 J gWW^{-1}, $p < 0.05$). Interannual trends were not consistent across all size fractions (Fig. 3.7). Notably, the 1-2 mm size fraction zooplankton had significantly higher ED during the 2021 survey than both the 2017 and 2019 surveys ($p < 0.05$), and there were very few statistically significant interannual differences in zooplankton ED in the 2-4 and >4 mm size fractions.

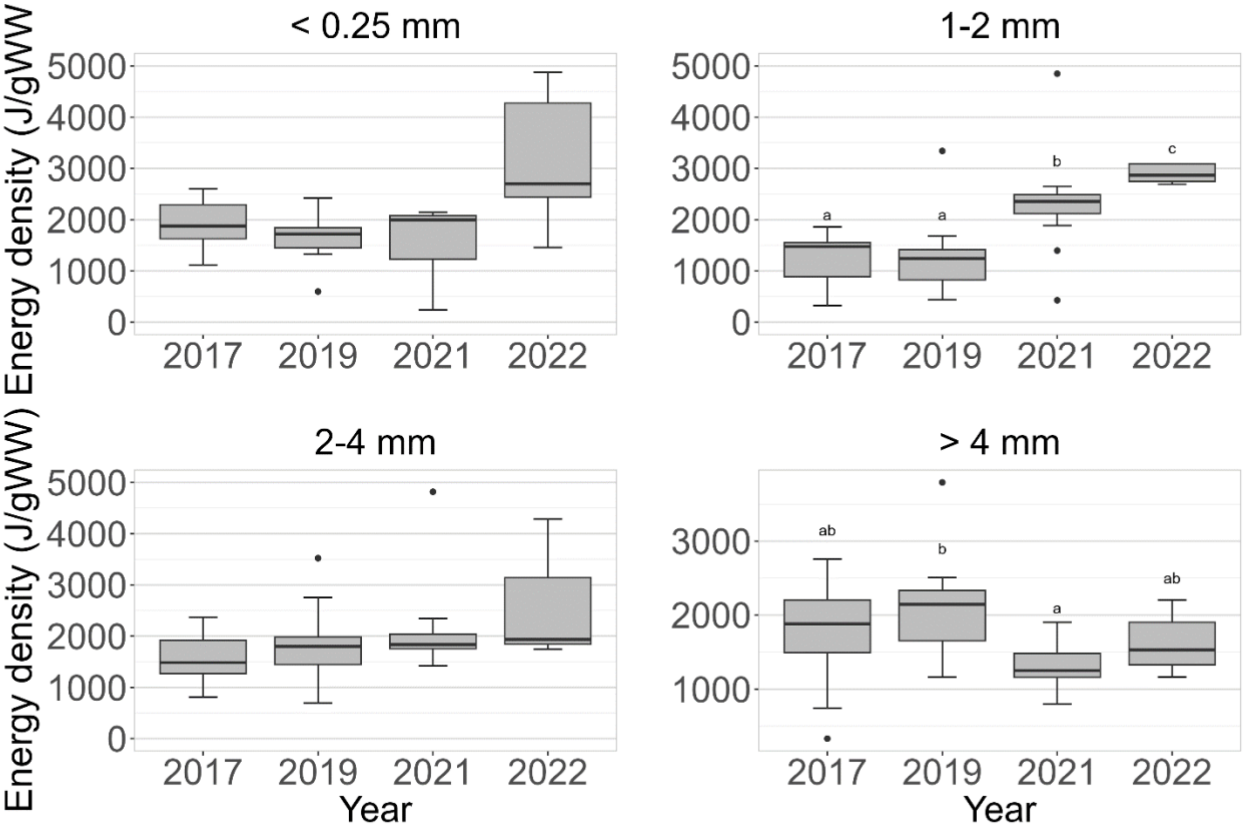


Figure 3.7: Interannual variability of size fractionated energy density (J gWW^{-1}) for bulk size fractionated zooplankton. Black dots represent outliers in the data. Significant differences are denoted by different letters.

The EDs of size fractionated bulk zooplankton are summarized in Table 3.3. In the first two surveys (2017 and 2019) the 1-2 mm zooplankton had significantly lower ED compared to other size fractions, while the 2021 survey found the inverse, whereby the zooplankton in the 1-2 mm size fraction were the most energy dense. Similarly, during the 2019 survey the >4 mm size fraction zooplankton had high ED relative to other size fractions, while the inverse was observed during the 2021 and 2022 surveys, whereby the >4 mm zooplankton had the lowest ED.

There were many significant correlations between the abundance of specific zooplankton taxonomic groups and total/size fractionated zooplankton ED, and these have been summarized in Table 3.5. The most significant of these was the negative correlation between doliolid abundance and total zooplankton ED measured during the 2017 and 2019 surveys ($R^2 = 0.66$ and 0.53 respectively).

Table 3.5: Summary tables for the R^2 values for significant ($p < 0.05$) linear correlations between relative abundance of taxonomic groups and size fractioned and total energy density, lipid content, and protein content. Bold values are considered strong correlations with a $R^2 > 0.5$. *Due to low sample sizes in 2022 (n = 5), there is high risk of Type 1 and 2 errors.

	R^2 values	Direction of Correlation	Year	Size Fraction (mm)
		Energy Density		
Doliolids	**0.66**	**-**	**2017**	**Total**
Doliolids	**0.53**	**-**	**2019**	**Total**
Annelids	0.21	-	2019	Total
Limacina helicina	0.24	+	2021	0.25 – 1
Neocalanus spp.	0.37	+	2021	1 – 2
Salps	0.32	-	2021	>4
Larvaceans*	**0.78**	**-**	**2022**	**Total**
Euphausiids*	**0.72**	**-**	**2022**	**Total**
		Total Lipids		
Doliolids	**0.58**	**-**	**2017**	**>4**
Doliolids	0.48	-	2019	Total
Ostracoda	**0.67**	**+**	**2019**	**1 – 2**
Neocalanus spp.	0.34	+	2019	2 – 4
***Neocalanus* spp.**	**0.69**	+	**2021**	**1 – 2**
Neocalanus spp.	0.41	+	2021	Total
Euphausiids*	**0.79**	+	**2022**	**2 – 4**
		Total Proteins		
Clione limacine	0.32	+	2019	1 – 2
Cephalopods	**0.53**	**-**	**2019**	**0.25 – 1**
Chaetognaths	0.32	-	2019	Total
Chaetognaths*	**0.65**	**-**	**2022**	**1 – 2**
Chaetognaths*	**0.73**	**-**	**2022**	**Total**
Doliolids	0.27	+	2021	>4
Cnidaria*	**0.71**	**-**	**2022**	**0.25 – 1**
Cnidaria*	**0.71**	**-**	**2022**	**Total**
Annelid*	**0.72**	**-**	**2022**	**0.25 – 1**
Annelid*	**0.86**	**-**	**2022**	**Total**
Ostracods*	**0.67**	**-**	**2022**	**1 – 2**

3.3.5 Zooplankton total lipid content

Mean bulk zooplankton TL content (%DW) during the 2021 survey (27 ± 3.4% DW) was significantly higher than in previous surveys (2017 = 16 ± 3%, 2019 = 14 ± 2.9% DW; Fig. 3.4), although interannual patterns were not the same for every zooplankton size fraction (Fig. 3.8). Zooplankton in the 1-2 mm, 2-4 mm, and >4 mm size fractions had higher TL contents during the 2021 and 2022 surveys relative to the 2017 and 2019 surveys. Zooplankton in the smallest size fraction (0.25-1 mm) zooplankton were the most lipid-rich during the 2017 survey and had significantly lower TL than other size fractions in the following surveys.

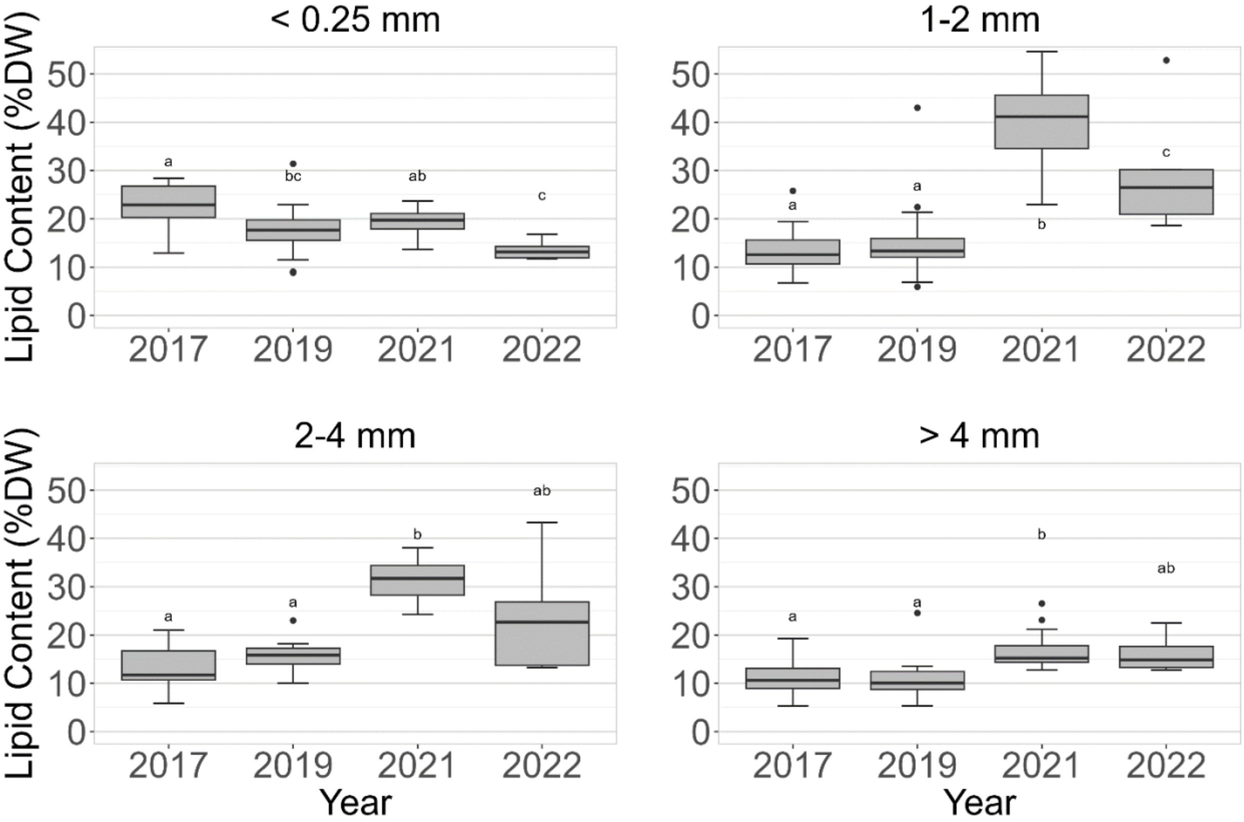


Figure 3.8: Interannual variability of size fractionated total lipid content (%DW) for bulk size fractionated zooplankton. Black dots represent outliers in the data. Insignificant differences are denoted by matching letters.

The TL contents of size fractionated zooplankton are summarized in Table 3.3. Typically, the largest zooplankton size fraction (>4 mm) had the lowest TL content in all but the 2022 survey which had the least TL content in the smallest size fraction (0.25-1 mm) zooplankton. Otherwise, the rank order of size fractionated zooplankton TL content was unique to each survey. However, the range of TL content between zooplankton size fractions was significantly greater during the 2021 and 2022 surveys, whereby there was 3x and 2.2x more TL between the most and least lipid-rich zooplankton size fraction (1-2 mm vs >4 mm). By comparison, TL content in the 2017 and 2019 surveys varied by ~1.5x between size fractions.

There were multiple significant correlations between the abundance of specific zooplankton taxonomic groups and both total and size fractionated zooplankton TL content (Table 3.5). Notably, doliolids were negatively correlated with total bulk zooplankton TL content in samples from the 2019 survey ($R^2 = 0.48$), as well as the TL content of zooplankton in the largest size fraction (>4 mm) during the 2017 survey ($R^2 = 0.58$). Additionally, the abundance of *Neocalanus* spp. was positively correlated with TL content of specific size fractions (1-2/2-4 mm) and total zooplankton sampled during the 2019 and 2021 surveys.

3.3.6 Zooplankton total protein content

Mean bulk zooplankton TP content (%DW) during the 2022 survey was significantly higher than in other surveys (12.5 ± 2% vs 6.7-7.0%; Fig. 3.4). Interannual variability in TP content was differed between size fractions (Fig. 3.9). Zooplankton in the 0.25-1 mm, 1-2 mm, and 2-4 mm size fractions had significantly higher (2x) TP content during the 2022 survey relative to previous surveys. Zooplankton TP content in the largest size fractions was not statistically different between surveys.

The protein content of size fractionated zooplankton is summarized in Table 3.3. There were no consistent trends in the rank-order of size fractionated TP content, but in the smaller size fractions (0.25-1 mm, 1-2 mm, and 2-4 mm) typically had lower TP content than the largest size fraction (>4 mm).

There were many significant correlations between the abundance of zooplankton taxonomic groups and both total and size fractionated zooplankton TP content, and the correlation coefficients have been summarized in Table 3.5. Most species-TP correlations occurred in 2022, where notably chaetognath, cnidarian, and annelid abundance were all negatively correlated with bulk TP content ($R^2 = 0.73$, $R^2 = 0.71$, and $R^2 = 0.86$ respectively).

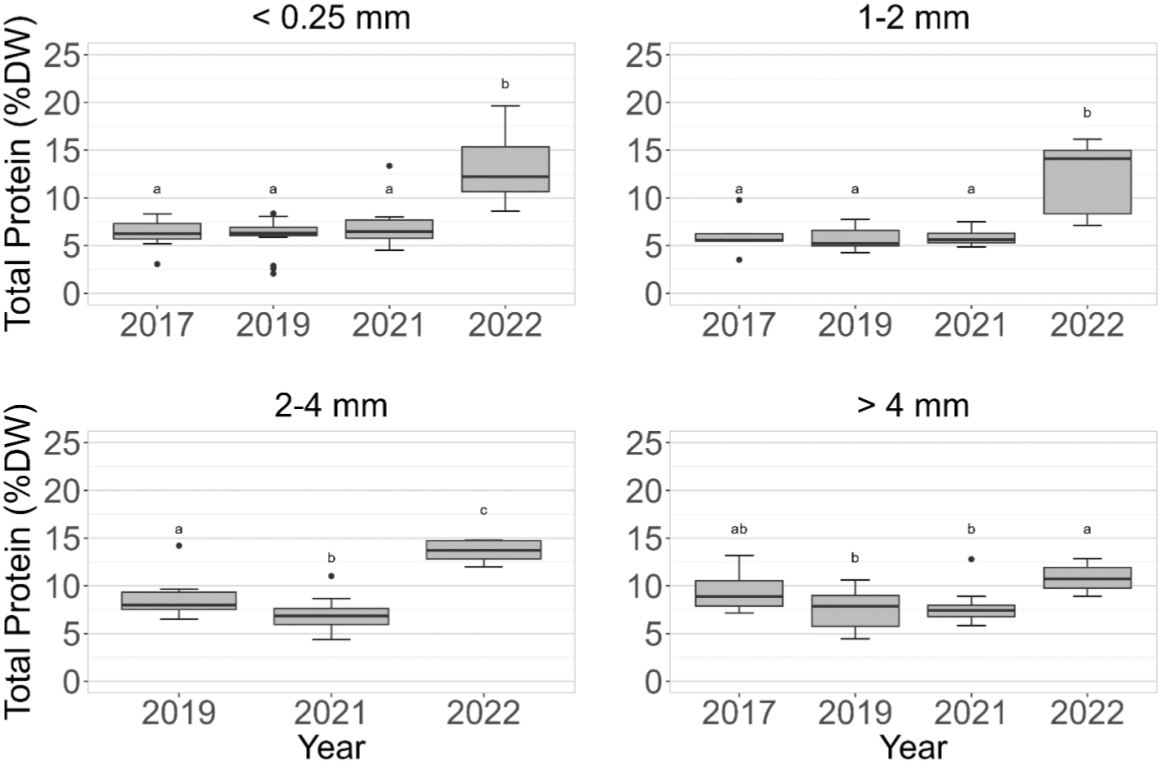


Figure 3.9: Interannual variability of size fractionated total protein content (%DW) for bulk size fractionated zooplankton. Black dots represent outliers in the data. Insignificant differences are denoted by matching letters.

3.3.7 Spatial variability of zooplankton energy density, total lipids, and total proteins

ED and TL content were significantly different between offshore and slope regions during the 2017 and 2022 surveys respectively, while TP was not significantly different between study regions on any survey (Fig. 3.6). During the 2017 survey, zooplankton ED was on average 400 J gWW^{-1} higher at sites that were located over the slope (p=0.042). During the 2022 survey, TL content at slope sites was significantly higher than at offshore sites (24 ± 12% vs 15 ± 5% DW, p=0.014). Other years did not show significant differences between offshore and slope zooplankton community ED, TL content, or TP content.

3.3.8 Linear correlations between zooplankton biomass, energy density, total lipid content, and total protein content

All significant linear correlation coefficients between size fractionated bulk zooplankton DW, ED, TL content, and TP content are summarized in Figure 3.10. A major trend during the 2021 and 2022 suvery was that total zooplankton DW was more heavily correlated with intermediate size zooplankton DW (1-2 and 2-4 mm), while total zooplankton DW during the 2017 and 2019 surveys was correlated with all four zooplankton size fractions. Zooplankton TL content and ED were correlated for various size fractions during the 2019, 2021, and 2022 surveys, but not during the 2017 survey. In 2019, 2021, and 2022, only about half of zooplankton size fractions had significant correlation between zooplankton TL and ED. The smallest zooplankton size fraction (0.25-1 mm) was not correlated with total zooplankton TL content and was also the most weakly correlated with any other metrics across all surveys.

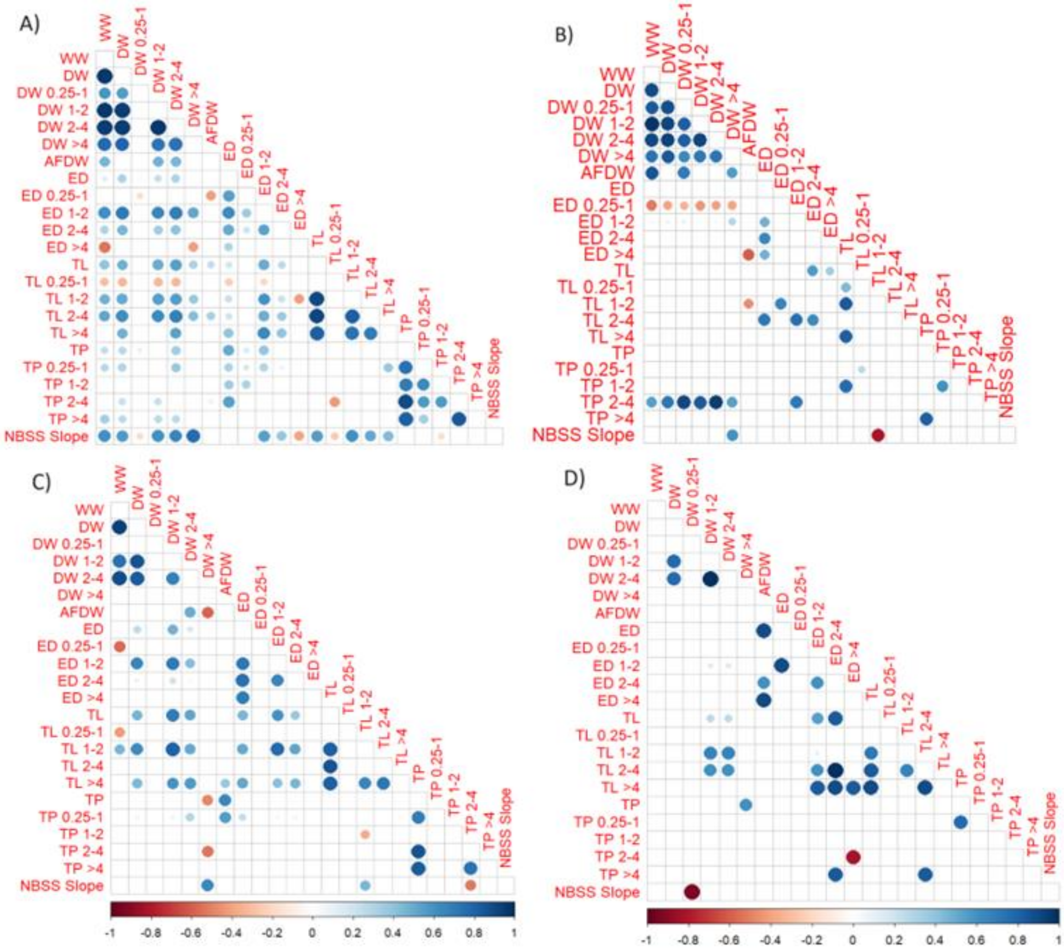


Figure 3.10. Spearman rank correlations ($p < 0.05$) between total and size fractionated (0.25 – 1 mm, 1 – 2 mm, 2 – 4 mm, and >4 mm) zooplankton compositional data from the (A) 2017, (B) 2019, (C) 2021, and (D) 2022 surveys. The x-axis is the spearman rank correlation, where red values (-) represent a negative correlation and blue (+) represent a positive correlation. The strength of the monotonic correlation is indicated by the size and darkness of the circles (*i.e.,* large dark blue circles represent a strong positive linear correlation). The metrics used for compositional information were wet weight (WW), dry weight (DW), energy density (ED), total lipid content (TL), and total protein content (TP). Metrics labelled without numbers are totals (WW and DW) or mean (ED, TL, and TP) of bulk zooplankton samples. The labels with associated number (XX #-#) are measurements of specific zooplankton size fractions (0.25 – 1, 1 – 2, 2 – 4, and >4 mm).

3.4 Discussion

This chapter explored the range of information that can be gained from the analysis of frozen and fixed bongo net samples to enhance our understanding of zooplankton communities. Although the present study was targeted specifically towards seamounts in the Canadian OPB, this multi-faceted approach can easily be applied elsewhere. Using these (ED, TL, and TP) and potentially other metrics, the variability of zooplankton nutritional quality among individual net tow samples can be used to describe and compare zooplankton standing stocks more accurately. In addition, correlations between zooplankton taxonomic composition and whole community macromolecular composition were identified and investigated.

3.4.1 Comparing methodologies for estimating zooplankton biomass

Across the 62 samples used in this study, there was a significant positive linear relationship between calculated and weighed biomass ($R^2 = 0.53$). However, far from the theoretical 1:1 relationship that might have been expected (slope = 0.28), the calculated biomass values were consistently higher than the directly weighed biomass values by a factor of ~3.5. For this reason, the weighed biomass measurements reported here may seem low compared to other studies reported from within this region, which have generally been based on calculated biomass. This seemingly large disparity may be due to the lack in sensitivity of length-weight regressions to the natural variability of taxonomic groups across seamounts and regions (Evanson et al., 2000; Lee et al., 2006; Stevens et al., 2022). Additionally, the weighed biomass samples experience greater handling through the sieving process, potentially damaging/destroying individuals (particularly fragile taxa) and thereby losing biomass. Neither method can be considered "better" or "more accurate", although each has its potential biases. Weighed biomass was chosen for this study because it is the most common method used in the literature (Postel et al., 2000; McEnnulty et al., 2020).

3.4.2 Analyses used in the quantification of zooplankton nutritional quality

Energy density of bulk zooplankton

Energy density (ED) determination was the most time and cost-efficient method employed in this study, making it an easily implemented method to characterize zooplankton nutritional quality. This method can be easily incorporated into current DFO biomass determination procedures, as ash-free dry weight (AFDW) measurement requires the same handling and preservation as standard dry weight (DW) methods. One drawback for the measurement of ED for bulk zooplankton nutritional quality is that this protocol uses wet weight (WW) as the reference for AFDW (Weil et al., 2019), and WW is a less reliable metric for bulk samples due to trapped interstitial water between organisms (Postel et al., 2000). Although this introduces a potential source of error in the ED of zooplankton, vacuum filtration was used to remove most interstitial water, therefore it was unlikely to significantly influence ED values. These ED estimates produce an accurate quantification of energy content in bulk zooplankton, offering a relatively cheap and fast method to provide a numerical representation of zooplankton quality which can be used in a variety of research programs.

Macromolecular quantification of bulk zooplankton

Macromolecular quantification was more time intensive than ED and requires specific sample handling and processing, but provides valuable information on zooplankton nutritional quality. The spatio-temporal distribution of TL and TP in zooplankton did not mirror those of ED, indicating macromolecules are likely measuring different aspects of nutritional quality which appear to be more variable metrics. This was particularly noticeable for the 2021 survey samples, where TL content was significantly higher than past years, but ED values were similar (Fig. 3.6). These differences between macromolecule quantity and ED were unexpected, as TL and TP are commonly interpreted as the building blocks which form the biologically available material (AFDW) which was used to determine ED (Cumminns and Wuycheck, 1971). Such variations in dietary components are likely important to higher trophic levels and can have substantial impacts on predator health (Beamish and Mahnken, 2001). Macromolecular quantification can therefore lead to a better understanding of zooplankton nutritional value that is not apparent from ED or total (or size fractionated) biomass alone.

The BCA method is the recommended protocol for TP determination in ecological studies (Smith et al., 1985; Zaguri et al., 2021). Although the results of this project (averaging 6.7-12.5% DW) indicate relatively low TP content in comparison to most studies (30-80% DW Postel et al. 2000, 21.5% DW Harmelin-Vivien et al. 2019, 26.81-60.51% DW Lobus et al. 2020, ~20% DW Zaguri et al. 2021; Wang and Jeffs 2014), similar absolute TP values (range from <0.01-7 mg m^{-3}, with an average 0.56 mg m^{-3}) have been reported using the BCA method near Australia (averages between 0.326-3.5 mg m^{-3}, McKinnon et al. 2015), in the Labrador sea in winter (averages between 0.65-5.35 mg m^{-3}, Yebra et al., 2009), and western Mediterranean coastal waters (0.73 ± 0.51 mg m^{-3}, Yebra et al. 2020). Although TP are often the most prevalent macromolecules in zooplankton, TL dominated the zooplankton samples from the Canadian OPB. This may be due to the dominance of lipid-rich subarctic zooplankton species in this region (particularly, large calanoids such as *Neocalanus* spp.) many of which have large lipid sacs which occupy much of their body cavity, making relative TP levels lower (Evanson et al., 2000; Lee et al., 2006; Kattner and Hagen, 2009). The low TP contents recorded here were unlikely to have resulted from methodological considerations (*i.e.,* storage temperature or drying method) as these procedures are commonly used in protein quantification methods (Morris and Hopkins, 1983; Postel et al., 2000; Chen et al., 2019; Harmelin-Vivien et al., 2019; Zaguri et al., 2021). In addition, there were no significant differences in zooplankton TP content between rinsed (*i.e.*, distilled water vs ammonium formate) or non-rinsed samples based on a *post-hoc* comparison performed on samples collected in Saanich inlet, BC, in September 2023 aboard the *RV John Strickland*. The differences in sample processing in 2022 (*i.e.*, -80ºC storage and rinsing with ammonium formate) should not have caused the 2-fold difference in TP concentrations from the 2017, 2019, and 2021 surveys to the 2022 survey.

3.4.3 Normalized biomass size-spectra

Although NBSS can indicate community productivity, energy transfer efficiency, and trophic structure (Zhou, 2006; Rykaczewski and Checkley, 2008; Décima, 2022), in this thesis the reported differences in NBSS were likely due to changes in the ratio of small:large copepods in the samples. It is plausible that NBSS in the Canadian OPB is strongly correlated with copepod size, as observed in other copepod-dominant regions such as the California current system (Rykaczewski, 2019). The Canadian OPB is likely similar to the California current system in this respect, since the shallowest slopes appeared in 2021 when large copepods (*Neocalanus* spp.) were in high abundance, while steeper slopes occurred in 2017 and 2019 when small copepod species dominated most of the samples (Fig. 3.6). In addition, slope sites had relatively steeper NBSS slopes and a higher abundance of small copepods in comparison to offshore sites during the 2017 survey (-1.2 vs -1.6; Fig. 3.5 and 3.7).

NBSS were estimated using size fractionated biomass, following Rykaczewski and Checkley (2008). Note, however, that the current study used four size bins as opposed to the 5-point estimation in Rykaczewski and Checkley (2008) and Décima (2022). Nonetheless, the NBSS slopes calculated in this study (range -0.3 to -2.2 with a mean slope of -1.1) are comparable to other studies that have used this estimation method (-0.5 to - 2.5 in Rykaczewski and Checkley 2008; -0.5 to -1.5 in Rykaczewski 2019). In addition, a comparison between 5-point estimation approach and high-resolution biomass size spectra using ZooScan imagery demonstrated similar conclusions between both methods (Rykaczewski 2019). This "coarse" NBSS method has clear potential as a useful tool to represent zooplankton size distribution.

3.4.4 Nutritional quality of bulk zooplankton samples in the Canadian Offshore Pacific Bioregion

The Canadian Offshore Pacific Bioregion zooplankton community

Bulk TL, TP, and energy measurements in the Canadian OPB indicate a lipid-rich and protein-poor zooplankton community with an intermediate ED. TL made up the largest proportion of bulk zooplankton biomass in all years and across all size fractions. In the literature, TL are frequently reported as the second most prevalent macromolecule in bulk zooplankton samples after TP (Jo et al., 2018; Chen et al., 2019; Harmelin-Vivien et al., 2019; Lobus et al., 2020), although there are cold-water species in which TL (>50%) are in higher proportion than TP (Wang and Jeffs, 2014; Stevens et al., 2022). Other studies have found relatively low TL contents in bulk zooplankton in the East/Japan Sea (8 ±3.9 % DW; Jo et al. (2018)), in the North-western Mediterranean Sea (10.5 ±8.9 % DW; Chen et al. 2019), and near the Kerguelen Islands (8.9 ± 4.4 %; DW Harmelin-Vivien et al., 2019). The TL content in the samples from this study (average 20 ± 6.84%, ranged from 9.3-34% DW) were higher, and more similar to zooplankton in arctic regions such as the Kara Sea (average 26.67 ± 2.28 %, range 15.86-46.97% DW; Lobus et al. 2020). In contrast to the patterns seen in TL, zooplankton in the Canadian OPB had much lower TP content (average 7.7 ± 2.3%, ranged from 4.9-15.1% DW) than other studies, where they accounted for 64.2 ± 35.1% (Jo et al., 2018), 26.8 ± 15.1% (Chen et al. 2019), 21.5 ± 8.4% (Harmelin- Vivien et al., 2019), and 43.39% (Lobus et al., 2020) of DW.

The ED of bulk zooplankton in the Canadian OPB was somewhat lower than might be expected in lipid-rich samples, ranging from 1000 - 2500 J gWW^{-1} during the 2017, 2019, and 2021 surveys, and 2000 – 5000 J gWW^{-1} in the 2022 survey. These values are lower than expected because lipids are the most energy dense macromolecule in zooplankton, and a high lipid content would be expected to indicate higher energy densities in zooplankton (Cummins et al. 1971; Weil et al. 2019). ED of the 2022 samples were in the same range as most crustacean species for this region, while the earlier surveys (2017-2021) had lower ED than most crustacean species (Tyler, 1973; Weil et al., 2020). Canadian OPB samples also contained large quantities of gelatinous and soft-bodied zooplankton (Fig. 3.5), which typically have quite low ED. Research by Lüskow et al. (2021) in the NE Pacific measured ED values <1500 J gWW^{-1} in most major classes of gelatinous/soft-bodied zooplankton. In comparison, the samples in this study from 2017-2021 were more energy dense than the measured ED of most gelatinous species but less so than many crustacean species. Consequently, bulk zooplankton samples seem to represent an intermediate ED between both types of organisms.

Differences in zooplankton nutritional quality between warm and cold mixed layer temperature years

The zooplankton community sampled from warmer MLT years (2017 and 2019) had a smaller total lipid-pool compared to those from colder MLT years (2021 and 2022). This was likely due to the shift between southern species (warmer MLT) to lipid-rich subarctic species (Colder MLT). In warmer years, samples contained less TL (10 - 20% of DW) but were still comparable to other cold-water regions, such as the Southern Ocean (Harmelin-Vivien et al., 2019) and the Kara Sea (Lobus et al., 2020). The taxonomic composition of the samples from warmer MLT surveys were dominated by *Oithona* spp. (Lipid = 13-15%

DW; Perumal et al. 2009), *Pseudocalanus* spp. (Lipid = 17.3% DW; Wang and Jeffs 2014), and thaliaceans (Lipid <5% DW; Dubischar et al. 2012). During warmer MLT surveys, there was also a larger presence of boreal (*i.e.*, *Pseudocalanus* spp. and *Acartia longiremis*) and southern copepods (*i.e.*, *Clausocalanus* spp.). In comparison, TL content in the colder years ranged between 15 – 34% of zooplankton DW and were dominated by large lipid-rich subarctic species, such as *Neocalanus cristatus* (Lipid = 36-60% DW), *N. plumchrus* (Lipid = 60-70% DW), *Metridia pacifica* (Lipid = 8-14% DW), and *Eucalanus bungii* (Lipid = 32-37 % DW; Ohman, 1988; Evanson et al., 2000; Saito and Kotani, 2000).

The difference in species observed between surveys is supported by past literature that reports positive biomass anomalies of southern zooplankton during warmer years in the region (*i.e.*, El Niño and "warm" PDO) (Mackas et al., 2001, 2004; Keister et al., 2011). In addition, these differences between "warm" and "cool" years may be associated with changes in large-scale current dynamics to the region contributing to different water masses being sampled (*e.g.* southern vs subarctic). The data presented in this thesis also indicated a near 5-fold increase in total zooplankton biomass in cold years, further increasing the absolute (mg m^{-3}) lipid pool within the Canadian OPB. Changes in prey quality with changing water temperature in this region have been discussed and predicted in the literature, often connecting taxonomic change to differences in lipid availability, but without providing direct measurements (Cavole et al., 2016; Pinchuk et al., 2021; McKinstry et al., 2022; Winans et al., 2023). These results provide empirical evidence for these assumed decreases in biologically-available lipids to higher trophic levels during relatively warm water years within the Canadian OPB.

3.4.5 Variability in bulk and size fractionated zooplankton biomass and nutritional composition

Magnitude of interannual change in total zooplankton quantity and quality

The range of interannual variability in zooplankton biomass (quantity) was more extreme than changes in relative ED, TL, and TP content (quality) across the Canadian OPB. When significant changes were detected, interannual differences in zooplankton biomass ranged between 1.2 to 7-fold between surveys. The largest interannual difference in biomass was a 7-fold increase between the 2019 and 2022 surveys. In comparison, the most variable aspect of zooplankton nutritional quality was bulk zooplankton ED, which resulted in 1.1 to 2-fold differences between surveys. The most significant difference in bulk zooplankton ED was a 2-fold change between the 2017 and 2022 survey. In comparison, zooplankton TL and TP content both had a maximum change of 1.9-fold between years. These changes happened across 62 net casts over a 6-year span on four separate surveys, and this time period likely represented the transition from warm to cool water regime years. Although similar magnitudes of biomass change (4 to 6-fold) were observed across a 15-year span off the west-coast of Vancouver Island (Mackas et al., 2001), measurement of multiple warm-cold water cycles would be needed to determine the full magnitude of biomass and nutritional variability.

Nutritional quality of zooplankton size fractions

The rank order of the TL, TP and ED of zooplankton size fractions differed between surveys. During the 2017 and 2019 surveys, there was an inconsistent rank-order of zooplankton size fractions in terms of ED and TP content, but often the smallest size fraction (0.25-1 mm) had the highest TL content. The 0.25-1 mm size range has been reported to be more TL, TP, and energy dense in comparison to larger size fractions in mid-latitude regions, such as the Bay of Marseille (Chen et al., 2019) and the Bay of Biscay (Dessier et al., 2018). This was attributed to the large quantities of nutrient-rich crustacean (primarily copepods) prey in this size-range. During the 2021 and 2022 surveys, the intermediate size fractions (1-2 and 2-4 mm) in the Canadian OPB were highest in TL and ED. Similarly, in high latitude regions, the 1-4 mm size range tends to have the highest quality zooplankton and generally larger zooplankton tend to be more TL and TP-rich (Guisande, 2006; Lee et al., 2006; Harmelin-Vivien et al., 2019). In the Canadian OPB, the largest size fraction (>4 mm) was not the most lipid and protein dense size fraction. This was likely from high proportions of large gelatinous species (*i.e.*, doliolids and salps) in the larger size fractions. Gelatinous species often have a lower macromolecular density than crustacean species (Wang and Jeffs, 2014; Weil et al., 2020; Lüskow et al., 2021), and therefore dilute the ED and macromolecule quantities per gram DW of the larger size fractions.

Small zooplankton biomass and ED were less variable across years than larger zooplankton. Zooplankton between 0.25-1 mm showed no significant changes in biomass and ED between surveys, although there was still some variability in TL and TP content. Small copepods, such as *Oithona similas*, *O. atlantica*, and *Pseudocalanus* spp. (primarily *P. mimus*) make up the majority of this size fraction. These copepods have relatively similar macromolecular compositions and EDs (Perumal et al., 2009; Wang and Jeffs, 2014), and therefore no matter the change in proportion of each species between surveys there was little change in biomass and ED. In addition, the smallest size fraction was least correlated with any other metric in comparison to the other size fractions, generally fluctuating independently within years (Fig. 3.20). The other size fractions (1-2, 2-4, and >4 mm) had more drastic changes in taxonomic composition, with a change from primary doliolids to a mixture of doliolids, salps, and large copepods. These taxa have large differences in macromolecular composition and ED (Wang and Jeffs, 2014; Lüskow et al., 2021), therefore yielding much larger variations with taxonomic change. Overall, it appears that taxonomic composition of large species with significant biomass contribution resulted in more interannual variability and a higher influence on bulk zooplankton nutritional quality than small species.

3.4.6 Species correlations with bulk zooplankton nutritional quality

There were some standout taxonomic groups that were frequently correlated with bulk zooplankton nutritional content, specifically with *Neocalanus* spp. and doliolids. *Neocalanus* spp. were correlated with the high TL content and ED, while doliolids were correlated with low TL content and ED. This indicates a high degree of influence in bulk zooplankton macromolecular composition, likely through high/low individual quantities of TL or energy. These species are likely significant drivers of zooplankton community change. In addition, both species are associated with environmental conditions. Specifically *Neocalanus* spp. tend to be more abundant in cold water years (Ashlock et al., 2021) while high doliolid abundance has been associated with anomalously warm years (Pinchuk et al., 2021). For these reasons they may have some potential as indicator species for zooplankton nutritional quality in the region.

Copepods of the genus *Neocalanus* (*N. plumchrus, N. cristatus, N. flemigeri*) had the largest impact of any taxonomic group on bulk nutritional quality of the zooplankton community. They were commonly correlated with high ED and TL content, across multiple surveys, including those in which they were not as prevalent (2019). Copepods make up the largest proportion of crustacean zooplankton abundance in most samples (Fig. 3.3) and tend to be particularly lipid-rich as many of them store lipids in the form of droplets or oil sacs (Lee et al., 2006). *Neocalanus* in particular, form large oil sacs (which contain wax esters) that fill the majority of their prosome, and are used as energy reserves during overwintering and fuel reproduction at depth where/when it is food limited (Evanson et al., 2000; Lee et al., 2006). As per their life-history, these lipid-rich copepods will enter diapause between 250-1000 m depth, representing a significant vertical displacement of high-quality zooplankton prey (Miller et al., 1984). It is plausible to assume this migration reduces zooplankton nutritional quality <250 m but provides a high-quality food source to predators which reside >250 m (*e.g*., benthic organisms and meso-/benthopelagic fishes), also presenting a potentially large energy influx to NE Pacific seamounts within this depth range.

The relative abundance of gelatinous species tended to be negatively associated with zooplankton nutritional quality. Doliolids and salps were the most common gelatinous taxa and were both correlated with negative energy density and lipid values across multiple years. Doliolids were frequently the dominant species in all years except 2022, which had significantly higher ED. Samples collected during the 2021 and 2022 surveys were characterized by a much higher proportion of large copepods relative to gelatinous species and were accompanied by significantly more TL than the other years. In addition, the regional difference between slope and offshore sites in 2017 demonstrated a taxonomic difference where slope sites had few to no doliolids and higher ED in comparison to low ED offshore sites with a high proportion of doliolids and fewer copepods (Fig. 3.5 & 3.7). Past research has found gelatinous species to be quite lipid-poor (Wang and Jeffs, 2014) and supports these observations.

3.4.7 The pervasive influence of *Neocalanus* spp.

Neocalanus spp. were responsible for the largest changes in bulk zooplankton biomass, TL, and ED, and skewed size-distribution measurements. Samples that were dominated by *Neocalanus* (2021 and 2022) had significantly higher bulk zooplankton biomass, TL content, and ED in the 1-2 and 2-4mm size fractions, which are the size fractions in which they settle. In fact, *Neocalanus* were commonly >4mm in length but copepods tend to sort into sieves based on body width and not length (Skjoldal, 2021). During the 2021 survey (highest *Neocalanus* abundance), only the biomass of intermediate size fractions were correlated with bulk zooplankton biomass, demonstrating that intermediate size fractions were directly correlated to total zooplankton biomass. Biomass of the smallest and largest size fractions did not have a significant influence on bulk zooplankton biomass for any given site. This indicates that when dominant, *Neocalanus* spp. are likely the key driver of total zooplankton biomass quantity and quality in the region.

The NBSS measured in years with high abundances of *Neocalanus* spp. often became less linear and more parabolic. High abundances of *Neocalanus* spp. increased the intermediate (1-2 and 2-4 mm) biomass values to greater than other size fractions used in the NBSS estimation. In samples from the 2021 and 2022 surveys, the NBSS became less linear (lower R^2) and more parabolic (Appendix 5). This change in shape produces shallower NBSS slopes, therefore indicating a community with a larger proportion of large organisms. The estimation of NBSS spectral slopes with this method requires a linear relationship between log biomass and size-bin (Rykaczewski and Checkley, 2008) and when *Neocalanus* spp. were in high abundances the relationship becomes more parabolic, becoming less accurate when treated with a linear model.

3.4.8 Research implications

Changes in the Canadian Offshore Pacific Bioregion marine ecosystem with a warming ocean

Warm-water anomalies have become more frequent over the past century, and are likely to continue with global climate change (Oliver et al., 2018). With a shift toward more anomalously warm years, the standing stock of zooplankton will likely resemble the samples collected in 2017 and 2019. This includes a shift in zooplankton taxonomic composition (including significantly less *Neocalanus* spp.; Ashlock et al., 2021), reducing bulk zooplankton biomass and therefore the absolute amount of all macromolecules and energy within the water column (as seen in Table. 3.3). This was emphasized in TL, as there was on average 1.6x more (less) TL per gram of biomass in the cold (warm) years. It is possible that predators may be able to compensate for reduced prey quality by increasing the quantity consumed or by shifting their range to regions of higher prey quality, but this does require typically greater energy expenditure by the predators

(Cruz-Rivera and Hay, 2000; Cavole et al., 2016). However, there are still clear indications of bird (Cassin's Auklet) and fish species (specifically Coho salmon, Chinook salmon, and Pollock) which are more successful when subarctic copepods are present (Hunt Jr et al., 2002; Cavole et al., 2016; Hipfner et al. 2020). When these subarctic species are not present, Chinook salmon can adjust their diet to include more Rockfish larva, but this still results in lower fitness in Chinook and may lower larval recruitment of Rockfish (Daly and Brodeur, 2015).

Changes in the pelagic ecosystem may also have significant impact on the marine snow exported to benthic regions. For example, salps and small-bodied copepods are responsible for relatively large amounts of fecal carbon export in comparison to large-bodied copepods; therefore, a community with many small-bodied copepods and salps would have a relatively higher carbon export from the euphotic zone to the mesopelagic and benthic regions (Stamieszkin et al., 2021). Further monitoring of the pelagic and benthic organisms would help determine the level of coupling between zooplankton taxonomic composition change with heat-events and the deep-sea organisms which are the target for protection within the TḥT MPA.

Future monitoring of the Canadian Offshore Pacific Bioregion MPAs

Time series of zooplankton biomass and nutritional quality can provide useful metrics to monitor ocean change. The techniques demonstrated here are easily incorporated into existing monitoring programs. DFO has two long-term oceanographic monitoring programs that sample near the TḥT MPA: La Perouse and Line P (https://www.dfo-mpo.gc.ca/science/oceanography-oceanographie/activities/index-eng.html). La Perouse is a biannual survey that occurs off the west coast of Vancouver Island, BC, and covers much of the self-break region. Line P is a triannual survey that traverses a transect from the shelf to the international offshore Pacific Ocean. The spatial coverage of both programs can provide insight into the conditions within the Canadian OPB across multiple seasons. Both programs regularly use bongos to collect biomass and taxonomic samples. Incorporation of the procedure developed in this thesis for both programs would yield a zooplankton nutritional quality time-series, allowing a more nuanced evaluation of the seasonal and interannual effects of environmental change on zooplankton communities in the Canadian OPB and wider NE Pacific. The propagation of these changes through higher trophic levels can also be evaluated by incorporating and comparing existing Canadian OPB fish and benthic survey data (Hake surveys, Salmon of the year assessments, and Northeast Pacific Deep-sea Exploration Project (NEPDEP) expeditions).

3.4.9 Conclusions

Zooplankton prey quantity and quality demonstrated substantial variability across interannual timescales and to a lesser extent, across offshore and deep-shelf bioregions in the Canadian OPB.

Zooplankton biomass and TL content were significantly higher in 2021 and 2022, while TP and ED was significantly increased in 2022; indicating that zooplankton sampled in 2022 were the most nutritious prey in our dataset. The decrease in total zooplankton abundance across these years also shows that although there was an increase in biomass and quality of zooplankton, macromolecules were concentrated into fewer individuals.

Changes in zooplankton quality were driven by the change from low quality gelatinous and sub-tropical crustacean species to high quality boreal/subarctic crustacean species characteristic of cool conditions. Zooplankton communities with higher proportions of gelatinous species have a lower nutritional value than those with greater proportions of crustacean species. *Neocalanus* copepods were the strongest positive driver of whole-community nutritional quality. Environmental factors that drive changes in the relative proportion of gelatinous *versus* crustacean zooplankton will exert large changes in total zooplankton quality. These changes may propagate to larger consumers if they do not have the ability to adapt feeding behaviour and change prey selection to meet their dietary requirements.

All zooplankton data in this chapter utilized bongo net samples to efficiently gather taxonomic and nutritional information on zooplankton as a food source to higher trophic levels. Zooplankton sampling requires significant ship-time resulting in limited sampling in any given survey/region. It is therefore important to optimize information gained by expanding the number of analyses routinely carried out on any given biomass sample. These procedures can be incorporated into existing monitoring systems to expand the understanding of spatiotemporal patterns in zooplankton quality.

Chapter 4: Implications for future research and monitoring of seamounts in the Canadian Offshore Pacific Bioregion

The main objective of this thesis was to help inform conservation and monitoring efforts of seamounts in the Canadian Offshore Pacific Bioregion (OPB) through the quantification of zooplankton as an energy source to higher trophic levels in the region. The secondary objective was to demonstrate the range of additional analyses that can be performed on zooplankton biomass samples, which are typically few in number and often underutilized. This thesis accomplished these objectives by using zooplankton biomass samples to quantify zooplankton nutritional quality using energy density (ED), total lipid (TL), and total protein (TP). In Chapter 2, zooplankton biomass distribution patterns and zooplankton nutritional quality were used to describe the allochthonous energy supply to 13 Canadian OPB seamounts. In Chapter 3, the spatiotemporal variability of zooplankton nutritional quality was quantified in the Canadian OPB, while also highlighting key indicator taxa associated with high and low nutritional quality. Throughout all chapters, suggestions were provided for future research and monitoring within the Canadian OPB.

4.1 Future research

4.1.1 Establishing food web connections within the Canadian Offshore Pacific Bioregion

In order to properly translate interannual and spatial variability in the allochthonous energy supply from zooplankton to seamount ecosystems, food-web connections between pelagic and benthic organisms must be identified and quantified. Such connectivity may be in the form of direct consumption of (for example) zooplankton by seamount-resident animals, but could also be via the sinking of marine snow in the overlying water column, including phytoplankton, zooplankton fecal pellets, moults, and carcasses, in addition to other biological byproducts (Alldredge and Silver, 1988). One way to explore such trophic relationships would be via the analysis of fatty acid profiles and stable isotope ratios between consumers and their potential food sources, as reviewed in Dalsgaard et al. (2003) and Fry (2006). This approach is based on the knowledge that many consumers integrate fatty acids from their diet into new tissues with little to no modification, and in a predictable manner. Similarly, the ratio of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotopes in predators and their prey can be used to corroborate trophic position and food sources, respectively (DeNiro and Epstein, 1978; Deniro and Epstein, 1981). Fatty acid and stable isotope analyses have recently been combined to study the coupling of pelagic and benthic food webs at Seine Seamount (Hirch and Christiansen, 2010) and more globally (Parzanini et al., 2019). Both analyses can be performed on phytoplankton, zooplankton, bentho-pelagic fish, benthic species, and marine snow.

Most seamounts in the Canadian OPB lie within MPAs, and therefore the sampling of bentho-pelagic fish and benthic invertebrates should be highly selective and accomplished without the use of trawls (*e.g.*, as used Hirch and Christiansen 2010). Instead, the use of baited pots or long-line fishing (ideally deployed for only short time periods) plus collections via remotely operated submersibles (ROVs) should be considered in order to avoid damage to the ecosystem. Zooplankton, phytoplankton, and marine snow can be collected with standard oceanographic techniques (*e.g.*, nets, rosette water sampling, and sediment traps). Species selection should be focused on those which dominate ecosystem biomass and/or are recognized as target conservation species on seamounts (*e.g.*, rockfish - *Sebastes* and *Sebastolobus* spp., sablefish, brittle stars, sea pens, various species of cold-water corals and sponges), as these are more likely to contribute to the major energy connections within seamount food webs (DFO, 2019).

Establishing food web connections between zooplankton and seamount organisms is important to provide additional support to operational objectives established in the monitoring framework for SK-B MPA, which will likely be used to inform for the future conservation of seamount ecosystems all across Canada's oceans (DFO, 2023). Evidence of significant bentho-pelagic food web coupling would provide support for the preservation of pelagic environments in these regions (Objective 1.2.b) in order to uphold key ecosystem functions and trophic structure (Objective 1.3.a).

4.1.2 Long-term monitoring of seamounts and zooplankton in the Canadian Offshore Pacific Bioregion

Long-term oceanographic monitoring is needed to accomplish operational objectives set out by the SK-B MPA monitoring framework (DFO, 2023) and to further the understanding of zooplankton nutritional quality variability and its influence on other ecosystems in the Canadian OPB. The research presented in this thesis is relevant to two operational objectives provided in the monitoring framework: Objective 1.2.b states that habitats within the MPA are protected and conserved, including pelagic and sea surface conditions remaining within a range of the natural state; and Objective 1.3.a states that ecosystem food webs are protected and conserved, including ecosystem function and trophic structure remaining within a range of the natural state (DFO, 2023). Continuing the oceanographic sampling started in this thesis will inform the "natural state" the pelagic conditions and trophic structure of the regions. Currently the existing zooplankton time series (*e.g.* Line P and La Perouse) in the Canadian OPB provide taxonomic and abundance data but does not include size-fractionated samples or any nutritional quality metrics. This research provides novel information to the natural variability of zooplankton size distribution and nutritional quality in the OPB but was not completed across a long enough period to adequately describe the whole range of variability in zooplankton nutritional quality experienced in the Canadian OPB across long-term climactic cycles, therefore not all variability in the environment has been sampled.

Zooplankton nutritional quality measurements from repeated oceanographic monitoring programs within the Canadian OPB can provide a finer-scale understanding of seasonal/annual/interannual changes in zooplankton communities (Mackas, 1992; Weil et al., 2020; Stevens et al., 2022). Ideally, this monitoring would include both offshore and slope zooplankton, which demonstrated significant taxonomic and nutritional quality differences throughout this thesis. Fortunately, these results suggest that basic long-term monitoring can be achieved using DFO's existing Line P and La Perouse programs which, together, provide adequate coverage to sample zooplankton from both offshore and slope regions. Matching time-series of zooplankton nutritional quality to other time-series in the region (*e.g.*, climatic fluctuations, fisheries catch, warm-water anomalies) would be informative for understanding the variability of energy availability to higher trophic levels and seamounts.

Long-term monitoring is a key part of effective marine conservation strategies and can aid in further study of seamounts in the Canadian OPB. Although ship-based oceanography and ROV surveys remain the gold-standard for marine monitoring, both are very expensive, time intensive, and provide only "snapshots" of *in-situ* conditions at the time of sampling. In contrast, the increased development of autonomous instruments (*e.g.,* gliders, AUVs, moorings, and sediment traps) and remote sensing (satellite) technologies offer a means to implement broader spatiotemporal sampling coverage. These tools could be particularly useful when investigating the existence/persistence of seamount effects, as they are capable of recording data continuously across long time periods (weeks to months). Satellite monitoring around seamounts could help to better constrain seasonal and spatial patterns of chlorophyll and sea surface temperature around seamounts, possibly indicating local primary productivity enhancement and upwelling (Demarcq et al., 2020; Leitner et al., 2020). Autonomous gliders or AUVs and moorings with CTD capabilities could be deployed to quantify longer-term patterns in local chemical and physical characteristics of the water column (Howatt et al., 2022; Wang et al., 2023). In addition, gliders and moorings with acoustic capabilities (*e.g.*, equipped with current meters or ADCPs) could help quantify zooplankton distribution patterns, vertical migration behaviours, and mesoscale currents and water dynamics (Powell and Ohman, 2015; Howatt et al., 2022; Wang et al., 2023; Cauchy et al., 2023). Finally, the deployment of sediment traps to collect marine snow (on moorings or at the seafloor) could be used to quantify and compare vertical carbon flux at seamounts and other benthic environments in the region (Gao et al., 2020). This would be important to measure, as marine snow has been deemed a substantial food source to seamount organisms (Genin and Dower, 2007). Taken together, this suite of techniques could be employed to provide further insight into Canadian OPB seamount processes through time, and the underlying energy flow which supports these biomass hotspots.

4.2 Conclusions

Zooplankton samples can be subjected to a wide array of analyses which can provide useful metrics to quantify zooplankton communities as a food source for higher trophic levels - including size fractionated biomass and dry weight, ash-free dry weight, total lipid and protein content, and energy density. When paired with taxonomic analysis, the influence of individual species on bulk biomass samples can also be identified and quantified. This multi-factor approach provides significantly more information than using either total zooplankton biomass or abundance alone, as it also considers variability in the macromolecular composition, and thus food quality, represented by zooplankton communities. Traditional zooplankton sampling requires large amounts of ship-time, so collecting more than a few biomass samples per station is unrealistic in most situations. Therefore, the ability to split one biomass sample into seven or more analyses, as demonstrated in this thesis, is an extremely valuable and cost-effective approach for studying and monitoring zooplankton communities. Using this approach, this thesis provides the first in-depth, multi-year, examination of spatiotemporal variability in zooplankton communities around seamounts in the Canadian OPB.

Changes in the taxonomic composition of zooplankton communities underlie differences in community size-structure, biomass, and nutritional quality between years and regions. In the OPB, specific taxonomic groups drove the differences between relatively high-quality and low-quality bulk zooplankton samples. *Neocalanus* spp. were associated with increased biomass and total lipid content of samples, thereby increasing both the quantity and quality of zooplankton available for zooplanktivorous predators. The abundance of copepod species also tended to be associated with higher energy density of bulk zooplankton samples. Alternatively, gelatinous species (*i.e.*, doliolids and salps) were associated with lower energy densities in bulk zooplankton, representing a decrease in overall zooplankton quality. Therefore, it is plausible to estimate bulk zooplankton nutritional qualities based on environmental conditions (*e.g.*, cold vs warm regime, coastal vs offshore) in which these species typically thrive.

Interannual difference in environmental conditions were the main drivers of variability in zooplankton taxonomic, biomass, and nutritional quality in the Canadian OPB. Although numerous within the region, seamounts do not appear to directly influence the distribution of zooplankton, at least during the periods when these 13 seamounts were sampled. All zooplankton community and compositional metrics measured in this thesis displayed some level of interannual variability. However, spatial differences were only detected in ED, size-distribution, and total species abundance (and all to a much lower magnitude than interannual variability). The largest magnitude of change was between relatively cool and relatively warm years, whereby cool years were characterized by low abundances of large high-quality zooplankton, while warm years had higher abundances of small, relatively, lower-quality zooplankton. Zooplankton are a vital food source to many higher trophic levels, therefore the patterns of zooplankton distribution within the Canadian OPB which were demonstrated in this thesis likely have significant implications for variability in trophic structure and energy flow through NE Pacific ecosystems.

References

Aarflot, J. M., Aksnes, D. L., Opdal, A. F., Skjoldal, H. R., and Fiksen, (2019). Caught in broad daylight: Topographic constraints of zooplankton depth distributions. Limnology and Oceanography, 64(3):849–859. doi: 10.1002/lno.11079.

Alldredge, A. L. and Silver, M. W. (1988). Characteristics, dynamics and significance of marine snow. Progress in Oceanography, 20(1):41–82. doi: 10.1016/0079-6611(88)90053-5.

Archer, S. K., Kahn, A. S., Leys, S. P., Norgard, T., Girard, F., Du Preez, C., and Dunham, A. (2018). Pyrosome consumption by benthic organisms during blooms in the northeast Pacific and Gulf of Mexico. Ecology, 99(4):981–984.

Ashlock, L., García-Reyes, M., Gentemann, C., Batten, S., and Sydeman, W. (2021). Temperature and Patterns of Occurrence and Abundance of Key Copepod Taxa in the Northeast Pacific. Frontiers in Marine Science, 8. doi: 10.3389/fmars.2021.670795.

Ban, S., Curtis, J. M. R., Germain, C. S., Perry, R. I., and Therriault, T. W. (2016). Identification of Ecologically and Biologically Significant Areas (EBSAs) in Canada's Offshore Pacific Bioregion. Canadian Science Advisory Secretariat Pacific Region Science Advisory Report 2016/011.

Bandara, K., Varpe, , Wijewardene, L., Tverberg, V., and Eiane, K. (2021). Two hundred years of zooplankton vertical migration research. Biological Reviews, 96(4):1547–1589. doi: 10.1111/brv.12715.

Banse, K. (1962). Net Zooplankton and Total Zooplankton. Cons. Internat. Explor. De la Mer, 153:211–215.

Barton, E. (2001). Island Wakes. In Encyclopedia of Ocean Sciences, pages 1397–1403. Elsevier. doi: 10.1006/rwos.2001.0140.

Batten, S. D. and Freeland, H. J. (2007). Plankton populations at the bifurcation of the North Pacific Current. Fisheries Oceanography, 16(6):536–546. doi: 10.1111/j.1365-2419.2007.00448.x.

Beamish, R. J. and Mahnken, C. (2001). A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography, 49(1):423–437. doi: 10.1016/S0079-6611(01)00034-9.

Benoit-Bird, K. J. (2004). Prey caloric value and predator energy needs: foraging predictions for wild spinner dolphins. Marine Biology, 145(3):435–444. doi: 10.1007/s00227-004-1339-1.

Bertram, D. F., Mackas, D. L., and McKinnell, S. M. (2001). The seasonal cycle revisited: interannual variation and ecosystem consequences. Progress in Oceanography, 49(1):283–307. doi: 10.1016/S0079-6611(01)00027-1.

Beukema, J. J. (1997). Caloric values of marine invertebrates with an emphasis on the soft parts of marine bivalves. Oceanography and Marine Biology: An Annual Review, 35:387–414.

Boehlert, G. W. and Genin, A. (1987). A Review of the Effects of Seamounts on Biological Processes. In Seamounts, Islands, and Atolls, pages 319–334. American Geophysical Union (AGU). doi: 10.1029/GM043p0319.

Bograd, S. J. and Lynn, R. J. (2001). Physical-biological coupling in the California Current during the 1997–99 El Niño-La Niña Cycle. Geophysical Research Letters, 28(2):275–278. doi: 10.1029/2000GL012047.

Brechner Owens, W. and Hogg, N. G. (1980). Oceanic observations of stratified Taylor columns near a bump. Deep Sea Research Part A. Oceanographic Research Papers, 27(12):1029–1045. doi: 10.1016/0198-0149(80)90063-1.

Brinton, E. (1967). Vertical Migration and Avoidance Capability of Euphausiids in the California Current. Limnology and Oceanography, 12(3):451–483. doi: 10.4319/lo.1967.12.3.0451.

Brodeur, R. D. (1989). Neustonic feeding by juvenile salmonids in coastal waters of the Northeast Pacific. Canadian Journal of Zoology, 67(8):1995–2007. doi: 10.1139/z89-284.

Brodeur, R. D. (2001). Habitat-specific distribution of Pacific ocean perch (Sebastes alutus) in Pribilof Canyon, Bering Sea. Continental Shelf Research, 21(3):207–224. doi: 10.1016/S0278-4343(00)00083-2.

Burd, B. J. and Thomson, R. E. (2019). Seasonal patterns in deep acoustic backscatter layers near vent plumes in the northeastern Pacific Ocean. FACETS, 4(1):183–209. Publisher: Canadian Science Publishing doi: 10.1139/facets-2018-0027.

Canessa, R. R., Conley, K. W., and Smiley, B. D. (2003). Bowie seamount pilot marine protected area: An ecosystem overview report. Canadian Technical Report of Fisheries and Aquatic Sciences 2461.

Cauchy, P., Heywood, K. J., Merchant, N. D., Risch, D., Queste, B. Y., and Testor, P. (2023). Gliders for passive acoustic monitoring of the oceanic environment. Frontiers in Remote Sensing, 4. doi: 10.3389/frsen.2023.1106533.

Cavole, L. M., Demko, A. M., Diner, R. E., Giddings, A., Koester, I., Pagniello, C. M., Paulsen, M.-L., Ramirez-Valdez, A., Schwenck, S. M., Yen, N. K., Zill, M. E., and Franks, P. J. (2016). Biological Impacts of the 2013–2015 Warm-Water Anomaly in the Northeast Pacific: Winners, Losers, and the Future. Oceanography, 29(2):273–285. Publisher: Oceanography Society.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Ñiquen C., M. (2003). From Anchovies to Sardines and Back: Multidecadal Change in the Pacific Ocean. Science, 299(5604):217–221. doi: 10.1126/science.1075880.

Chavez, F. P., Strutton, P. G., Friederich, G. E., Feely, R. A., Feldman, G. C., Foley, D. G., and McPhaden, M. J. (1999). Biological and Chemical Response of the Equatorial Pacific Ocean to the 1997-98 El Niño. Science, 286(5447):2126–2131. Publisher: American Association for the Advancement of Science.

Chen, B., Masunaga, E., Smith, S. L., and Yamazaki, H. (2021). Diel vertical migration promotes zooplankton horizontal patchiness. Journal of Oceanography, 77(1):123–135. doi: 10.1007/s10872-020-00564-4.

Chen, C.-T., Bănaru, D., Carlotti, F., Faucheux, M., and Harmelin-Vivien, M. (2019). Seasonal variation in biochemical and energy content of size fractionated zooplankton in the Bay of Marseille (North-Western Mediterranean Sea). Journal of Marine Systems, 199:103223. doi: 10.1016/j.jmarsys.2019.103223.

Christiansen, B., Martin, B., and Hirch, S. (2009). The benthopelagic fish fauna on the summit of Seine Seamount, NE Atlantic: Composition, population structure and diets. Deep Sea Research Part II: Topical Studies in Oceanography, 56(25):27052712. doi: 10.1016/j.dsr2.2008.12.032.

Clark, M. R., Watling, L., Rowden, A. A., Guinotte, J. M., and Smith, C. R. (2011). A global seamount classification to aid the scientific design of marine protected area networks. Ocean & Coastal Management, 54(1):19–36. doi: 10.1016/j.ocecoaman.2010.10.006.

Colton Jr, J. B., Green, J. R., Byron, R. R., and Frisella, J. L. (1980). Bongo Net Retention Rates as Effected by Towing Speed and Mesh Size. Canadian Journal of Fisheries and Aquatic Sciences, 37(4):606–623. Publisher: NRC Research Press doi: 10.1139/f80-077.

Contreras, T., Olivar, M. P., González-Gordillo, J. I., and Hulley, P. A. (2020). Feeding patterns of transforming and juvenile myctophids that migrate into neustonic layers. Marine Ecology Progress Series, 650:239–252. doi: 10.3354/meps13234.

Copeman, L. A. and Laurel, B. J. (2010). Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. Marine Ecology Progress Series, 412:259272. doi: 10.3354/meps08661.

Copeman, L. A., Parrish, C. C., Brown, J. A., and Harel, M. (2002). Effects of docosahexaenoic, eicosapentaenoic, and arachidonic acids on the early growth, survival, lipid composition and pigmentation of yellowtail flounder (Limanda ferruginea): a live food enrichment experiment. Aquaculture, 210(1):285–304. doi: 10.1016/S00448486(01)00849-3.

Costalago, D., Forster, I., Nemcek, N., Neville, C., Perry, R. I., Young, K., and Hunt, B. P. V. (2020). Seasonal and spatial dynamics of the planktonic trophic biomarkers in the Strait of Georgia (northeast Pacific) and implications for fish. Scientific Reports, 10:8517. doi: 10.1038/s41598-020-65557-1.

Crochelet, E., Barrier, N., Andrello, M., Marsac, F., Spadone, A., and Lett, C. (2020). Connectivity between seamounts and coastal ecosystems in the Southwestern Indian Ocean. Deep Sea Research Part II: Topical Studies in Oceanography, 176:104774. doi: 10.1016/j.dsr2.2020.104774.

Cruz-Rivera, E. and Hay, M. E. (2000). Can Quantity Replace Quality? Food Choice, Compensatory Feeding, and Fitness of Marine Mesograzers. Ecology, 81(1):201–219. doi: 10.1890/0012-9658(2000)081[0201:CQRQFC]2.0.CO;2.

Cumminns, K. W. and Wuycheck, J. C. (1971). Caloric Equivalents for Investigations in Ecological Energetics: With 2 figures and 3 tables in the text. SIL Communications, 1953-1996, 18(1):1–158. doi: 10.1080/05384680.1971.11903918.

Dai, S., Zhao, Y., Li, X., Wang, Z., Zhu, M., Liang, J., Liu, H., and Sun, X. (2022). Seamount effect on phytoplankton biomass and community above a deep seamount in the tropical western Pacific. Marine Pollution Bulletin, 175:113354. doi: 10.1016/j.marpolbul.2022.113354.

Dai, S., Zhao, Y., Li, X., Wang, Z., Zhu, M., Liang, J., Liu, H., Tian, Z., and Sun, X. (2020). The seamount effect on phytoplankton in the tropical western Pacific. Marine Environmental Research, 162:105094. doi: 10.1016/j.marenvres.2020.105094.

Dalsgaard, J., St. John, M., Kattner, G., Müller-Navarra, D., and Hagen, W. (2003). Fatty acid trophic markers in the pelagic marine environment. In Advances in Marine Biology, volume 46, pages 225–340. Academic Press. doi: 10.1016/S00652881(03)46005-7.

Daly, E. A. and Brodeur, R. D. (2015). Warming Ocean Conditions Relate to Increased Trophic Requirements of Threatened and Endangered Salmon. PLOS ONE, 10(12):e0144066. Publisher: Public Library of Science doi: 10.1371/journal.pone.0144066.

De Leo, F. C., Ogata, B., Sastri, A. R., Heesemann, M., Mihály, S., Galbraith, M., and Morley, M. G. (2018). High-frequency observations from a deep-sea cabled observatory reveal seasonal overwintering of Neocalanus spp. in Barkley Canyon, NE Pacific: Insights into particulate organic carbon flux. Progress in Oceanography, 169:120–137. doi: 10.1016/j.pocean.2018.06.001.

De Robertis, A., Schell, C., and Jaffe, J.S. (2003). Acoustic observations of the swimming behaviour of the euphausiid Euphausia pacifica Hansen. ICES Journal of Marine Science, 60:885-898. doi: 10.1016/S0079-6611(99)00012-9

De Souza, C. S., Da Conceição, L. R., Freitas, T. S. S., Aboim, I. L., Schwamborn, R., Neumann-Leitão, S., and Mafalda Junior, P. D. O. (2020). Size Spectra Modeling of Mesozooplankton over a Tropical Continental Shelf. Journal of Coastal Research, 36(4):795. doi: 10.2112/JCOASTRES-D-19-00102.1.

Demarcq, H., Noyon, M., and Roberts, M. J. (2020). Satellite observations of phytoplankton enrichments around seamounts in the South West Indian Ocean with a special focus on the Walters Shoal. Deep-Sea Research Part II: Topical Studies in Oceanography, 176:104800. doi: 10.1016/j.dsr2.2020.104800.

Denda, A., Stefanowitsch, B., and Christiansen, B. (2017). From the epipelagic zone to the abyss: Trophic structure at two seamounts in the subtropical and tropical Eastern Atlantic - Part I zooplankton and micronekton. Deep Sea Research Part I: Oceanographic Research Papers, 130:63–77. doi: 10.1016/j.dsr.2017.10.010.

DeNiro, M. J. and Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta, 42(5):495–506. doi: 10.1016/0016-7037(78)90199-0.

Deniro, M. J. and Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta, 45(3):341–351. doi: 10.1016/0016-7037(81)90244-1.

Denman, K. and Dower, J. (2001). Patch Dynamics. In Encyclopedia of Ocean Sciences, pages 2107–2114. Elsevier. doi: 10.1006/rwos.2001.0290.

Deslauriers, D., Heironimus, L. B., and Chipps, S. R. (2016). Test of a foraging-bioenergetics model to evaluate growth dynamics of endangered pallid sturgeon (Scaphirhynchus albus). Ecological Modelling, 336:1–12. doi: 10.1016/j.ecolmodel.2016.05.017.

Dessier, A., Dupuy, C., Kerric, A., Mornet, F., Authier, M., Bustamante, P., and Spitz, J. (2018). Variability of energy density among mesozooplankton community: New insights in functional diversity to forage fish. Progress in Oceanography, 166:121–128. doi: 10.1016/j.pocean.2017.10.009.

DFO (2004). Identification of Ecologically and Biologically Significant Areas. National Capital Region Ecosystem Status Report 2004/006.

DFO (2009). Development of a Framework and Principles for the Biogeographic Classification of Canadian Marine Areas. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2009/056.

DFO (2019). Biophysical and Ecological Overview of the Offshore Pacific Area of Interest (AOI). Canadian Science Advisory Secretariat Science Response 2019/011.

DFO (2023). Monitoring Framework for SGaan Kinghlas-Bowie Seamount Marine Protected Area, British Columbia, Canada. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2023/011.

Doty, M. S. and Oguri, M. (1956). The Island Mass Effect. ICES Journal of Marine Science, 22(1):33–37. doi: 10.1093/icesjms/22.1.33.

Dower, J., Freeland, H., and Juniper, K. (1992). A strong biological response to oceanic flow past Cobb Seamount. Deep Sea Research Part A. Oceanographic Research Papers, 39(7-8):1139–1145. doi: 10.1016/0198-0149(92)90061-W.

Dower, J. F. and Mackas, D. L. (1996). "Seamount effects" in the zooplankton community near Cobb Seamount. Deep Sea Research Part I: Oceanographic Research Papers, 43(6):837–858. doi: 10.1016/0967-0637(96)00040-4.

Du Preez, C. and Norgard, T. (2022). Identification of Representative Seamount Areas in the Offshore Pacific Bioregion, Canada. Canadian Science Advisory Secretariat (CSAS) Research Document 2022/042, pages viii + 136.

Dubischar, C. D., Pakhomov, E. A., von Harbou, L., Hunt, B. P. V., and Bathmann, U. V. (2012). Salps in the Lazarev Sea, Southern Ocean: II. Biochemical composition and potential prey value. Marine Biology, 159(1):15–24. doi: 10.1007/s00227011-1785-5.

Dunham, J. S. and Duffus, D. A. (2001). Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. Marine Ecology Progress Series, 223:299–310. doi: 10.3354/meps223299.

Décima, M. (2022). Zooplankton trophic structure and ecosystem productivity. Marine Ecology Progress Series, 692:23–42. doi: 10.3354/meps14077.

Evans, R., English, P. A., Gauthier, S., and Robinson, C. L. (2023). Quantifying the effects of extreme events and oceanographic variability on the spatiotemporal biomass and distribution of two key euphausiid prey species. Frontiers in Marine Science, 10. doi: 10.3389/fmars.2023.1031485.

Evanson, M., Bornhold, E. A., Goldblatt, R. H., Harrison, P. J., and Lewis, A. G. (2000). Temporal variation in body composition and lipid storage of the overwintering, subarctic copepod Neocalanus plumchrus in the Strait of Georgia, British Columbia (Canada). Marine Ecology Progress Series, 192:239–247. doi: 10.3354/meps192239.

Fisher, J. L., Peterson, W. T., and Rykaczewski, R. R. (2015). The impact of El Niño events on the pelagic food chain in the northern California Current. Global Change Biology, 21(12):4401–4414. doi: 10.1111/gcb.13054.

Fock, H. O., Matthiessen, B., Zidowitz, H., and Westernhagen, H. v. (2002). Diel and habitat-dependent resource utilisation by deep-sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. Marine Ecology Progress Series, 244:219–233. doi: 10.3354/meps244219.

Folch, J., Lees, M., and Sloane Stanley, G. H. (1957). A simple method for the isolation and purification of total lipides from animal tissues. The Journal of Biological Chemistry, 226(1):497–509.

Folt, C. L. and Burns, C. W. (1999). Biological drivers of zooplankton patchiness. Trends in Ecology & Evolution, 14(8):300–305. doi: 10.1016/S0169-5347(99)01616X.

Foy, R. and Norcross, B. (1999). Spatial and temporal variability in the diet of juvenile Pacific herring (Clupea pallasi) in Prince William Sound, Alaska. Canadian Journal of Zoology, 77(5):697–706. doi: 10.1139/cjz-77-5-697.

Freeland, H. J. and Cummins, P. F. (2005). Argo: A new tool for environmental monitoring and assessment of the world's oceans, an example from the N.E. Pacific. Progress in Oceanography, 64(1):31–44. doi: 10.1016/j.pocean.2004.11.002.

Fry, B. (2006). Stable isotope ecology. Springer, New York, NY.

Fudge, H. (1968). Biochemical Analysis of Preserved Zooplankton. Nature, 219(5152):380–381. doi: 10.1038/219381a0.

Gao, M., Huang, B., Liu, Z., Zhao, Y., and Zhang, Y. (2020). Observations of marine snow and fecal pellets in a sediment trap mooring in the northern South China Sea. Acta Oceanologica Sinica, 39(3):141–147. doi: 10.1007/s13131-020-1561-9.

Genin, A. (2004). Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems, 50(1):3–20. doi: 10.1016/j.jmarsys.2003.10.008.

Genin, A. and Boehlert, G. W. (1985). Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. Journal of Marine Research, 43(4):907–924. doi: 10.1357/002224085788453868.

Genin, A., Dayton, P. K., Lonsdale, P. F., and Spiess, F. N. (1986). Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature, 322(6074):59–61. doi: 10.1038/322059a0.

Genin, A. and Dower, J. F. (2007). Seamount Plankton Dynamics. In Pitcher, T. J., Morato, T., Hart, P. J. B., Clark, M. R., Haggan, N., and Santos, R. S., editors, Seamounts: Ecology, Fisheries & Conservation, pages 87–100. doi: 10.1002/9780470691953.ch5.

Genin, A., Greene, C., Haury, L., Wiebe, P., Gal, G., Kaartvedt, S., Meir, E., Fey, C., and Dawson, J. (1994). Zooplankton patch dynamics: daily gap formation over abrupt topography. Deep Sea Research Part I: Oceanographic Research Papers, 41(5):941–951. doi: 10.1016/0967-0637(94)90085-X.

Genin, A., Haury, L., and Greenblatt, P. (1988). Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep Sea Research Part A. Oceanographic Research Papers, 35(2):151–175. doi: 10.1016/0198-0149(88)90034-9.

Gilljam, D., Thierry, A., Edwards, F. K., Figueroa, D., Ibbotson, A. T., Jones, J. I., Lauridsen, R. B., P*etc*hey, O. L., Woodward, G., and Ebenman, B. (2011). Seeing Double:: Size-Based and Taxonomic Views of Food Web Structure. In Belgrano, A., editor, Advances in Ecological Research, volume 45 of The Role of Body Size in Multispecies Systems, pages 67–133. Academic Press. doi: 10.1016/B978-0-12386475-8.00003-4.

Goldblatt, R. H., Mackas, D. L., and Lewis, A. G. (1999). Mesozooplankton community characteristics in the NE subarctic Pacific. Deep Sea Research Part II: Topical Studies in Oceanography, 46(11):2619–2644. doi: 10.1016/S0967-0645(99)00078-8.

Graeve, M., Hagen, W., and Kattner, G. (1994) Herbivorous or omnivorous? On the significance of lipid compositions as trophic markers in Antarctic copepods. Deep Sea Research Part I: Oceanographic Research Papers, 41, 915–924.

Greenblatt, P., Shulenberger, E., and Wormuth, J. (1982). Small-scale distributions of zooplankton biomass. Deep Sea Research Part A. Oceanographic Research Papers, 29(4):443–457. doi: 10.1016/0198-0149(82)90069-3.

Guisande, C. (2006). Biochemical fingerprints in zooplankton. Limnetica, 25(1):369–376. doi: 10.23818/limn.25.25.

Guo, B., Wang, W., Shu, Y., He, G., Zhang, D., Deng, X., Liang, Q., Yang, Y., Xie, Q., Wang, H., and Wang, J. (2020). Observed Deep Anticyclonic Cap Over Caiwei Guyot. Journal of Geophysical Research: Oceans, 125(10):e2020JC016254. doi: 10.1029/2020JC016254.

Hardy, A. C. (1936). Observations on the uneven distribution of oceanic plankton. Discovery Reports, 11:511–538.

Harmelin-Vivien, M., Bnaru, D., Dromard, C. R., Ourgaud, M., and Carlotti, F. (2019). Biochemical composition and energy content of size fractionated zooplankton east of the Kerguelen Islands. Polar Biology, 42(3):603–617. Publisher: Springer Verlag doi: 10.1007/s00300-019-02458-8.

Harris, R., Wiebe, P., Lenz, J., Skjoldal, H.-R., and Huntley, M. (2000). ICES Zooplankton Methodology Manual. Elsevier.

Haury, L. R. (1976). Small-scale pattern of a California current zooplankton assemblage. Marine Biology, 37(2):137–157. doi: 10.1007/BF00389124.

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia, 503(1):163–170. doi: 10.1023/B:HYDR.0000008476.23617.b0.

Hays, G. C., Doyle, T. K., and Houghton, J. D. R. (2018). A Paradigm Shift in the Trophic Importance of Jellyfish? Trends in Ecology & Evolution, 33(11):874–884. doi: 10.1016/j.tree.2018.09.001.

Hays, G. C., Kennedy, H., and Frost, B. W. (2001). Individual variability in diel vertical migration of a marine copepod: Why some individuals remain at depth when others migrate. Limnology and Oceanography, 46(8):2050–2054. doi: 10.4319/lo.2001.46.8.2050.

Hertz, E., Trudel, M., Tucker, S., Beacham, T., Parken, C., Mackas, D., and Mazumder, A. (2016). Influences of ocean conditions and feeding ecology on the survival of juvenile Chinook Salmon (Oncorhynchus tshawytscha). Fisheries Oceanography, 25(4):407–419. doi: 10.1111/fog.12161.

Hipfner, J., Galbraith, M., Bertram, D. F., and Green, D. J. (2020). Basin-scale oceanographic processes, zooplankton community structure, and diet and reproduction of a sentinel North Pacific seabird over a 22-year period. Progress in Oceanography, 182:102290. doi: 10.1016/j.pocean.2020.102290.

Hirch, S. and Christiansen, B. (2010). The trophic blockage hypothesis is not supported by the diets of fishes on Seine Seamount: Trophic blockage not supported by diets of fishes. Marine Ecology, 31:107–120. doi: 10.1111/j.1439-0485.2010.00366.x.

Howatt, T., Ross, T., and Waterman, S. (2022). Canyon Downwelling and Water Mass Influences on Winter Zooplankton Distributions in the Coastal Northeast Pacific. Journal of Geophysical Research: Oceans, 127(11):e2022JC018540. doi: 10.1029/2022JC018540.

Hubbs, C. L. (1959). Initial discouveries of fish faunuas on seamounts and offshore banks in the eastern pacific. Pacific Science, 13:311–316.

Hunt Jr, G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., and Bond, N. A. (2002). Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Research Part II: Topical Studies in Oceanography, 49(26):5821–5853. doi: 10.1016/S0967-0645(02)00321-1.

Huntley, M. and Brooks, E. R. (1982). Effects of age and food availability on diel vertical migration of Calanus pacificus. Marine Biology, 71(1):23–31. doi: 10.1007/BF00396989.

Hébert, M.-P., Beisner, B. E., and Maranger, R. (2016). A meta-analysis of zooplankton functional traits influencing ecosystem function. Ecology, 97(4):1069–1080.

Isaacs, J. D. and Schwartzlose, R. A. (1965). Migrant Sound Scatterers: Interaction with the Sea Floor. Science, 150(3705):1810–1813. Publisher: American Association for the Advancement of Science doi: 10.1126/science.150.3705.1810.

Jo, N., Kang, J. J., Park, W. G., Lee, B. R., Lee, J. H., Kim, Y., Ahn, S. H., Lee, D., Min, J.-O., Kang, C.-K., and Lee, S. H. (2018). Carbohydrate-dominant Phytoplankton and Protein-high Zooplankton in the Northern Part of the Southwestern East/Japan Sea in 2015. Journal of Coastal Research, pages 371–375. Publisher: Coastal Education & Research Foundation, Inc.

Jo, N., Kang, J. J., Park, W. G., Lee, B. R., Yun, M. S., Lee, J. H., Kim, S. M., Lee, D., Joo, H., Lee, J. H., Ahn, S. H., and Lee, S. H. (2017). Seasonal variation in the biochemical compositions of phytoplankton and zooplankton communities in the southwestern East/Japan Sea. Deep Sea Research Part II: Topical Studies in Oceanography, 143:82–90. doi: 10.1016/j.dsr2.2016.12.001.

Ju, S.-J., Scolardi, K., Daly, K. L., and Harvey, H. R. (2004). Understanding the trophic role of the Antarctic ctenophore, Callianira antarctica, using lipid biomarkers. Polar Biology, 27(12):782–792. doi: 10.1007/s00300-004-0652-y.

Kaiser, M. J. and Williams, P. J. l. (2011). Marine Ecology: Processes, Systems, and Impacts. OUP Oxford. Google-Books-ID: WYKcAQAAQBAJ.

Kattner, G. and Hagen, W. (1998). Lipid metabolism of the Antarctic euphausiid Euphausia crystallorophias and its ecological implications. Marine Ecology Progress Series, 170:203–213. Publisher: Inter-Research Science Center.

Kattner, G. and Hagen, W. (2009). Lipids in marine copepods: latitudinal characteristics and perspective to global warming. In Kainz, M., Brett, M. T., and Arts, M. T., editors, Lipids in Aquatic Ecosystems, pages 257–280. Springer, New York, NY. doi: 10.1007/978-0-387-89366-2_11.

Kattner, G., Hagen, W., Graeve, M., and Albers, C. (1998). Exceptional lipids and fatty acids in the pteropod Clione limacina (Gastropoda) from both polar oceans. Marine Chemistry, 61(3):219–228. doi: 10.1016/S0304-4203(98)00013-9.

Keister, J. E., Di Lorenzo, E., Morgan, C. A., Combes, V., and Peterson, W. T. (2011). Zooplankton species composition is linked to ocean transport in the Northern California Current. Global Change Biology, 17(7):2498–2511. doi: 10.1111/j.1365-2486.2010.02383.x.

Kelley, D., Richards, C., and Layton, C. (2023). Oce: Analysis of Oceanography Data.

Larson, R. J. and Harbison, G. R. (1989). Source and Fate of Lipids in Polar Gelatinous Zooplankton. Arctic, 42(4):339–346. Publisher: Arctic Institute of North America.

Lebrato, M., Pahlow, M., Frost, J. R., Küter, M., de Jesus Mendes, P., Molinero, J.-C., and Oschlies, A. (2019). Sinking of Gelatinous Zooplankton Biomass Increases Deep Carbon Transfer Efficiency Globally. Global Biogeochemical Cycles, 33(12):1764–1783. doi: 10.1029/2019GB006265.

Lee, R., Hagen, W., and Kattner, G. (2006). Lipid storage in marine zooplankton. Marine Ecology Progress Series, 307:273–306. doi: 10.3354/meps307273.

Lee, R. F. and Hirota, J. (1973). Wax Esters in Tropical Zooplankton and Nekton and the Geographical Distribution of Wax Esters in Marine Copepods1. Limnology and Oceanography, 18(2):227–239. doi: 10.4319/lo.1973.18.2.0227.

Lee, R. F., Hirota, J., and Barnett, A. M. (1971). Distribution and importance of wax esters in marine copepods and other zooplankton. Deep Sea Research and Oceanographic Abstracts, 18(12):1147–1165. doi: 10.1016/0011-7471(71)90023-4.

Leitner, A. B., Neuheimer, A. B., and Drazen, J. C. (2020). Evidence for long-term seamount-induced chlorophyll enhancements. Scientific Reports, 10(1):12729. doi: 10.1038/s41598-020-69564-0.

Li, H., Gu, Y., Cai, Q., Dong, X., and Ye, L. (2022). Zooplankton Size Structure in Relation to Environmental Factors in the Xiangxi Bay of Three Gorges Reservoir, China. Frontiers in Ecology and Evolution, 10:800025. doi: 10.3389/fevo.2022.800025.

Lobus, N. V., Flint, M. V., Flerova, E. A., and Shcheglova, Y. V. (2020). Biochemical Composition and Energy Content in the Zooplankton of the Kara Sea. Oceanology, 60(6):778–786. doi:10.1134/S0001437020050136.

Longhurst, A.R., and Harrison, G.W. (1989). The biological pump: Profiles of plankton production and consumption in the upper ocean. Progress in Oceanography, 22(1):47-123. doi: 10.1016/0079-6611(89)90010-4

Lorance, P., Uiblein, F., and Latrouite, D. (2002). Habitat, behaviour and colour patterns of orange roughy Hoplostethus atlanticus (Pisces: Trachichthyidae) in the Bay of Biscay. Journal of the Marine Biological Association of the United Kingdom, 82(2):321–331. Publisher: Cambridge University Press doi: 10.1017/S0025315402005519.

Lüskow, F., Galbraith, M., Hunt, B., Perry, R., and Pakhomov, E. (2021). Gelatinous and soft-bodied zooplankton in the Northeast Pacific Ocean: organic, elemental, and energy contents. Marine Ecology Progress Series, 665:19–35. doi: 10.3354/meps13663.

Lüskow, F., Galbraith, M. D., Kwong, L. E., and Pakhomov, E. A. (2022). Biology and distribution of salps in the subarctic Northeast Pacific. Marine Biology, 169(6):84. doi: 10.1007/s00227-022-04067-2.

Mackas, D. L. (1984). Spatial autocorrelation of plankton community composition in a continental shelf ecosystem. Limnology and Oceanography, 29(3):451–471. doi: 10.4319/lo.1984.29.3.0451.

Mackas, D. L. (1992). Seasonal Cycle of Zooplankton off Southwestern British Columbia: 1979–89. Canadian Journal of Fisheries and Aquatic Sciences, 49(5):903–921. Publisher: NRC Research Press doi: 10.1139/f92-101.

Mackas, D. L., Batten, S., and Trudel, M. (2007). Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. Progress in Oceanography, 75(2):223–252. doi: 10.1016/j.pocean.2007.08.010.

Mackas, D. L. and Beaugrand, G. (2010). Comparisons of zooplankton time series. Journal of Marine Systems, 79(3-4):286–304. doi: 10.1016/j.jmarsys.2008.11.030.

Mackas, D. L., Denman, K. L., and Abbott, M. R. (1985). Plankton patchiness: biology in the physical vernacular. Bulletin of Marine Science, 37(2):652–674.

Mackas, D. L. and Galbraith, M. (2002a). Zooplankton community composition along the inner portion of Line P during the 1997–1998 El Niño event. Progress in Oceanography, 54(1):423–437. doi: 10.1016/S0079-6611(02)00062-9.

Mackas, D. L. and Galbraith, M. D. (2002b). Zooplankton Distribution and Dynamics in a North Pacific Eddy of Coastal Origin: I. Transport and Loss of Continental Margin Species. Journal of Oceanography, 58:725–738.

Mackas, D. L., Peterson, W. T., and Zamon, J. E. (2004). Comparisons of interannual biomass anomalies of zooplankton communities along the continental margins of British Columbia and Oregon. Deep Sea Research Part II: Topical Studies in Oceanography, 51(6):875–896. doi: 10.1016/j.dsr2.2004.05.011.

Mackas, D. L., Thomson, R. E., and Galbraith, M. (2001). Changes in the zooplankton community of the British Columbia continental margin, 1985-1999, and their covariation with oceanographic conditions. Canadian Journal of Fisheries and Aquatic Sciences, 58(4):685–702. doi: 10.1139/f01-009.

Mackas, D. L. and Tsuda, A. (1999). Mesozooplankton in the eastern and western subarctic Pacific: community structure, seasonal life histories, and interannual variability. Progress in Oceanography, 43(2):335-363. doi: 10.1016/S0079-6611(99)00012-9.

Mantua, N. J. and Hare, S. R. (2002). The Pacific Decadal Oscillation. Journal of Oceanography, 58(1):35–44. doi: 10.1023/A:1015820616384.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C. (1997). A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production*. Bulletin of the American Meteorological Society, 78(6):1069–1080. Publisher: American Meteorological Society Section: Bulletin of the American Meteorological Society doi: 10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.

Martin, B. and Christiansen, B. (2009). Distribution of zooplankton biomass at three seamounts in the NE Atlantic. Deep Sea Research Part II: Topical Studies in Oceanography, 56(25):2671–2682. doi: 10.1016/j.dsr2.2008.12.026.

Martin, B. and Nellen, W. (2004). Composition and distribution of zooplankton at the Great Meteor Seamount, subtropical North-east Atlantic. Archive of Fishery and Marine Research, 51(1-3):89–100. doi: 0944-1921/2004/51/1-3-89.

Martínez, I., Herrera, A., Tames-Espinosa, M., Bondyale-Juez, D. R., Romero-Kutzner, V., Packard, T. T., and Gómez, M. (2020). Protein in marine plankton: A comparison of spectrophotometric methods. Journal of Experimental Marine Biology and Ecology, 526:151357. doi: 10.1016/j.jembe.2020.151357.

McEnnulty, F. R., Davies, C. H., Armstrong, A. O., Atkins, N., Coman, F., Clementson, L., Edgar, S., Eriksen, R. S., Everett, J. D., Anthony Koslow, J., Lønborg, C., McKinnon, A. D., Miller, M., O'Brien, T. D., Pausina, S. A., Uribe-Palomino, J., Rochester, W., Rothlisberg, P. C., Slotwinski, A., Strzelecki, J., Suthers, I. M., Swadling, K. M., Tonks, M. L., van Ruth, P. D., Young, J. W., and Richardson, A. J. (2020). A database of zooplankton biomass in Australian marine waters. Scientific Data, 7(1):297. doi: 10.1038/s41597-020-00625-9.

McKinnon, A. D., Doyle, J., Duggan, S., Logan, M., Lønborg, C., and Brinkman, R. (2015). Zooplankton Growth, Respiration and Grazing on the Australian Margins of the Tropical Indian and Pacific Oceans. PLOS ONE, 10(10):e0140012. doi: 10.1371/journal.pone.0140012.

McKinstry, C. A., Campbell, R. W., and Holderied, K. (2022). Influence of the 2014–2016 marine heatwave on seasonal zooplankton community structure and abundance in the lower Cook Inlet, Alaska. Deep Sea Research Part II: Topical Studies in Oceanography, 195:105012. doi: 10.1016/j.dsr2.2021.105012.

Miller, C. B., Frost, B. W., Batchelder, H. P., Clemons, M. J., and Conway, R. E. (1984). Life histories of large, grazing copepods in a subarctic ocean gyre: Neocalanus plumchrus, Neocalanus cristatus, and Eucalanus bungii in the Northeast Pacific. Progress in Oceanography, 13(2):201–243. doi: 10.1016/00796611(84)90009-0.

Miller, E. J., Potts, J. M., Cox, M. J., Miller, B. S., Calderan, S., Leaper, R., Olson, P. A., O'Driscoll, R. L., and Double, M. C. (2019). The characteristics of krill swarms in relation to aggregating Antarctic blue whales. Scientific Reports, 9(1):16487. doi: 10.1038/s41598-019-52792-4.

Morris, M. J. and Hopkins, T. L. (1983). Biochemical composition of crustacean zooplankton from the eastern Gulf of Mexico. Journal of Experimental Marine Biology and Ecology, 69(1):1–19. doi: 10.1016/0022-0981(83)90169-7.

Murphy, D. J. (2012). The dynamic roles of intracellular lipid droplets: from archaea to mammals. Protoplasma, 249(3):541–585. doi: 10.1007/s00709-011-0329-7.

Nelson, M. M., Phleger, C. F., Mooney, B. D., and Nichols, P. D. (2000). Lipids of gelatinous antarctic zooplankton: Cnidaria and Ctenophora. Lipids, 35(5):551–559. doi: 10.1007/s11745-000-555-5.

Newman, M., Alexander, M. A., Ault, T. R., Cobb, K. M., Deser, C., Lorenzo, E. D., Mantua, N. J., Miller, A. J., Minobe, S., Nakamura, H., Schneider, N., Vimont, D. J., Phillips, A. S., Scott, J. D., and Smith, C. A. (2016). The Pacific Decadal Oscillation, Revisited. Journal of Climate, 29(12):4399–4427. Publisher: American Meteorological Society Section: Journal of Climate doi: 10.1175/JCLI-D-15-0508.1.

Noyon, M., Rasoloarijao, Z., Huggett, J., Ternon, J.-F., and Roberts, M. (2020). Comparison of mesozooplankton communities at three shallow seamounts in the South West Indian Ocean. Deep Sea Research Part II: Topical Studies in Oceanography, 176:104759. doi: 10.1016/j.dsr2.2020.104759.

Ohman, M. (1988). Sources of variability in measurements of copepod lipids and gut fluorescence in the California Current coastal zone. Marine Ecology Progress Series, 42:143–153. doi: 10.3354/meps042143.

Ohman, M. D., Frost, B. W., and Cohen, E. B. (1983). Reverse Diel Vertical Migration: An Escape from Invertebrate Predators. Science, 220(4604):1404–1407. Publisher: American Association for the Advancement of Science doi: 10.1126/science.220.4604.1404.

Oksanen, J., Blanchet, F., Friendly, M., and Kindt, R. (2022). Package ’vegan’.

Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., and Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. Nature Communications, 9(1):1324. Publisher: Nature Publishing Group doi: 10.1038/s41467018-03732-9.

Omori, M. (1978). Some Factors Affecting on Dry Weight, Organic Weight and Concentrations of Carbon and Nitrogen in Freshly Prepared and in Preserved Zooplankton. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 63(2):261–269. doi: 10.1002/iroh.19780630211.

Österblom, H., Olsson, O., Blenckner, T., and Furness, R. W. (2008). Junk-food in marine ecosystems. Oikos, 117(7):967–977. doi: 10.1111/j.0030-1299.2008.16501.x.

Parrish, C. C. (1999). Determination of Total Lipid, Lipid Classes, and Fatty Acids in Aquatic Samples. In Arts, M. T. and Wainman, B. C., editors, Lipids in Freshwater Ecosystems, pages 4–20. Springer New York, New York, NY. doi: 10.1007/978-14612-0547-0_2.

Parzanini, C., Parrish, C. C., Hamel, J.-F., and Mercier, A. (2019). Reviews and syntheses: Insights into deep-sea food webs and global environmental gradients revealed by stable isotope (15N, 13C) and fatty acid trophic biomarkers. Biogeosciences, 16(14):2837–2856. Publisher: Copernicus GmbH doi: 10.5194/bg-162837-2019.

Pata, P. R., Galbraith, M., Young, K., Margolin, A. R., Perry, R. I., and Hunt, B. P. (2022). Persistent zooplankton bioregions reflect long-term consistency of community composition and oceanographic drivers in the NE Pacific. Progress in Oceanography, 206:102849. doi: 10.1016/j.pocean.2022.102849.

Pearcy, W. G., Krygier, E. E., Mesecar, R., and Ramsey, F. (1977). Vertical distribution and migration of oceanic micronekton off Oregon. Deep Sea Research, 24(3):223–245. doi: 10.1016/S0146-6291(77)80002-7.

Perfect, B., Kumar, N., and Riley, J. J. (2020). Energetics of Seamount Wakes. Part I: Energy Exchange. Journal of Physical Oceanography, 50(5):1365–1382. doi: 10.1175/JPO-D-19-0105.1.

Perumal, P., Rajkumar, M., and Santhanam, P. (2009). Biochemical composition of wild copepods, Acartia spinicauda and Oithona similis, from Parangipettai coastal waters in relation to environmental parameters. Journal of Environmental Biology, 30(6):995–1005.

Picheral, M., Catalano, C., Brousseau, D., Claustre, H., Coppola, L., Leymarie, E., Coindat, J., Dias, F., Fevre, S., Guidi, L., Irisson, J. O., Legendre, L., Lombard, F., Mortier, L., Penkerch, C., Rogge, A., Schmechtig, C., Thibault, S., Tixier, T., Waite, A., and Stemmann, L. (2021). The Underwater Vision Profiler 6: an imaging sensor of particle size spectra and plankton, for autonomous and cabled platforms. Limnology and Oceanography: Methods. doi: 10.1002/lom3.10475.

Pinchuk, A. I., Batten, S. D., and Strasburger, W. W. (2021). Doliolid (Tunicata, Thaliacea) Blooms in the Southeastern Gulf of Alaska as a Result of the Recent Marine Heat Wave of 2014–2016. Frontiers in Marine Science, 8:625486. doi: 10.3389/fmars.2021.625486.

Platt, T. and Denman, K. (1977). Organisation in the pelagic ecosystem. Helgoländer wissenschaftliche Meeresuntersuchungen, 30(1):575–581. Publisher: BioMed Central doi: 10.1007/BF02207862.

Posgay, J. A. and Marak, R. R. (1980). The MARMAP bongo zooplankton samplers. J. Northw. Atl. Fish. Sci., 1, 91-99.

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., and Montaña, C. G. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia, 152, 179–189.

Powell, J. R. and Ohman, M. D. (2015). Changes in zooplankton habitat, behavior, and acoustic scattering characteristics across glider-resolved fronts in the Southern California Current System. Progress in Oceanography, 134:77–92. doi: 10.1016/j.pocean.2014.12.011.

Rainuzzo, J. R., Reitan, K. I., and Olsen, Y. (1997). The significance of lipids at early stages of marine fish: a review. Aquaculture, 155(1):103–115. doi: 10.1016/S00448486(97)00121-X.

Ratnarajah, L., Abu-Alhaija, R., Atkinson, A., Batten, S., Bax, N. J., Bernard, K. S., Canonico, G., Cornils, A., Everett, J. D., Grigoratou, M., Ishak, N. H. A., Johns, D., Lombard, F., Muxagata, E., Ostle, C., Pitois, S., Richardson, A. J., Schmidt, K., Stemmann, L., Swadling, K. M., Yang, G., and Yebra, L. (2023). Monitoring and modelling marine zooplankton in a changing climate. Nature Communications, 14(1):564. doi: 10.1038/s41467-023-36241-5.

Richardson, A. J. (2008). In hot water: zooplankton and climate change. ICES Journal of Marine Science, 65(3):279–295. doi: 10.1093/icesjms/fsn028.

Robinson, K. L., Sponaugle, S., Luo, J. Y., Gleiber, M. R., and Cowen, R. K. (2021). Big or small, patchy all: Resolution of marine plankton patch structure at micro to submesoscales for 36 taxa. Science Advances, 7(47):eabk2904. doi: 10.1126/sciadv.abk2904.

Roden, G. I. (1991). Mesoscale flow and thermohaline structure around Fieberling seamount. Journal of Geophysical Research: Oceans, 96(C9):16653–16672. doi: 10.1029/91JC01747.

Roe, H. S. J. (1984). The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 4. The copepods. Progress in Oceanography, 13(3):353–388. doi: 10.1016/0079-6611(84)90013-2.

Rogers, A. D. (2018). The Biology of Seamounts: 25 Years on. In Advances in Marine Biology, volume 79, pages 137–224. Elsevier. doi: 10.1016/bs.amb.2018.06.001.

Rowden, A. A., Dower, J. F., Schlacher, T. A., Consalvey, M., and Clark, M. R. (2010). Paradigms in seamount ecology: fact, fiction and future. Marine Ecology, 31(s1):226–241. doi: 10.1111/j.1439-0485.2010.00400.x.

Rykaczewski, R. R. (2019). Changes in mesozooplankton size structure along a trophic gradient in the California Current Ecosystem and implications for small pelagic fish. Marine Ecology Progress Series, 617-618:165–182. doi: 10.3354/meps12554.

Rykaczewski, R. R. and Checkley, D. M. (2008). Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings of the National Academy of Sciences, 105(6):1965–1970. doi: 10.1073/pnas.0711777105.

Saito, H. and Kotani, Y. (2000). Lipids of four boreal species of calanoid copepods: origin of monoene fats of marine animals at higher trophic levels in the grazing food chain in the subarctic ocean ecosystem. Marine Chemistry, 71(1):69–82. doi: 10.1016/S0304-4203(00)00041-4.

Saito, R., Yamaguchi, A., Yasuda, I., Ueno, H., Ishiyama, H., Onishi, H., and Imai, I. (2014). Influences of mesoscale anticyclonic eddies on the zooplankton community south of the western Aleutian Islands during the summer of 2010. Journal of Plankton Research, 36(1):117–128. doi: 10.1093/plankt/fbt087.

Sargent, J. R. and Lee, R. F. (1975). Biosynthesis of lipds in zooplankton from Saanich Inlet, British Columbia, Canada. Marine Biology, 31(1):15–23. doi: 10.1007/BF00390643.

Schaafsma, F. L., Cherel, Y., Flores, H., van Franeker, J. A., Lea, M.-A., Raymond, B., and van de Putte, A. P. (2018). Review: the energetic value of zooplankton and nekton species of the Southern Ocean. Marine Biology, 165(8):129. doi: 10.1007/s00227-018-3386-z.

Schlacher, T. A., Rowden, A. A., Dower, J. F., and Consalvey, M. (2010). Seamount science scales undersea mountains: new research and outlook: Seamount science scales undersea mountains. Marine Ecology, 31:1–13. doi: 10.1111/j.14390485.2010.00396.x.

Seki, M. P. and Somerton, D. A. (1994). Feeding ecology and daily ration of the pelagic armorhead, Pseudopentaceros wheeleri, at Southeast Hancock Seamount. Environmental Biology of Fishes, 39(1):73–84. doi: 10.1007/BF00004758.

Sieburth, J. M., Smetacek, V., and Lenz, J. (1978). Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions 1. Limnology and Oceanography, 23(6):1256–1263. doi: 10.4319/lo.1978.23.6.1256.

Skjoldal, H. R. (2021). Species composition of three size fractions of zooplankton used in routine monitoring of the Barents Sea ecosystem. Journal of Plankton Research, 43(5):762–772. doi: 10.1093/plankt/fbab056.

Skjoldal, H. R., Wiebe, P. H., Postel, L., Knutsen, T., Kaartvedt, S., and Sameoto, D. D. (2013). Intercomparison of zooplankton (net) sampling systems: Results from the ICES/GLOBEC sea-going workshop. Progress in Oceanography, 108:1–42. doi: 10.1016/j.pocean.2012.10.006.

Smetacek, V. and Passow, U. (1990). Spring bloom initiation and Sverdrup’s critical-depth model. Limnology and Oceanography, 35(1):228–234. doi: 10.4319/lo.1990.35.1.0228.

Smith, P. K., Krohn, R. I., Hermanson, G. T., Mallia, A. K., Gartner, F. H., Provenzano, M. D., Fujimoto, E. K., Goeke, N. M., Olson, B. J., and Klenk, D. C. (1985). Measurement of protein using bicinchoninic acid. Analytical Biochemistry, 150(1):76–85. doi: 10.1016/0003-2697(85)90442-7.

Sogawa, S., Sugisaki, H., Saito, H., Okazaki, Y., Ono, T., Shimode, S., and Kikuchi, T. (2016). Seasonal and regional change in vertical distribution and diel vertical migration of four euphausiid species (Euphausia pacifica, Thysanoessa inspinata, T. longipes, and Tessarabrachion oculatum) in the northwestern Pacific. Deep Sea Research Part I: Oceanographic Research Papers, 109:1–9. doi: 10.1016/j.dsr.2015.12.010.

Spitz, J. and Jouma’a, J. (2013). Variability in energy density of forage fishes from the Bay of Biscay (north-east Atlantic Ocean): reliability of functional grouping based on prey quality. Journal of Fish Biology, 82(6):2147–2152. doi: 10.1111/jfb.12142.

Spitz, J., Mourocq, E., Schoen, V., and Ridoux, V. (2010). Proximate composition and energy content of forage species from the Bay of Biscay: high- or low-quality food? ICES Journal of Marine Science, 67(5):909–915. doi: 10.1093/icesjms/fsq008.

Stamieszkin, K., Steinberg, D. K., and Maas, A. E. (2021). Fecal pellet production by mesozooplankton in the subarctic Northeast Pacific Ocean. Limnology and Oceanography, 66(7):2585–2597. doi: 10.1002/lno.11774.

Star, J. L. and Mullin, M. M. (1981). Zooplanktonic assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. Deep Sea Research Part A. Oceanographic Research Papers, 28(11):1303–1322. doi: 10.1016/01980149(81)90036-4.

Steinberg, D. K., Carlson, C. A., Bates, N. R., Goldthwait, S. A., Madin, L. P., and Michaels, A. F. (2000). Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. Deep Sea Research Part I: Oceanographic Research Papers, 47(1):137–158. doi: 10.1016/S09670637(99)00052-7.

Stevens, C. J., Deibel, D., and Parrish, C. C. (2004) Species-specific differences in lipid composition and omnivory indices in Arctic copepods collected in deep water during autumn (North Water Polynya). Marine Biology, 144, 905–915.

Stevens, C. J., Sahota, R., Galbraith, M. D., Venello, T. A., Bazinet, A. C., Hennekes, M., Yongblah, K., and Juniper, S. K. (2022). Total lipid and fatty acid composition of mesozooplankton functional group members in the NE Pacific over a range of productivity regimes. Marine Ecology Progress Series, 687:43–64. doi: 10.3354/meps14004.

Surma, S., Pakhomov, E. A., and Pitcher, T. J. (2018). Energy-based ecosystem modelling illuminates the ecological role of Northeast Pacific herring. Marine Ecology Progress Series, 588:147–161. doi: 10.3354/meps12430.

Taipale, S. J., Kahilainen, K. K., Holtgrieve, G. W., and Peltomaa, E. T. (2018). Simulated eutrophication and browning alters zooplankton nutritional quality and determines juvenile fish growth and survival. Ecology and Evolution, 8(5):26712687. doi: 10.1002/ece3.3832.

Tanaka, H., Sassa, C., Ohshimo, S., and Aoki, I. (2013). Feeding ecology of two lanternfishes Diaphus garmani and Diaphus chrysorhynchus. Journal of Fish Biology, 82(3):1011–1031. doi: 10.1111/jfb.12051.

Tanasichuk, R. W. (1998). Interannual variations in the population biology and productivity of Euphausia pacifica in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Marine Ecology Progress Series, 173:163180. doi: 10.3354/meps173163.

Teles, A. O., Couto, A., Enes, P., and Peres, H. (2020). Dietary protein requirements of fish – a meta-analysis. Reviews in Aquaculture, 12(3):1445–1477. doi: 10.1111/raq.12391.

Thavarajah, R., Mudimbaimannar, V. K., Elizabeth, J., Rao, U. K., and Ranganathan, K. (2012). Chemical and physical basics of routine formaldehyde fixation. Journal of Oral and Maxillofacial Pathology, 16(3):400. doi: 10.4103/0973029X.102496.

Tsuda, A., Saito, H., and Kasai, H. (2001). Life history strategies of subarctic copepods Neocalanus flemingeriand N. plumchrus, especially concerning lipid accumulation patterns.

Turner, J. T. (2002). Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquatic Microbial Ecology, 27(1):57–102. doi: 10.3354/ame027057.

Tyler, A. V. (1973). Caloric values of some North Atlantic invertebrates. Marine Biology, 19(3):258–261. doi: 10.1007/BF02097146.

Urmy, S. S. and Benoit-Bird, K. J. (2021). Fear dynamically structures the ocean's pelagic zone. Current Biology, 31(22):5086–5092.e3. doi: 10.1016/j.cub.2021.09.003.

Venello, T. A., Sastri, A. R., Galbraith, M. D., and Dower, J. F. (2021). Zooplankton functional group responses to environmental drivers off the west coast of Vancouver Island, Canada. Progress in Oceanography, 190:102482. doi: 10.1016/j.pocean.2020.102482.

Wahl, R. J. and Teague, W. J. (1983). Estimation of Brunt-Väisälä Frequency from Temperature Profiles. Journal of Physical Oceanography, 13(12):2236–2240. Publisher: American Meteorological Society

Section: Journal of Physical Oceanography doi: 10.1175/1520-0485(1983)013<2236:EOBVFF>2.0.CO;2.

Wang, M. and Jeffs, A. G. (2014). Nutritional composition of potential zooplankton prey of spiny lobster larvae: a review. Reviews in Aquaculture, 6(4):270–299. doi: 10.1111/raq.12044.

Wang, Y., Zhang, J., Yu, J., Wu, Q., and Sun, D. (2023). Anticyclonic mesoscale eddy induced mesopelagic biomass hotspot in the oligotrophic ocean. Journal of Marine Systems, 237:103831. doi: 10.1016/j.jmarsys.2022.103831.

Watkins, J., Rudstam, L., and Holeck, K. (2011). Length-weight regressions for zooplankton biomass calculations – A review and a suggestion for standard equations. Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J., Freidank, M., Cai, J., and Protivinsky, T. (2021). Visualization of a Correlation Matrix.

Weil, J., Duguid, W., and Juanes, F. (2020). Fine-scale taxonomic and temporal variability in the energy density of invertebrate prey of juvenile Chinook salmon Oncorhynchus tshawytscha. Marine Ecology Progress Series, 655:185–198. doi: 10.3354/meps13513.

Weil, J., Trudel, M., Tucker, S., Brodeur, R. D., and Juanes, F. (2019). Percent ash-free dry weight as a robust method to estimate energy density across taxa. Ecology and Evolution, 9(23):13244–13254. doi: 10.1002/ece3.5775.

White, J. R., Zhang, X., Welling, L. A., Roman, M. R., and Dam, H. G. (1995). Latitudinal gradients in zooplankton biomass in the tropical Pacific at 140°W during the JGOFS EqPac study: Effects of El Niño. Deep Sea Research Part II: Topical Studies in Oceanography, 42(2):715–733. doi: 10.1016/0967-0645(95)00033-M.

White, M., Bashmachnikov, I., Arstegui, J., and Martins, A. (2007). Physical Processes and Seamount Productivity. In Pitcher, T. J., Morato, T., Hart, P. J. B., Clark, M. R., Haggan, N., and Santos, R. S., editors, Seamounts: Ecology, Fisheries & Conservation, pages 62–84. Blackwell Publishing Ltd, Oxford, UK. doi: 10.1002/9780470691953.ch4.

Wiebe, P., Boyd, S., Davis, B., and Cox, J. (1982). Avoidance of towed nets by the euphausiid Nematoscelis megalops. Fishery Bulletin, 80(1):75–91.

Wiebe, P. H. and Benfield, M. C. (2003). From the Hensen net toward four-dimensional biological oceanography. Progress in Oceanography, 56(1):7–136. doi: 10.1016/S0079-6611(02)00140-4.

Wiebe, P. H., Madin, L. P., Haury, L. R., Harbison, G. R., and Philbin, L. M. (1979). Diel vertical migration bySalpa aspera and its potential for large-scale particulate organic matter transport to the deep-sea. Marine Biology, 53(3):249–255. doi: 10.1007/BF00952433.

Winans, A. K., Herrmann, B., and Keister, J. E. (2023). Spatio-temporal variation in zooplankton communitycompositioninthe southern Salish Sea: changes during the 2015-2016 Pacific marine heatwave. Progress in Oceanography. doi: 10.1016/j.pocean.2023.103022.

Xu, H., Wang, J., Mai, K., Xu, W., Zhang, W., Zhang, Y., and Ai, Q. (2016). Dietary docosahexaenoic acid to eicosapentaenoic acid (DHA/EPA) ratio influenced growth performance, immune response, stress resistance and tissue fatty acid composition of juvenile Japanese seabass, Lateolabrax japonicus (Cuvier). Aquaculture Research, 47(3):741–757. doi: 10.1111/are.12532.

Yebra, L., Espejo, E., Putzeys, S., Giráldez, A., Gómez-Jakobsen, F., León, P., Salles, S., Torres, P., and Mercado, J. M. (2020). Zooplankton Biomass Depletion Event Reveals the Importance of Small Pelagic Fish Top-Down Control in the Western Mediterranean Coastal Waters. Frontiers in Marine Science, 7:608690. doi: 10.3389/fmars.2020.608690.

Yebra, L., Harris, R. P., Head, E. J. H., Yashayaev, I., Harris, L. R., and Hirst, A. G. (2009). Mesoscale physical variability affects zooplankton production in the Labrador Sea. Deep Sea Research Part I: Oceanographic Research Papers, 56(5):703–715. doi: 10.1016/j.dsr.2008.11.008.

Yebra, L., Kobari, T., Sastri, A., Gusmão, F., and Hernández-León, S. (2017a). Advances in Biochemical Indices of Zooplankton Production. In Advances in Marine Biology, volume 76, pages 157–240. Elsevier. doi: 10.1016/bs.amb.2016.09.001.

Yebra, L., Kobari, T., Sastri, A. R., Gusmão, F., and Hernández-León, S. (2017b). Chapter Four - Advances in Biochemical Indices of Zooplankton Production. In Curry, B. E., editor, Advances in Marine Biology, volume 76, pages 157–240. Academic Press. doi: 10.1016/bs.amb.2016.09.001.

Zaguri, M., Kandel, S., Rinehart, S. A., Torsekar, V. R., and Hawlena, D. (2021). Protein quantification in ecological studies: A literature review and empirical comparisons of standard methodologies. Methods in Ecology and Evolution, 12(7):12401251. doi: 10.1111/2041-210X.13601.

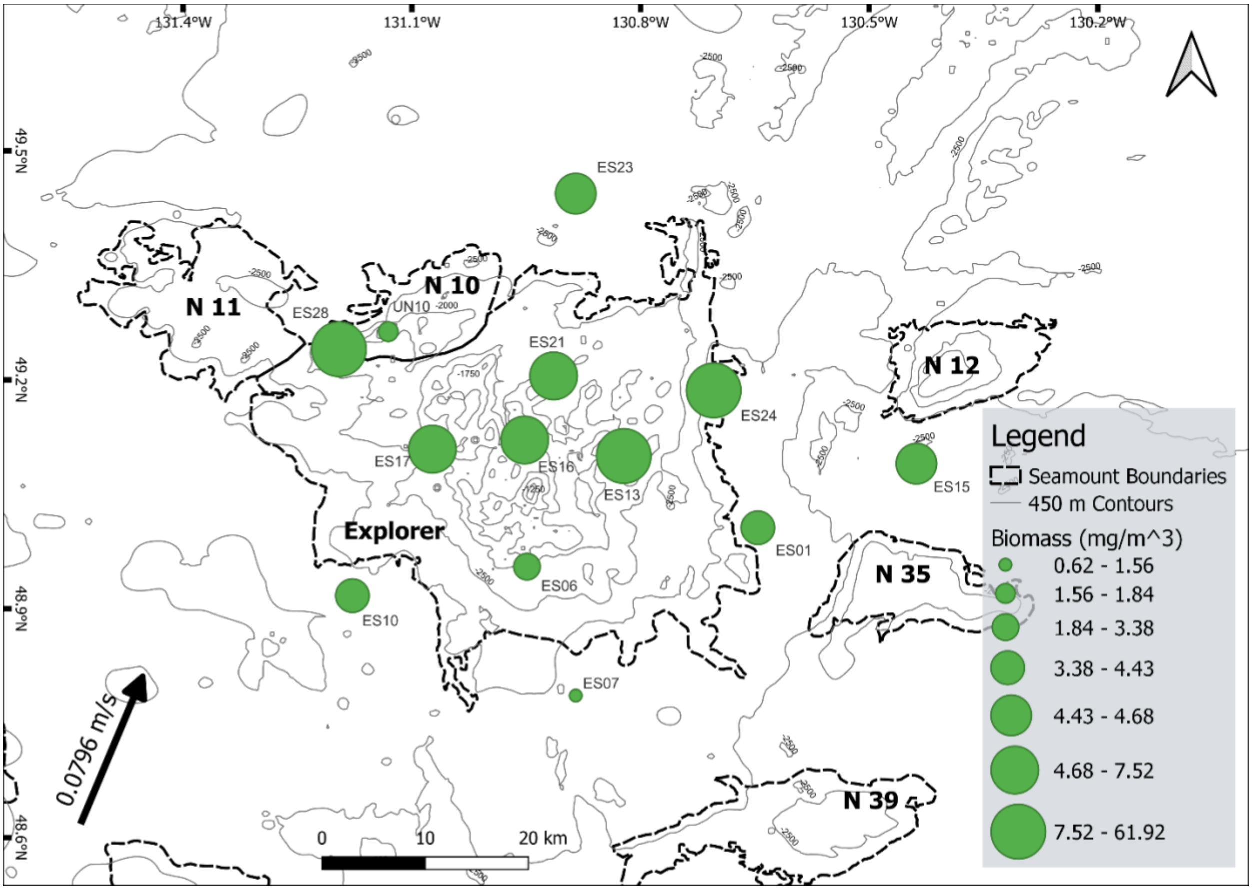
Zhang, Y., Kieft, B., Hobson, B. W., Raanan, B.-Y., Urmy, S. S., Pitz, K. J., Preston, C. M., Roman, B., Benoit-Bird, K. J., Birch, J. M., Chavez, F. P., and Scholin, C. A. (2021). Persistent Sampling of Vertically Migrating Biological Layers by an Autonomous Underwater Vehicle Within the Beam of a Seabed-Mounted Echosounder. IEEE Journal of Oceanic Engineering, 46(2):497–508. doi: 10.1109/JOE.2020.2982811.

Zhou, M. (2006). What determines the slope of a plankton biomass spectrum? Journal of Plankton Research, 28(5):437–448. doi: 10.1093/plankt/fbi119.

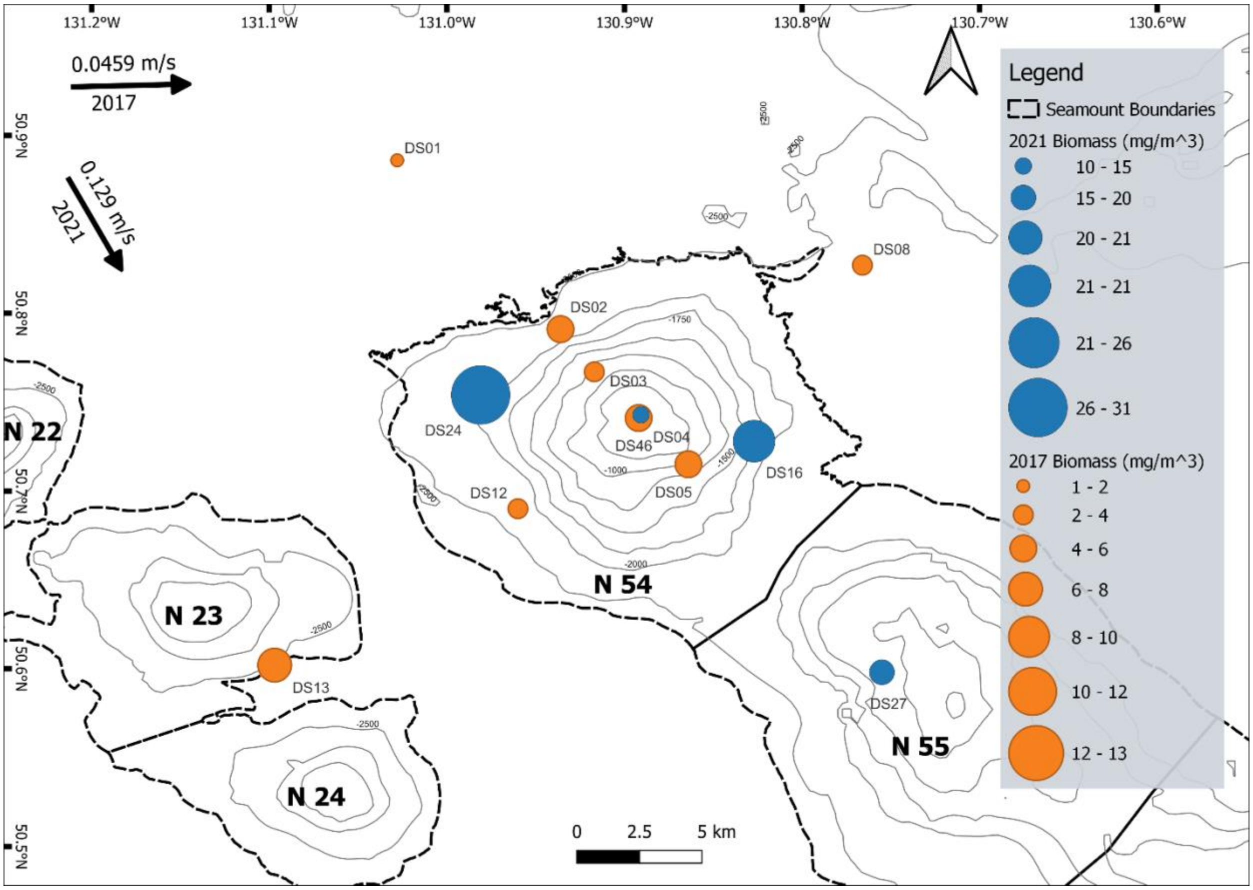
Zhou, M. and Huntley, M. (1997). Population dynamics theory of plankton based on biomass spectra. Marine Ecology Progress Series, 159:61–73. doi: 10.3354/meps159061.

Appendix

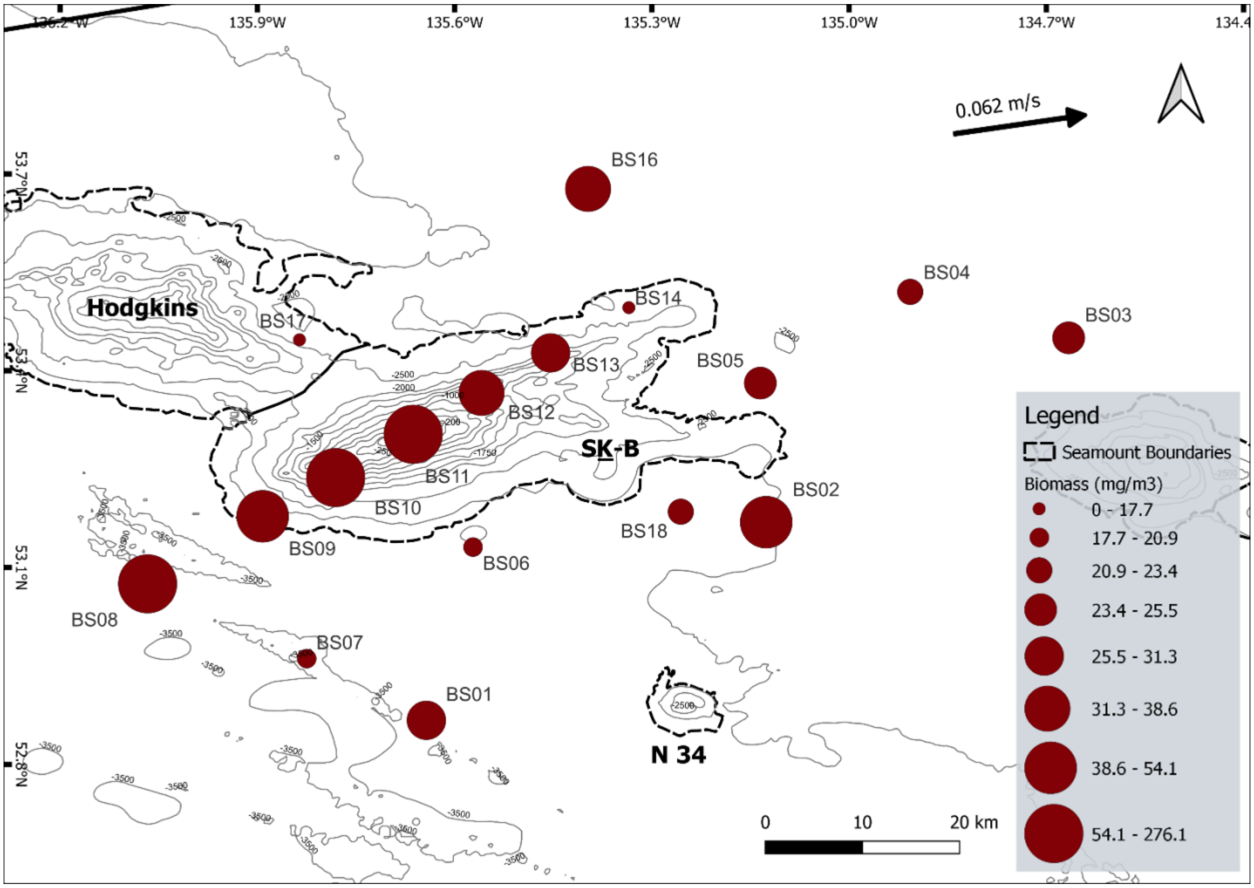
Appendix 1. Dendrogram of zooplankton community composition sorted using Bray-Curtis dissimilarity among all sites from 2017, 2019, and 2021. The nearest node connecting two sites indicates the dissimilarity between those sites. Sites tend to cluster primarily based on year, but within years there was some clustering of seamount. Sites sampled in 2015 were excluded because they were exclusively collected from SGáan Kínghlas-Bowie SeamountSeamount, therefore confounding between spatial and temporal clustering. Colours denote statistically significant groupings identified using a bootstrap analysis.



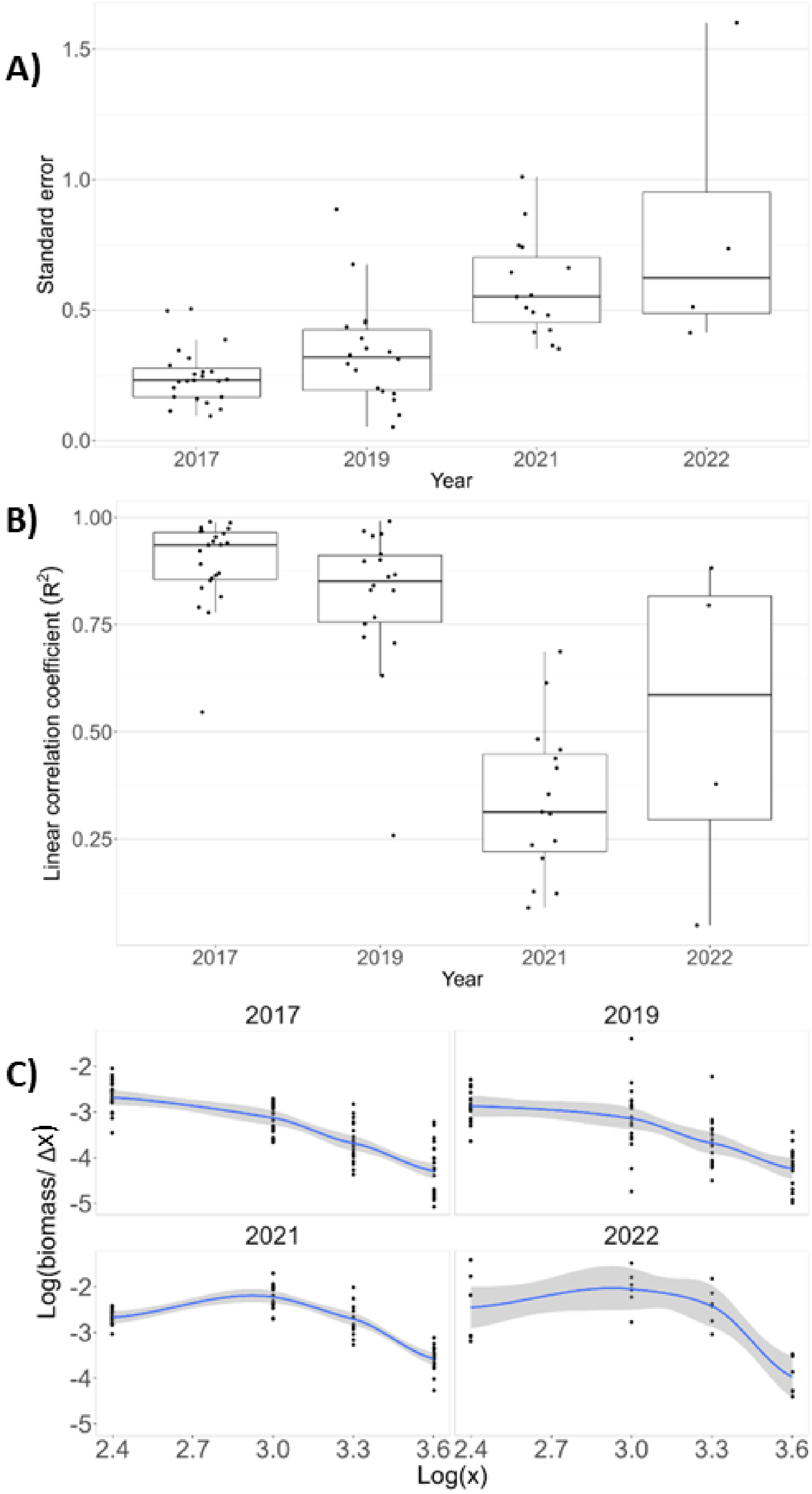
Appendix 2: Total zooplankton biomass distribution around Explorer Seamount during the 2019 survey. Site numbers are included, and surface current direction and speed are indicated using an arrow in the bottom left of the map. The GEBCO (2021) contours (https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2021/) were used were used to delineate demonstrate the topography of the region. Surface current direction and velocity were estimated using data from CMEMS multi-model reanalysis currents from the NE Pacific (NEP; https://doi.org/10.48670/moi-00024).



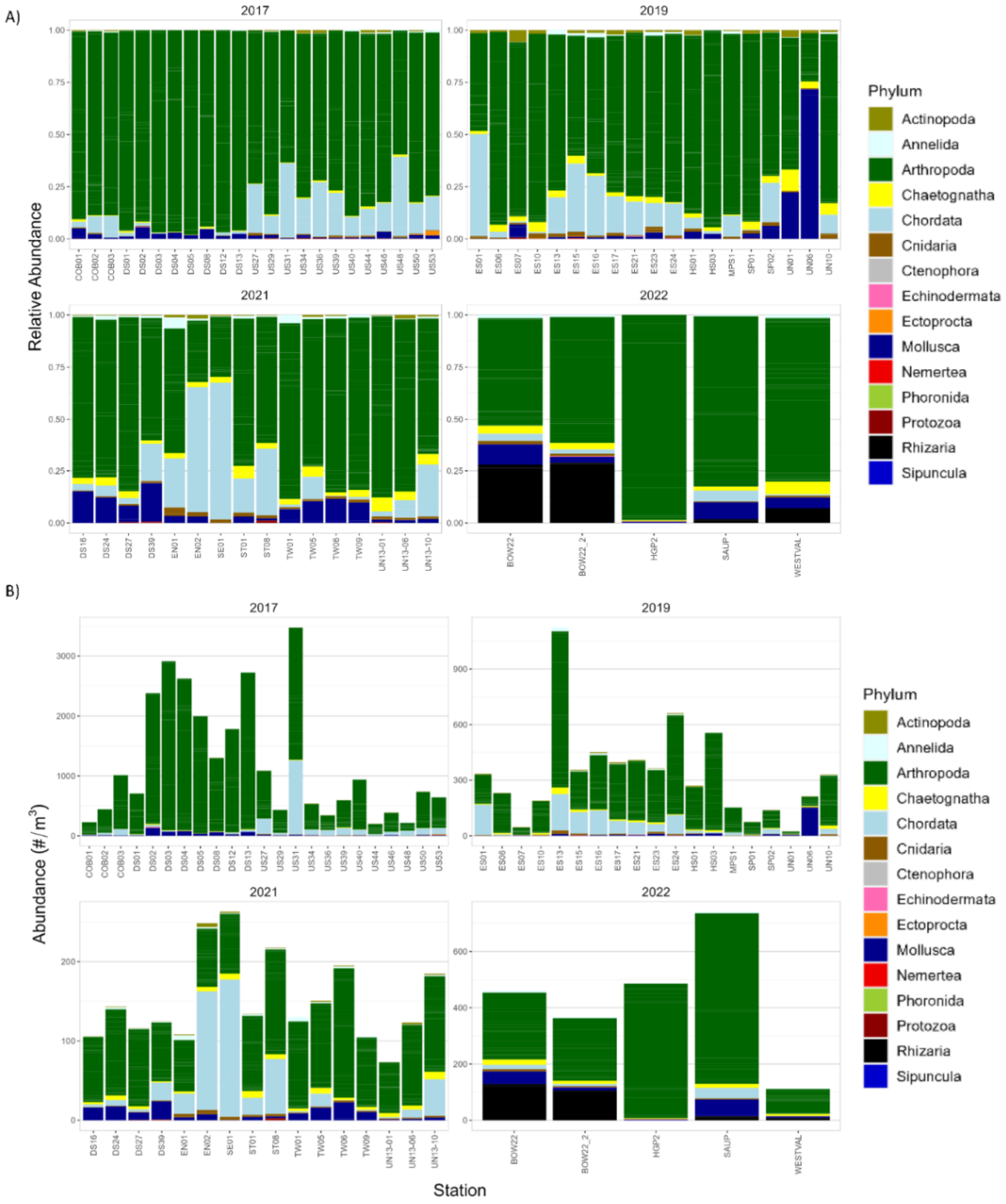
Appendix 3: Total zooplankton biomass distribution around NEPDEP 54 Seamount during the 2017 and 2021 surveys. Site numbers are included and surface current direction and speed are indicated using an arrow in the top left of the map. Note the difference in scale between surveys, during the 2021 survey there was significantly more zooplankton biomass per cubic meter. The GEBCO (2021) contours (https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2021/) were used were used to delineate demonstrate the topography of the region. Surface current direction and velocity were estimated using data from CMEMS multi-model reanalysis currents from the NE Pacific (NEP; https://doi.org/10.48670/moi-00024).



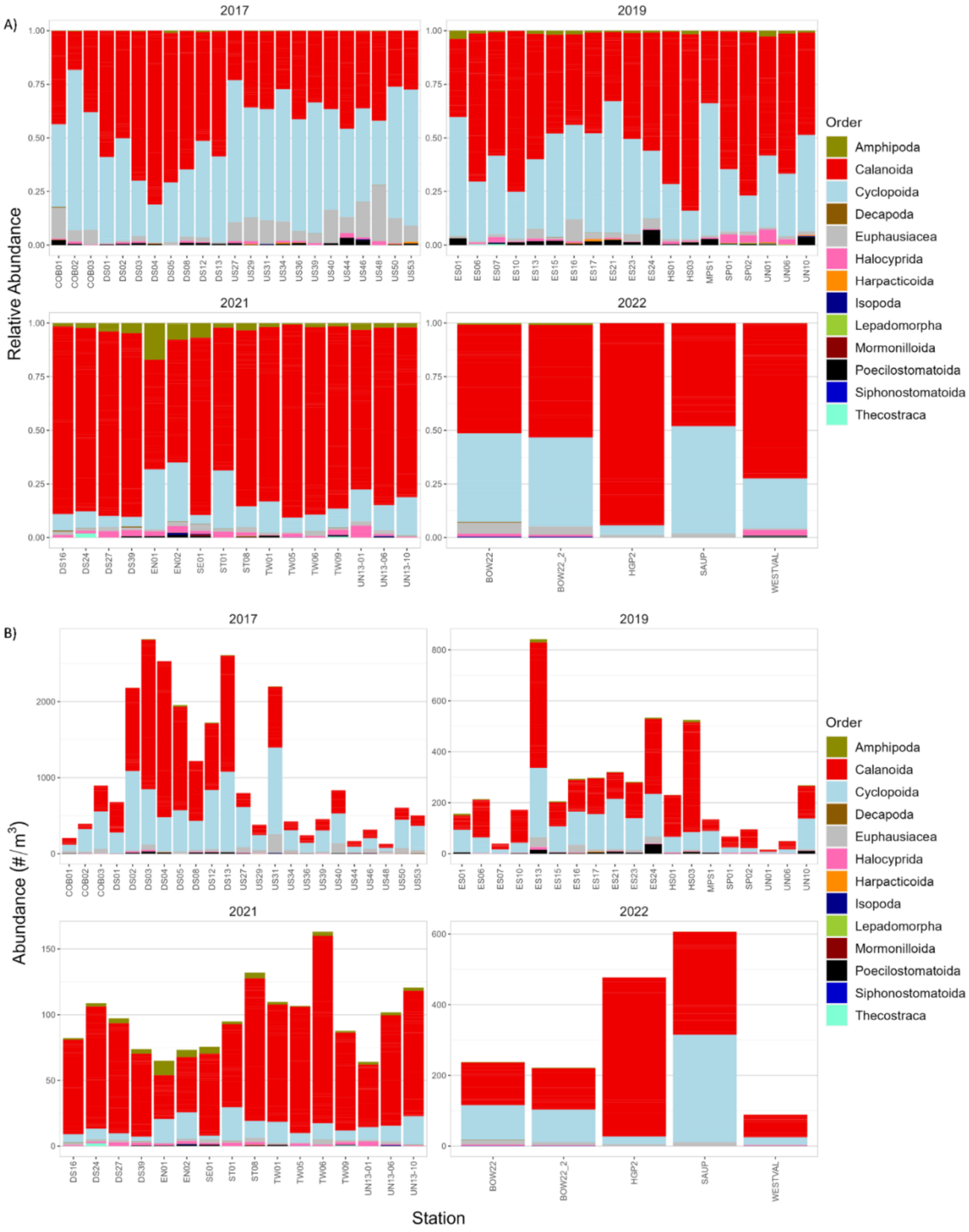
Appendix 4: Total zooplankton biomass distribution around SG̲áan K̲ínghlas-Bowie Seamount during the 2015 survey. Site numbers are included, and surface current direction and speed are indicated using an arrow in the top right of the map. Calculated biomass was used for zooplankton biomass. Seamount boundaries collected from Du Preez and Norgard (2022). The GEBCO (2021) contours (https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_2021/) were used were used to delineate demonstrate the topography of the region. Surface current direction and velocity were estimated using data from CMEMS multi-model reanalysis currents from the NE Pacific (NEP; https://doi.org/10.48670/moi-00024).



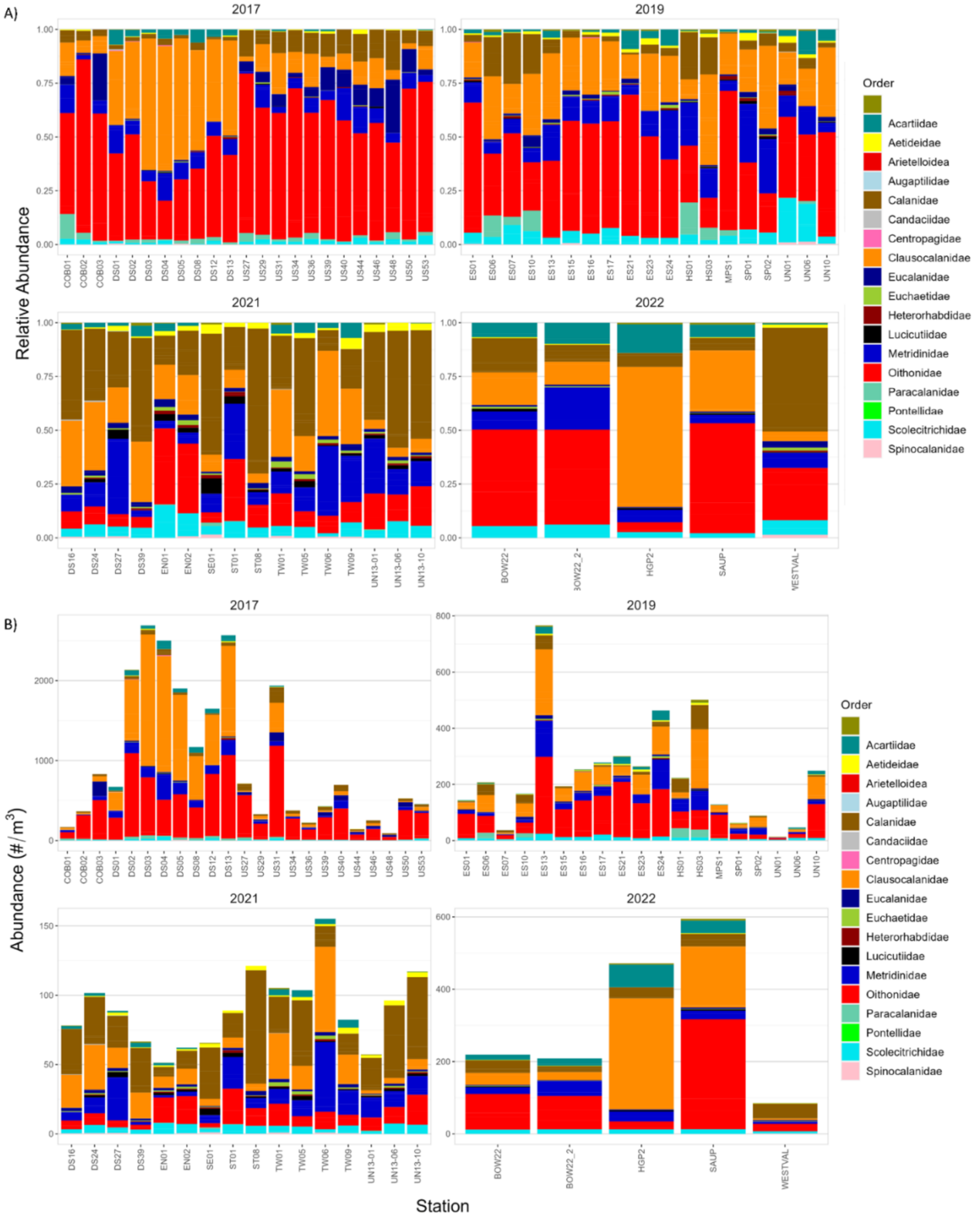
Appendix 5. Graphs demonstrating the differences in zooplankton NBSS (A) standard error, (B) linear correlation coefficient (R2), and (C) mean four-point loess curves between surveys.



Appendix 6. The (A) relative and (B) absolute abundance (# m^{-3}) of zooplankton phyla at each station and the years they were sampled. Note the difference in the y-axis scales between (B) graphs.



Appendix 7. The (A) relative and (B) absolute abundance (# m^{-3}) of Arthropoda orders at each station and the years they were sampled. Note the difference in the y-axis scales between (B) graphs.



Appendix 8. The (A) relative and (B) absolute abundance (# m^{-3}) of Calanoid and Cyclopoid copepod families at each station and the years they were sampled. Note the difference in the y-axis scales between (B) graphs.