Linking Zooplankton Community Composition to Ecosystem Functioning Off the West Coast of
Vancouver Island and in the Northeast Subarctic Pacific

by

Theresa Ann Venello
B.Sc., Stockton University, 2012
M.Res., University of Plymouth, 2014

A Dissertation Submitted in Partial Fulfillment
of the Requirements for the Degree of

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University of Victoria

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Abstract

Zooplankton play a key role in the functioning of marine ecosystems by transferring energy from phytoplankton to higher trophic levels. Additionally, because of their short generation times and ability to respond rapidly to oceanographic conditions, they have been used as indicators of ecosystem health. Despite their use as ecosystem indicators, there are still critical knowledge gaps in our understanding of zooplankton communities. This includes links between zooplankton biodiversity and ecosystem functions, such as productivity and energy transfer. Difficulties making empirical measurements of ecosystem functions has also created a barrier in addressing these gaps. Lastly, functional role assessments of zooplankton communities can give more insight into the ecological roles of zooplankton species/groups, how they affect ecosystem function, and how community roles may reorganize under climate change scenarios.

Chapter 1 introduces zooplankton as crucial to the functioning of marine ecosystems and as key ecological indicators. It also discusses measures of ecosystem function and biodiversity, and drivers of variation in zooplankton communities. Chapter 1 also outlines the objectives of this thesis and describes the regional oceanographic setting of the subarctic northeast Pacific in the context of those objectives.

Chapter 2 applies a functional traits-based approach to a 35-year time series of mesozooplankton biomass on the southern shelf along the west coast of Vancouver Island, Canada. Eight functional groups were identified using a functional-trait similarity approach from which biomass anomaly time series for each group were calculated. Generalized additive modeling (GAM) was used to identify drivers of functional group biomass anomaly variability. GAM results found that the key drivers were a local sea surface temperature, the Southern Oscillation Index (SOI), the Pacific Decadal Oscillation (PDO), as well as the North Pacific Gyre Oscillation (NPGO). Functional group biomass anomalies for gelatinous zooplankton were strongest in 2015, with comparably little change in crustacean zooplankton group biomass anomalies throughout the time series. This suggests a degree of functional redundancy within these groups, with endemic species dominating in cool years and southern species replacing them in warm years.

Chapter 3 quantifies patterns of spatiotemporal variability in crustacean zooplankton production rates (BPR) using the chitobiase method and assesses regional drivers of BPR variability. As an alternative to traditional, labor-intensive, and species-specific production rates, the chitobiase method provides a community-level estimate of somatic production for all developing crustacean zooplankton. BPR was measured along the west coast of Vancouver Island and in the subarctic NE Pacific during 2005, 2009-2011, and 2015-2018. GAMs determined that sea surface temperature, satellite chlorophyll *a* and crustacean zooplankton biomass significantly influenced the BPR of crustacean zooplankton, although the relationships between BPR and predictor variables differed between regions. High BPR values occurred in years with a high biomass of large-bodied cold-water indicator species, while low BPR values were associated with a biomass dominated by small-bodied warm-water species.

Chapter 4 estimates trophic transfer efficiency (TTE) using BPR and net community production rates from 2015-2018. TTE varied from just greater than 0% to 35%, with annual means both below the oft-assumed 10% average (6% and 5.1% in 2015 and 2018 respectively)

and above 10% (14% and 15% in 2016 and 2017, respectively). The effect of zooplankton community composition and functional and taxonomic diversity on TTE was also investigated. Functional dispersion, functional divergence, species evenness, and mixed layer depth temperature were identified as significant explanatory variables of TTE across the study area. Zooplankton community composition differed significantly between high and low TTE communities, driven primarily by differences in the abundance of the Omnivore-Herbivores and Active Ambush Omnivores from a functional trait perspective and by the abundances of Boreal-Shelf, *Oithona* spp., and Southern copepods from a geographic-taxonomic one. This chapter presents routine rate-based TTE estimates across a variety of oceanographic conditions - an area of research that is critical to our understanding of marine ecosystems but which has many poorly understood components. This chapter therefore helps to bridge that knowledge gap.

Chapter 5 includes some general conclusions on what may become a “new normal” for zooplankton communities in the subarctic northeast Pacific under increased ocean warming, and considers potential consequences for higher trophic levels. Additionally, this chapter highlights some long-standing ecological assumptions that have been challenged within this thesis. This thesis concludes by exploring the future work that will be needed to refine our understanding of pelagic marine ecosystems and the relationships between production rates and oceanographic regimes.

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Dedication

I dedicate this thesis to my parents (Theresa and James) and sister (Jamie), for they have always encouraged me to pursue my childhood dream of being a 'marine biologist'. I wouldn't be where I am today without their constant support and encouragement for this life-long dream.

Chapter 1. Introduction

1.1 The Importance of Zooplankton in Marine Food Webs

Zooplankton are the major link between primary producers and higher-level consumers including fish, seabirds, and marine mammals and play a central role in the transfer of energy through marine ecosystems. Zooplankton play an active role in the biological pump, helping to export carbon from surface waters to the deep ocean, helping benthic communities via the deposition of faecal pellets and carcasses (Ruhl and Smith, 2004) while also supporting the microbial loop via the regeneration of nitrogen (through excretion). Zooplankton communities are considered a particularly sensitive gauge of ecosystem change due to non-linear responses which can amplify subtle environmental changes (Taylor *et al.*, 2002). The prolific nature and short life cycles of marine zooplankton make them sensitive indicators of ecosystem health and changes within marine ecosystems, especially as a result of climate change (Beaugrand, 2005; Hooff and Peterson, 2006; Mackas and Beaugrand, 2010; Mackas *et al.*, 2012). More specifically, spatiotemporal oceanographic variability can influence zooplankton community composition - thereby affecting metrics of ecosystem functions, such as production rates and energy transfer (e.g. Hooff and Peterson, 2006; Paterson *et al.*, 2012). However, there are still critical knowledge gaps in our understanding of zooplankton communities, especially with regard to empirical measures and variability of ecosystem functions as well as functional role assessments of zooplankton communities. Additionally, links between zooplankton diversity and measures of ecosystem function such as zooplankton production rates and trophic transfer efficiency are virtually non-existent for marine zooplankton communities. A better

understanding of how zooplankton community composition affects energy transfer and productivity is needed as changes to the base of marine food webs can propagate upwards. As such, slight changes in the amount or the availability of energy to be transferred can have large impacts on the abundances of top predators (Eddy *et al.*, 2021). Therefore, the processes controlling ecosystem functions need to be more fully resolved, and particularly to better constrain models that address potential changes in marine ecosystems and fisheries production due to anthropogenic stressors.

1.2 Crustacean Zooplankton Production Rates and Trophic Transfer Efficiency as Measures of Ecosystem Function

1.2.1 Defining and Measuring Ecosystem Functions

The biodiversity-ecosystem function (BEF) theory established the concept that ecosystem functions (e.g. productivity and nutrient cycling) and ecosystem stability directly rely on differing levels of biodiversity - including genotypes, taxonomic, and functional groups (Doherty and Zedler, 2018). BEF has been investigated using a variety of biodiversity and ecosystem function measures (Cardinale *et al.*, 2006; Naeem *et al.*, 2009). As such, there are often several conflicting definitions of ecosystem function (and variables considered as functions), where the choice of which one to use is determined by the research question that needs to be addressed. However, a holistic definition of ecosystem function includes: 1) the stocks of energy and materials within the system; 2) the fluxes of energy and materials; and 3) relative stability over time (Pacala and Kinzig, 2002; Paterson *et al.*, 2009; Paterson *et al.*, 2012). Therefore, ecosystem functions are usually determined by “*processes through which materials are transformed within an ecosystem*”. In marine ecosystems, the majority of studies have

focused on primary production and nutrient turnover (Paterson *et al.*, 2012). Functional measures include nutrient fluxes, net primary production, and secondary productivity defined by static measures (Paterson *et al.*, 2012 and references therein). However, difficulties in acquiring direct empirical measurements of ecosystem functions, specifically rate measurements, remain a persistent challenge in advancing the biodiversity-ecosystem function field.

Empirical measurements of ecosystem function in marine systems such as primary and secondary production, including mesozooplankton production rates, are limited largely due to difficulties in estimating/measuring rate-based parameters (Paterson *et al.*, 2012). Although methods for primary production rates have been in use for decades (Steemann-Nielsen, 1952), methods for estimating zooplankton production rates have proven more challenging. Methods for measuring zooplankton production rates have historically been restricted to select copepod species, requiring labor intensive incubation methods or the application of empirical models with broad growth rate assumptions across species (Avila *et al.*, 2012; Kobari *et al.*, 2019). More recently, biochemical methods for estimating zooplankton production rates have grown in popularity and have had some demonstrated success in the field and laboratory, where methods such as RNA:DNA ratios, aminoacyl-tRNA synthetases (AARS) for specific growth rates, and chitobiase for crustacean zooplankton production rates are in use today (Yebra *et al.*, 2017; Kobari *et al.*, 2019).

1.2.2 Primary and Secondary Production Rates

Community-level primary production rates have measured the photosynthetic rates of phytoplankton in seawater *in situ* for nearly 70 years via ^{14}C (Steeman-Neilson, 1952), oxygen evolution (Colijn *et al.*, 1983), carbon assimilation by mass spectrometry (Slawyk *et al.*, 1977), and the rate of nitrogen assimilation and production (Neess *et al.*, 1962; Dugdale and Goering, 1967). Continued development of routine field measures for primary production rates include net community production rates from O_2/Ar or O_2/N_2 mass spectrometry (Kaiser *et al.*, 2005; Hamme *et al.*, 2012; Izett *et al.*, 2018; Izett and Tortell, 2020) as well as diatom production *via* silica utilization (Geisbrecht and Varela, 2021), and nitrate (NO_3^-) utilization to measure new production (Giesbrecht *et al.*, 2019). However, comparable *in situ* estimates of community-level production rates for crustacean zooplankton communities remain scarce (Sastri *et al.*, 2012; Suchy *et al.*, 2016).

Typically, estimates of zooplankton production require both biomass and growth rate and are most commonly calculated as $P = B \times g$, where P is production (m T^{-1}), B is biomass and g is specific growth rate (Kimmerer, 1987; Huntley and Lopez, 1992). Biomass is one of the metrics most commonly reported in zooplankton studies (e.g. Hays *et al.*, 2005), yet difficulties in growth rate determination can result limited production rate measurements that are restricted to select species. This may result from the labor intensive nature of collecting direct measures of growth rate or the restrictions and/or assumptions made in empirical modeling of growth rate (Avila *et al.*, 2012).

Experimental designs estimating zooplankton productivity typically use the egg production, egg ratio or size-frequency (cohort) techniques, which all require the collection, sorting, incubation, and enumeration of samples (Kimmerer 1987; Kimmerer and Mckinnon,

1987; Poulet *et al.*, 1995; Jónasdóttir *et al.*, 2005; Temperoni *et al.*, 2011; Riquelme-Bugueño *et al.*, 2013). However, these methods are often restricted to copepods due to their general dominance, relatively short generation times, and recognizable stage structure – thus resulting in a species-specific bias. In addition, egg production and egg ratio methods also exclude male presence, focusing solely on gravid or post-release females (Jónasdóttir *et al.*, 2005; Temperoni *et al.*, 2011). An alternative, the growth increment summation method (Downing and Rigler, 1984; Kimmerer, 1987) follows changes in the size-frequency distribution of a culture to calculate zooplankton production as the sum of daily somatic and molt production, but may be limited in some instances by not taking into account egg production (Riquelme-Bugueño *et al.*, 2013). The biomass size spectrum approach may also be used to estimate zooplankton production rates, where production is relative to body mass class size (Sheldon *et al.*, 1972). More recently, biomass size spectra approaches use predator-prey biomass ratios (Jennings *et al.*, 2002; Blanchard *et al.*, 2009), normalized biomass size spectra slopes (Zhou and Huntley, 1997) or both (Kwong *et al.*, 2020). Here, a log-log relationship between biomass and body size is applied, working under two assumptions: (i) that biomass and production decrease in progressively larger body mass sizes and (ii) that weight-specific metabolic rates (P:B ratios) follow allometric relationships (Gaedke and Straile, 1994). Ultimately, the established ratio between different biomass size classes has also been used to calculate trophic transfer efficiency (Gaedke and Straile, 1994; Jennings *et al.*, 2002).

In addition to direct measures of growth rate, several empirical models have also been widely used. These include the temperature-dependent growth rate model (Huntley and Lopez, 1992), in addition to weight-specific fecundity and growth rate models (Hirst and Lampitt, 1998;

Hirst and Bunker, 2003). Such models rely on some common assumptions. For example, when applying the temperature-dependent model (Huntley and Lopez, 1992) to copepods, it is assumed that the growth rate is exponential and can be directly estimated from egg weights, adult weights, generation times, and temperature integrated through said generation time. For the Hirst and Lampitt (1998) model, adult weight-specific growth rate is assumed to be linear while juvenile growth rate is assumed to be exponential. The Hirst and Bunker (2003) model considers mean chlorophyll *a* concentration in addition to body weight and temperature, while otherwise following the same growth rate assumptions as Hirst and Lampitt (1998). In most cases, these empirical model estimations of growth rate are limited to single copepod species or copepod communities, and usually overestimate copepod production likely due to net selectivity and an underestimation of biomass (Avila *et al.*, 2012; Dvoretzky and Dvoretzky, 2012).

Several biochemical techniques have also been used to estimate zooplankton production rates, and a recent review has highlighted the advances of such methods (Yebra *et al.*, 2017). Nucleic acid production, most commonly applied using RNA concentration and RNA:DNA ratios, has been used to index zooplankton somatic growth or egg production (e.g. Gorokhova, 2003; Yebra *et al.*, 2011). Nucleic acid methods rely on two assumptions: (i) synthesized proteins are indicative of weight-specific growth and (ii) that DNA is fairly constant and represents the cell number. However, the lack of a universally applicable relationship between nucleic acid content and growth rate makes it difficult for nucleic acid indices to be used at the community level (Yebra *et al.*, 2017). Additionally, aminoacyl-tRNA synthetases (AARS) assays have been modified as an index of somatic growth rate in planktonic crustaceans

(Yebra and Hernández-León, 2004). AARS are a group of enzymes that catalyze amino acid activation, which is directly related to protein synthesis and can give an indication of feeding and developmental history. Although the AARS approach to zooplankton production rates can be applied across taxonomic groups, protein synthesis is not a direct measurement of growth. Therefore, a calibration of the method with somatic growth rate is required (Yebra *et al.*, 2017).

1.2.3 Chitobiase-based Production Rates

The measurement of the chitobiase enzyme to estimate zooplankton production at the community level for crustacean zooplankton has gained popularity (Oosterhuis *et al.*, 2000; Sastri and Roff, 2000; Sastri and Dower, 2006, 2009; Avila *et al.*, 2011, 2012; Sastri *et al.*, 2012; Suchy *et al.*, 2016). Chitobiase is a chitinolytic enzyme used by crustaceans to catalyze the partial recycling of chitin. At the time of molt, chitobiase is released into the water column by the shedding of the exoskeleton, observed as an enzyme increase coincident to the animal's location (Vrba and Machacek, 1994). The amount of chitobiase released into the water column has been shown to be proportional to an individual's body size (Sastri and Dower, 2006). The "chitobiase method" works under the assumptions that (i) chitobiase activity in the water column is proportional to the developing biomass of the crustacean zooplankton community; and (ii) that there is a steady rate of chitobiase production by molting crustaceans and decay by marine bacteria (Sastri and Roff, 2000; Sastri and Dower, 2006). Therefore, the rate of production of chitobiase in the water column is considered a proxy for the biomass production rate (BPR) of the entire crustacean zooplankton community. By using the chitobiase method to estimate crustacean zooplankton production rates, the sampling bias against smaller copepod species (i.e. that exists in other methods) is removed. The chitobiase approach is routinely

applicable in the field (i.e. relatively simple) and analogous to community-level production rate estimates for phytoplankton. As such, it can also be used to estimate trophic transfer efficiencies (Sastri *et al.*, 2012; Suchy *et al.*, 2016).

Chitobiase-based estimates of crustacean zooplankton production have been compared to empirical models in previous studies (Avila *et al.*, 2012; Suchy *et al.*, 2016; Kwong *et al.*, 2020). The Hirst and Bunker (2003) empirical growth rate model was found to be the most consistent with chitobiase-based values (Kwong *et al.*, 2020), whereas estimates derived from the Huntley and Lopez (1992) model and Hirst and Lampitt (1998) were more variable (Kwong *et al.*, 2020) and higher than chitobiase-based estimates (Suchy *et al.*, 2016). Inconsistencies between empirical models and chitobiase-based estimates may be due to the nature of the models themselves, wherein the Huntley and Lopez model only considered specific-sized copepods in their 'average' growth rate calculation. Therefore, larger slower growing non-copepod crustaceans were excluded from the global model. Similarly, the global model incorporating chlorophyll concentrations (Hirst and Bunker, 2003), only considers food quantity and not quality - which may play major role in estimate discrepancies (Suchy *et al.*, 2016). Additionally, when applying any of the empirical growth rate models to biomass for entire zooplankton communities it assumes that all individuals are growing at rates defined by the model. This is a particularly questionable assumption because all animals within a community may not be actively growing or growing at the same rate, and especially between different species (Hirst and Sheader, 1997). In contrast, the chitobiase method captures only the growth and production of crustacean zooplankton individuals that are actively growing.

Throughout the thesis, the term “crustacean zooplankton biomass production rates (BPR)” derived from chitobiase-based estimates of productivity will be used in place of “secondary production rates” since some of the species captured in the production rate estimates presented here do not occupy the second trophic level. Additionally, many non-crustacean zooplankton also act as secondary consumers (e.g. chaetognaths, pteropods, gelatinous taxa) but are excluded from our chitobiase-based production estimates.

1.2.4 Trophic Transfer Efficiency

Another facet of the ecosystem function definition includes energy and nutrient flux as well as biomass production (Paterson *et al.*, 2012). One measure of energy exchange between trophic levels within an ecosystem is the trophic transfer efficiency (TTE). As a core principle in ecology, TTE was originally defined as “*the efficiency of productivity of any (trophic) level relative to the productivity of any previous level*”, where productivity was defined as being the general rate of production (Lindeman, 1942). TTE has traditionally been assumed to be 10% between trophic levels in both aquatic and terrestrial systems (Semper, 1881; Lindeman, 1942; Pauly and Christensen, 1995). Despite this long-standing assumption, it has been previously noted that TTE estimates can vary greatly, ranging from <1% to 50% in both freshwater and marine ecosystems (e.g. Cushing 1973; Jennings *et al.*, 2002; Bradford-Grieve *et al.*, 2003; Anderson *et al.*, 2009; Trebilco *et al.*, 2013; Suchy *et al.*, 2016). In fact, TTE may not be directly related to ecosystem productivity, *per se* (San Martin *et al.*, 2006). Rather it likely represents a combination of factors, both environmental and biological, that will determine the efficiency at which energy is transferred up the food web (Cushing, 1971, 1973; Gaedke and Straile, 1994;

San Martin *et al.*, 2006; Dickman *et al.*, 2008; Peace, 2015; Garcia-Comas *et al.*, 2016). These factors therefore not only help to determine TTE but can also affect zooplankton diversity, composition, and productivity.

1.3 Zooplankton Biodiversity

Biodiversity encompasses many levels of organization and can be described as the number of genotypes, species, the evenness of distribution and the range of functional traits present, or ecosystems (Hooper *et al.*, 2005). Traditionally, the term biodiversity has been synonymous with species richness (Hooper *et al.*, 2005); however, a combination of richness, relative abundance, and composition can affect ecosystem functions differently. Ecological research in terrestrial ecosystems has a long-standing record of linking changes in biodiversity to ecosystem functions (Naeem and Li, 1997; Tilman, 1999; Loreau *et al.*, 2001, 2002; Petchey *et al.*, 2002). Although calculating taxonomic diversity remains common practice and is a well-established way of assessing patterns of biodiversity, additional knowledge regarding the biology and ecology of the individual species present within a given system may provide deeper insight into ecosystem processes and functions, such as TTE (McGill *et al.*, 2006). The functional analogue to taxonomic diversity uses species functional traits to quantify functional diversity (FD) (Chapin *et al.*, 2000; Naeem *et al.*, 2002) and functional group diversity (Tilman, 2001; Pomerleau *et al.*, 2015; Benedetti *et al.*, 2015, 2018, Venello *et al.*, 2021a). FD is defined as “the value and range of organismal traits that influence their performance and ecosystem functioning” (Díaz and Cabido, 2001), where the traits can be defined as the morphological, physiological, and behavioral characteristics which represent the functional role of a given

species within the ecosystem, as well as the ecological niche that the species occupies (Litchman *et al.*, 2013). Together, these dictate critical ecological functions and affect key ecosystem processes such as productivity and energy transfer (Hébert *et al.*, 2017). FD has been characterized by several indices: functional richness (*FRic*), functional evenness (*FEve*), functional divergence (*FDiv*) (Mason *et al.*, 2005; Villéger *et al.*, 2008) as well as functional dispersion (*FDis*) (Laliberté and Legendre, 2010), and where *FRic*, *FEve*, and *FDiv* are analogous to species richness (*S*), species evenness (*J'*), the Shannon diversity index (*H'*) respectively.

Like taxonomic diversity, functional diversity has been commonly used to relate community composition to ecosystem function in terrestrial and freshwater ecosystems (Diaz and Cabido, 2001; Barnett *et al.*, 2007; Roscher *et al.*, 2013; Russell *et al.*, 2014; Schmitz *et al.*, 2015; Russo *et al.*, 2016; Hébert *et al.*, 2017). However, functional diversity studies of marine zooplankton communities have been limited to descriptions of functional traits within a community (Kiorboe, 2011; Barton *et al.*, 2013; Litchman *et al.*, 2013; Hébert *et al.*, 2016), to establish functional groups (Pomerleau *et al.*, 2015; Benedetti *et al.*, 2015, 2018; Venello *et al.*, 2021a), or to compare taxonomic *versus* functional diversity metrics (Pomerleau *et al.*, 2015). To date, few direct links have been established between functional diversity and ecosystem function. Functional diversity has been shown to have a greater influence than taxonomic diversity on ecosystem functions, such as productivity (Hooper and Dukes, 2004; Hooper *et al.*, 2005; Schittko *et al.*, 2014). As such, functional approaches in assessing marine zooplankton communities are important to further our understanding of potential changes in ecosystem functions, such as productivity and energy transfer that may occur in response to environmental variability, and including anthropogenic stressors (Jennings *et al.*, 2002).

1.4 Drivers of Variability in Zooplankton Production Rates, Energy Transfer, and Biodiversity

The extent to which oceanographic variability influences the biodiversity of marine zooplankton communities remains a critical issue for biological oceanographers (González *et al.*, 2020). Zooplankton communities are known to be influenced by temperature, salinity, oxygen concentration, and stratification (Beaugrand *et al.*, 2002; Mackas *et al.*, 2006; Mackas *et al.*, 2007). Temperature, in particular, is a major factor influencing the rate of physiological processes in zooplankton, including growth rate (Kimmerer, 1987; Huntley and Lopez, 1992). Additionally, temperature plays a fundamental role in structuring marine biodiversity (Tittensor *et al.*, 2010), and it is expected that changes to ecosystem functions, such as energy transfer, will be partially due to shifts in species/community assemblages as a response to climate change (Tittensor *et al.*, 2010; du Pontavice *et al.*, 2020). In fact, reductions in TTE have been linked to rising temperatures across a range of marine and freshwater ecosystems (du Pontavice *et al.*, 2020; Barneche *et al.*, 2021). Increased temperatures may also increase predation on zooplankton from within and between trophic levels, limiting the efficiency between primary producers and their consumers (Dickman *et al.*, 2008; Tanaka and Mano, 2012).

As one example, productive upwelling regions usually have surface waters that are cool and well mixed, with high nutrient concentrations, and phytoplankton communities that are dominated by large centric diatoms. In such instances, large copepods usually dominate the zooplankton community with a food web that is considered simple, efficient and able to support a high biomass of higher trophic levels (Richardson, 2008). In contrast, surface waters

in oligotrophic/nutrient limited regions surface waters are warmer and more stratified with the phytoplankton community often dominated by smaller-celled taxa and flagellates. Zooplankton communities under these conditions are usually dominated by small crustaceans and a large biomass of gelatinous animals, producing a potentially more complex and less efficient food web that doesn't usually support a high biomass of upper trophic level organisms (Richardson, 2008). However, the productivity of a given ecosystem isn't necessarily indicative of the efficiency of energy transfer processes. In fact, TTE can be very low in productive upwelling regions where grazing by zooplankton simply cannot keep up with primary production (Cushing, 1971). For example, productive regions of the Atlantic Ocean were found to be no more efficient than adjacent oligotrophic regions (San Martin *et al.*, 2006). Additionally, studies within this thesis showed that high crustacean zooplankton biomass within the northeast subarctic Pacific may not necessarily equate to high production rates (Venello *et al.*, 2021b; Chapter 3).

1.5 Regional Oceanographic Setting for This Thesis

Within the northeast subarctic Pacific and along the west coast of Vancouver Island (WCVI), a range of oceanographic and productivity regimes have been observed (Mackas and Sefton, 1982; Mackas, 1992; Varela and Harrison, 1999; Ware and Thomson, 2005; Harris *et al.*, 2009). These regimes include a seasonal upwelling zone along the WCVI, a transitional oceanic region characterized by nutrient limitation during summer, and a high nitrate low chlorophyll (HNLC) regime furthest offshore in our area of reference (Boyd and Harrison, 1999; Varela and Harrison, 1999; Whitney *et al.*, 2005; Mackas and Coyle, 2005). The WCVI is a highly productive

region that resides in a transition area, where the eastward flowing North Pacific current splits to form both the northward flowing Alaska and southward flowing California current (Freeland, 2006). Oceanographic conditions along the WCVI transition seasonally between upwelling and downwelling which result in seasonal variation in upper-water column temperature, salinity, oxygen, and nutrients. During the summer months, biological productivity along the southern shelf of Vancouver Island is driven by the Juan de Fuca eddy (Mackas and Sefton, 1982; Freeland, 1988). Spatiotemporal variability of phytoplankton biomass is considerable, but generally higher on-shelf than off-shelf, with inshore seasonal maxima in summer and offshore in March/April and October (Mackas and Sefton, 1982; Harris *et al.*, 2009).

The region seaward of the WCVI continental shelf is generally not influenced by coastal upwelling and experiences summer nitrate (NO_3) depletion which limits primary productivity (Whitney *et al.*, 1998; Peña and Varela, 2007). Even further offshore is a region characterized by high-nitrate low-chlorophyll (HNLC) conditions, where primary productivity is limited by the availability of iron (Harrison *et al.*, 2004). Productivity and phytoplankton biomass are generally lower in the HNLC region with the occasional increase due to nutrient enrichment from mesoscale eddies (Whitney and Robert, 2002; Whitney *et al.*, 2005) and broad-scale events such as volcanic ash deposition (Hamme *et al.*, 2010).

Variation of zooplankton biomass and community composition in the study area is characterized by a gradient from nearshore to open-ocean environments which generally aligns with the oceanographic regimes described above (Mackas and Coyle, 2005). Nearshore/shelf zooplankton communities are not highly diverse and are comprised of species which are omnivorous/herbivorous, with narrow vertical migration ranges, small body size, and which

have multiple cohorts present (Mackas and Coyle, 2005; Venello *et al.*, 2021a). In contrast, the off-shelf to oceanic zooplankton communities in the region are more diverse, and dominated by zooplankton where vertical migration is more common, are larger in body size, and have strongly seasonal reproduction cycles (Mackas and Coyle, 2005). Copepod species in the study area have been classified into geographically separated groups: 'Boreal-Shelf', 'Subarctic', and 'Southern', whereby 'Boreal-Shelf' and 'Subarctic' groups dominate in cooler than average and typical years, whereas species from the 'Southern' group are more abundant during El Niño years and with anomalous warm water events (Mackas and Galbraith, 2002a; Mackas *et al.*, 2004; Galbraith and Young, 2019).

The range of oceanographic regimes that occur off the WCVI and within the subarctic NE Pacific has long been of interest to oceanographers and, as such, has been extensively surveyed by Fisheries and Oceans Canada since the 1970s. Additionally, the HNLC region is home to Ocean Station Papa, a long-standing weather ship station turned oceanographic sampling line where modern sampling of biological, chemical, and physical oceanographic data has been collected since 1980 (Freeland, 2007). Twice yearly surveys along the WCVI occurs via the La Perouse zooplankton monitoring program, as well as thrice yearly surveys of "Line P" which extends seaward from coastal WCVI to Ocean Station Papa. The biological, chemical, and physical parameter data set available from these programs, as well as opportunities provided to students to collect their own data during the surveys, is invaluable to both governmental and academic scientists in this area. As such the work conducted for this thesis and the ancillary data used here would not have been possible without access to these survey programs.

1.6 Thesis Objectives and Structure

Despite established links to temperature and differences in community composition (Mackas and Galbraith 2002; Mackas *et al.*, 2004; Galbraith and Young, 2019; Venello *et al.*, 2021a), little work has been done to explicitly address links between diversity metrics and ecosystem function (i.e. production rates and energy transfer), especially for marine zooplankton. With recent advances in *in situ* methods for estimating ecosystem functions the opportunity to link zooplankton biodiversity to ecosystem function has become more feasible. As such we can further refine our understanding of ecosystem functions within the subarctic NE Pacific marine ecosystem and evaluate its response to environmental variability with applications to future climate scenarios. This is especially important as community composition and diversity likely play a crucial role in determining energy transfer within an ecosystem (Edwards and Richardson, 2004; Hays *et al.*, 2005). Thus, as climate change alters plankton communities, it is likely that production rates and energy transfer at the base of marine food webs will also be altered, whereby these changes may propagate upward to higher trophic levels. Therefore, we need to improve our understanding of the factors that drive variability in functional/taxonomic diversity, crustacean zooplankton biomass production rates, and TTE across a range of oceanographic regimes to help address potential community-wide responses to environmental variability including anthropogenic stressors.

With that motivation in mind, the three primary research questions of this thesis are:

- 1) What are the drivers of functional group community assembly and how might these communities be altered by a changing marine ecosystem? (Chapter 2).** This question is addressed in chapter 2 and has been published in *Progress in Oceanography* in 2020 as ‘Zooplankton functional group responses to environmental drivers off the west coast of Vancouver Island, Canada’ by Venello, T.A., Sastri, A.R., Galbraith, M.D., and Dower, J.F.
- 2) How do community-level crustacean zooplankton production rates vary within and across regions of the subarctic northeast Pacific? (Chapter 3).** This chapter is currently under review and revision at the *ICES Journal of Marine Science* as ‘Drivers of variation in crustacean zooplankton production rates differ across regions off the west coast of Vancouver Island and in the subarctic NE Pacific’ by Venello, T.A., Sastri, A.R., Suchy, K.D., Galbraith, M.D., and Dower, J.F.
- 3) How does zooplankton community composition/diversity affect the spatiotemporal variability in trophic transfer efficiency? (Chapter 4).**

The thesis concludes with a synthesis of the major findings (Chapter 5), addressing the importance of routine estimates of crustacean productivity as well as the applied use of functional group analysis and the implications that the results from Chapters 2 to 4 have on future research in the field of functional diversity, crustacean zooplankton production rates, and energy transfer in marine ecosystems.

Chapter 2. Zooplankton Functional Group Responses to Environmental Drivers off the West Coast of Vancouver Island, Canada

Citation:

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2.1 Abstract

Zooplankton diversity and biomass are integral to marine ecosystem functioning. Functional trait-based approaches enable an examination of ecosystem dynamics in which species groups are defined by their functional roles (i.e. functional groups) within the ecosystem, rather their taxonomic identity. Changes in the relative and absolute biomass of zooplankton functional groups may affect the productivity of higher trophic levels via change in secondary production rates and the efficiency of energy transfer. Traits from 55 mesozooplankton species were assembled from the literature and applied to a 35-year time series (1980-2016) for the southern shelf area off the west coast of Vancouver Island, Canada. Eight functional groups were identified by clustering species on the basis of functional trait similarity. A time series of biomass anomalies was calculated for each functional group, after which links between functional group biomass anomalies and several environmental variables were examined. Generalized additive modeling (GAM) identified local sea surface temperature as the most important driver of biomass anomaly patterns for three groups: Doliolids, Omnivore-Herbivores, and the Active Ambush Omnivores. The Southern Oscillation Index (SOI) was also a main driver for three groups: Egg-Brooding Carnivores, Broadcast Carnivores, and Cruise Carnivores-A. The Ocean Niño Index (ONI) was significant for Active Ambush Omnivores and Egg-Brooding Carnivores, whereas the Pacific Decadal Oscillation (PDO) was a driver of Broadcast Carnivores and Cruise Carnivores-A. The Doliolids group also varied with surface salinity, and Cruise Carnivores-B with the North Pacific Gyre Oscillation (NPGO). The relative contribution of several zooplankton functional groups to the overall biomass showed no temporal trends but some groups had increased or decreased abundance contributions. This

suggests functional redundancy within groups, as smaller or larger species may dominate based on environmental conditions. Our analysis demonstrates that functional group biomass anomalies vary with environmental variables, where conditions may favor certain functional groups, therefore dictating how the ecosystem is functioning.

2.2 Introduction

Zooplankton, including both gelatinous and crustacean species, are major contributors in moderating global ecosystem functioning (i.e. aide in the biological cycling of carbon via the biological pump and energy transfer to higher trophic levels), whereby the strength and function of this system is dependent not only on biomass and production of pelagic producers/consumers but also on the composition and number of species within those communities (Duffy and Stachowicz, 2006). Zooplankton can also serve as indicators of climate change (Richardson, 2008), as their non-linear responses allow them to rapidly respond to change (Taylor *et al.*, 2002), by which they may accurately reflect changes in temperature and ocean currents, since zooplankton physiological processes are sensitive to temperature (Mauchline, 1998; Richardson, 2008).

One way to assess pelagic ecosystem dynamics is to use functional groupings; an approach which defines the functional roles of zooplankton by grouping species with similar functional traits (Tilman, 2001; Pomerleau *et al.*, 2015; Benedetti *et al.*, 2015, 2018). Functional traits can be defined as those morphological, physiological, and behavioral characteristics which define the functional role and ecological niche of a given species within the ecosystem, as well as the ecological niche that species occupy (Litchman *et al.*, 2013). These traits influence a

species/organism's fitness, represent different critical ecological functions, and can affect key ecosystem processes such as productivity and energy transfer (Hébert *et al.*, 2016). Functional groups are therefore defined as clusters of species with similar effects on ecosystem functions, which are likely to respond similarly to changes in environmental conditions (Lavorel *et al.*, 1997). A functional group approach to assessing changes in zooplankton community structure may thus help to reduce the complexity of dealing with many species at once while still retaining enough information to understand community selection pressures and environmental drivers (Litchman *et al.*, 2013). Traditional taxonomic-based approaches not only provide little indication as to why particular species co-occur within an area (e.g. where environmental conditions may favor certain assemblage types) but also do not indicate what the impact of the presence/absence of any given species would have on ecosystem functioning.

Previous studies have suggested that a functional traits approach can provide a link between the functional roles of species and the community response to environmental changes. For instance, Barnett and Beisner (2007) found that variation in functional diversity was better explained by chemical factors than traditional species-richness metrics across 18 lakes. Functional traits such as adult body size and trophic group were found to be most related to lake productivity. Additionally, lakes dominated by diatoms/chrysophytes and low total phosphorus concentration promoted zooplankton functional diversity, whereas lakes dominated by cyanobacteria and with high total phosphorus had low functional diversity (Barnett and Beisner, 2007). Similarly, Cardoso *et al.* (2017), showed that phytoplankton functional and taxonomic diversity in Amazonian lakes was driven primarily by total phosphorus

and zooplankton density - explaining more variation in functional versus taxonomic diversity during low water seasons.

The majority of previous studies dedicated to planktonic functional groups were focused on phytoplankton or freshwater zooplankton (Barnett and Beisner 2007; Litchman and Klausmeier 2008; Litchman *et al.*, 2012; Edwards *et al.*, 2013; Litchman *et al.*, 2013; Cardoso *et al.*, 2017; Josué *et al.*, 2019; Ma *et al.*, 2019). The approach has not been as widely applied to marine zooplankton, largely because species-specific trait information is lacking, except for a limited number of well-known species in a few well-studied areas (Hébert *et al.*, 2016, 2017; Brun *et al.*, 2017). Some progress has been made in creating trait frameworks for marine crustacean zooplankton; however, few studies have focused on applied questions or addressed the potential utility of this approach to current metrics, such as species-specific biomass and abundance. Pomerleau *et al.* (2015) identified seven zooplankton functional groups for the NE Pacific, while linking broad-scale oceanographic and climate variables to both taxonomic and functional diversity over a 16-year time series. Benedetti *et al.* (2016) established copepod functional groups in the Mediterranean Sea, distinguishing two groups of carnivores and four non-carnivore groups. An in-depth analysis of these groups (Benedetti *et al.*, 2018) subsequently identified seven copepod functional groups with differing distributions along an environmental gradient. For example, carnivorous functional groups in the Mediterranean Sea were more strongly associated with oligotrophic/tropical conditions, whereas herbivores were associated with colder and seasonally productive areas (Benedetti *et al.*, 2018).

Campos *et al.* (2017) identified two major functional groups of copepods from the Tropical Southwestern Atlantic, chiefly separated by spawning strategy. These functional

groups also had distinct cross-shelf distributions, linking certain functional groups to specific continental shelf locations (Campos *et al.*, 2017). Similarly, McGinty *et al.* (2018) found that in the North Atlantic, sea surface temperature, depth, salinity, and chlorophyll separated omnivores and herbivores from carnivores in copepod niches. However, in the Southern Ocean differences between copepod trophic groups were found to be separated primarily by chlorophyll and wind stress (McGinty *et al.*, 2018).

Changes in ocean climate, such as increased warming and stratification, can also alter the composition and size structure of primary producers, where cyanobacteria, dinoflagellates, and pico-phytoplankton are expected to dominate under warmer, more stratified conditions (Sommer *et al.*, 2002; Morán *et al.*, 2010; Peña *et al.*, 2019). Changes in phytoplankton community structure could alter phytoplankton-zooplankton interactions and ultimately impact higher trophic levels relying on specific prey.

As such, zooplankton communities will have to respond to changes in prey community structure, which in turn may alter zooplankton functional groups by changing the contribution of species-specific abundances. Thus, it is important to assess the utility and efficacy of new approaches, as either improvements or complementary to existing metrics for time series analyses. These new approaches may also help improve our understanding of mechanisms driving variations in zooplankton community structure and the representation of zooplankton in marine ecosystem models. A functional approach to zooplankton community time series can thus provide insight into potential community reorganizations under a changing marine ecosystem by identifying environmental drivers of community assembly.

Previous studies of the zooplankton community off the west coast of Vancouver Island, Canada has focused on biomass anomalies of several selected species (Mackas, 1992; Mackas *et al.*, 2001). Here, we have used four traits for the most commonly observed gelatinous and crustacean mesozooplankton species to define functional groups for the southern shelf area off the west coast of Vancouver Island (Figure 2.1). These traits are: size class, feeding type, trophic group, and reproduction mode. Spring functional group biomass anomalies (defined as departures from the climatological mean biomass from 1980-2010) as well as anomalies of environmental drivers that were calculated from 1980-2016. Relationships between functional group biomass anomalies and environmental driver anomalies were examined, including: localized sea surface temperature and salinity (Amphitrite Point), localized upwelling strength (as a proxy for food availability, recorded at 48°N 125°W), the North Pacific Gyre Oscillation (NPGO), the Pacific Decadal Oscillation (PDO), the Ocean Niño Index (ONI), and the Southern Oscillation Index (SOI).

2.3 Study Area and Methods

2.3.1 West Coast Vancouver Island

The west coast of Vancouver Island (WCVI) is a highly productive seasonal upwelling region located at the northernmost end of the California current ecosystem, off the coast of British Columbia, Canada. The WCVI has been sampled routinely by Fisheries and Oceans Canada (DFO) since the early 1980s, with stations spanning the entire shelf (Figure 2.1). The southern extent of the WCVI is a transition zone between the southward-flowing California current and the northward-flowing Alaska current. Along the WCVI, local conditions can resemble the

biological and physical characteristics of both currents - the degree of resemblance varying seasonally and annually (Mackas *et al.*, 2001). The Vancouver Island coastal current dominates circulation patterns within 20 km of the coast; driven by freshwater input from mainland British Columbia (BC) it maintains a northward flow from the Strait of Juan de Fuca to Brooks Peninsula throughout the year. The WCVI experiences seasonal and interannual variability in upwelling and downwelling intensity. In winter, the Aleutian Low pressure system generally drives southerly coastal winds and a poleward downwelling current dominates; while in summer, the North Pacific High drives northerly winds that favor upwelling with the equatorward current flowing along the shelf break. (Thomson, 1981). These strong upwelling and downwelling cycles also cause highly variable cycles in subsurface temperature, oxygen, salinity and nutrients.

Summer productivity along the southern part of Vancouver Island is driven by the Juan de Fuca eddy, which controls circulation in the area during this time (Mackas and Sefton, 1982; Freeland, 1988). Primary productivity off the WCVI ranges from 1-13 g C m⁻² d⁻¹ (Harris *et al.*, 2009). Spatiotemporal variability in phytoplankton biomass is considerable; with biomass generally higher on-shelf than off-shelf, with inshore peaks (>5 mg/m³) during summer and offshore peaks in March/April and October (Mackas and Sefton, 1982; Harris *et al.*, 2009).

A similar seasonal cycle for mesozooplankton biomass has also been observed, with a biomass maximum in the spring-summer and a minimum in fall-winter (Mackas, 1992). Prevailing currents and bathymetry usually determine the boundaries of zooplankton aggregations and phytoplankton biomass in the region, although this is highly variable (Mackas, 1984; Mackas *et al.*, 2001). During summer, cross-shelf transport associated with seasonal upwelling advect zooplankton seaward from the inner shelf to the continental slope and

eventually off-shelf via cross-shore export (Mackas and Coyle, 2005). In spring, the WCVI shelf mesozooplankton biomass is dominated by the copepods *Calanus marshallae* and *Pseudocalanus* spp, whereas *Neocalanus cristatus* and *N. plumchrus* dominate at the shelf break/off-shelf (Mackas, 1992). In summer, *Acartia longiremis* dominates on the shelf, and moving into late summer *C. marshallae* and *Pseudocalanus* spp. are advected toward the shelf break/off-shelf. *Metridia pacifica* is present throughout the spring and summer (Mackas, 1992). Several euphausiid species also contribute to total biomass along the shelf break and areas seaward, dominated by *Euphausia pacifica*, *Thysanoessa spinifera* and *Thysanoessa inspinata* (Mackas, 1992).

Figure 2.1. Location of sampling stations (1980-2016) for the southern shelf area of WCVI. Contour lines occur at 250m, 500m, 1000m, 1500m, and 2000m to define shelf.

2.3.2 Environmental Variable Anomaly Time Series

Seven environmental variables were selected to best represent the known ecosystem drivers within the study area (Table 2.1). The North Pacific Gyre Oscillation (NPGO), Pacific Decadal Oscillation (PDO), Ocean Niño Index (ONI), and Southern Oscillation Index (SOI) were chosen to represent large-scale ocean processes known to influence regional productivity and community composition (Harrison *et al.*, 2004; Di Lorenzo *et al.*, 2008; Patterson *et al.*, 2013). Coastal upwelling intensity recorded from a coastal buoy located at 48°N 145°W (Upwelling, PFEL, NOAA, Table 2.1) was selected because zooplankton biomass relies on phytoplankton blooms driven by nutrient-rich waters upwelled seasonally off the WCVI (Thomson, 1981). Daily sea surface temperature, and surface salinity from Amphitrite Point Lighthouse (Amp SST and Amp Sal, respectively, Fisheries and Oceans Canada, Table 2.1) were chosen to represent local indicators of oceanographic conditions for the southern shelf area of Vancouver Island (Chandler *et al.*, 2016, 2017). Anomaly time series for each variable were constructed by subtracting the climatological mean from daily values for Amp SST, Amp Sal and Upwelling. Daily and monthly anomalies were then averaged to produce an annual anomaly value. Annual anomalies were averaged over spring months only (April-June). Northern Oscillation Index was also considered but displayed strong significant collinearity with PDO (-0.8, p-value = 0.002) and was therefore not included in our analysis.

Variable	Abbreviation	Description	Source
North Pacific Gyre Oscillation	NPGO	Climate pattern that emerges as the 2 nd dominant mode of sea surface height variability developed from sea surface temperature and height anomalies over the Northeast Pacific (180°W-110°W; 25°N-62°N)	Di Lorenzo et al. 2008; http://www.o3d.org/npgo/
Pacific Decadal Oscillation	PDO	Standardized values derived as the leading PC of monthly SST anomalies in the North Pacific Ocean poleward of 20°N, where monthly mean global average SST anomalies are removed	Zhang et al. 1997, Mantua et al. 1997; Joint Institute for the Study of the Atmosphere and Ocean, National Oceanic and Atmospheric Administration http://research.jisao.washington.edu/pdo/
Upwelling Index at 48N 125W (cubic meters per second along 100m of coastline)	Upwelling	Bakun Index values at 48°N 125°W, values are daily average of wind driven cross-shore transports computed from six-hourly surface pressure analyses	Pacific Fisheries Environmental Laboratory, National Oceanic and Atmospheric Administration https://coastwatch.pfeg.noaa.gov/erddap/search/index.html?page=1&itemsPerPage=1000&searchFor=upwelling
Amphitrite Point Lighthouse Sea Surface Temperature (°C)	Amp SST	Daily daytime high tide surface water temperature at Amphitrite Point Lighthouse	Fisheries and Oceans Canada http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lightstations-phares/index-eng.html https://open.canada.ca/data/en/dataset/719955f2-bf8e-44f7-bc26-6bd623e82884
Amphitrite Point Lighthouse Sea Surface Salinity (psu)	Amp Sal	Daily daytime high tide surface water salinity at Amphitrite Point Lighthouse	Fisheries and Oceans Canada http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lightstations-phares/index-eng.html https://open.canada.ca/data/en/dataset/719955f2-bf8e-44f7-bc26-6bd623e82884
Ocean Niño Index	ONI	Running 3-month average sea surface temperature Niño 3.4 region (120°W-170°W), which is then compared to a 30-year average	National Centers for Environmental Prediction, Climate Prediction Center, National Oceanic and Atmospheric Administration https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_change.shtml
Southern Oscillation Index	SOI	Computed from sea level pressure anomalies (monthly sea level pressure minus climatology) between Tahiti and Darwin	Pacific Fisheries Environmental Laboratory, National Oceanic and Atmospheric Administration https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensocycle/soi.shtml

Table 2.1. Description and sources of variables used to explore relationships between the environment and functional group biomass anomalies from 1980-2016.

2.3.3 Zooplankton Abundance and Biomass

Abundance and biomass data were extracted from the zooplankton database maintained by Fisheries and Oceans Canada (Institute of Ocean Sciences, Sidney, BC, Canada). Southern shelf zooplankton samples used in this analysis were collected during DFO's La Perouse monitoring cruises in April, May, and June from 1980-2016. Vertical net hauls were conducted using a black-meshed bongo net (0.25 m² mouth area, 0.23 mm mesh) fitted with a TSK flowmeter, from near-bottom to sea surface (when bottom depth was < 250 m) on the continental shelf and upper slope, and from 250 m to surface at deeper locations and off the shelf. Samples were identified and enumerated to species and developmental stage (*as per* Mackas, 1992; Mackas *et al.*, 2001; Mackas and Galbraith, 2002a,b). Briefly, raw counts were transformed to abundance per square meter using a subsampled fraction, volume of water, and tow depth. Species and stage-specific length:dry-weight relationships (from the literature or locally measured relationships; Mackas, 1992) were used to convert abundance to species-specific biomass.

2.3.4 Functional Group Anomalies

We selected 55 crustacean and gelatinous mesozooplankton species that occur within the study area and for which we could also find trait information in the literature. Functional traits for most of the crustacean species were established following Pomerleau *et al.* (2015), while a wider literature review was conducted to assess these same traits for the gelatinous species selected (Table 2.2). Ultimately, four key functional traits were used in this study: size class of average body length or max body size/diameter, feeding type (ambush, cruise, current, and

mixed), trophic group (carnivore, detritivore, omnivore and herbivore), and reproductive mode (alternation of generations, broadcast spawners, egg-brooding, egg-brooding sac) (Table 2.2). Size classes were determined by a k-means cluster analysis using the NBClust package (Charrad *et al.*, 2014) within the R statistical framework (R Development Core Team, 2017), where the number of k-means size class clusters was determined by the silhouette method. Four size classes were established: Size 1: 0.65-4.6 mm, average: 1.8 mm; Size 2: 4.98-11 mm, average: 7.4 mm; Size 3: 20-26.5 mm, average: 24.3 mm; Size 4: 90-120 mm, average: 105 mm. The complex life history of the Doliolids group (*Dolioletta gegenbauri*), which includes alternation of sexual and asexual generations and a polymorphic asexual phase (Deibel and Lowen, 2012) significantly affects their reproductive output and as such was chosen to represent their reproductive mode. These four traits are commonly used for describing zooplankton (Barnett *et al.*, 2007; Benedetti *et al.*, 2015; Pomerleau *et al.*, 2015), and were chosen to represent various key ecological functions, such as reproduction and consumption on an organismal level and zooplankton biomass/secondary productivity, algal biomass/composition, and biogeochemical cycles at the ecosystem level (Kiorboe, 2011; Litchman *et al.*, 2013).

To delineate functional groups, a multiple correspondence analysis (MCA) was applied to the resultant trait matrix, *as per* Benedetti *et al.* (2016). MCA operates as an ordination method in reduced space for the multivariate analysis of categorical variables (Husson *et al.*, 2017). Hierarchical clustering was performed on the MCA-derived distance matrix (Ward's; Husson *et al.*, 2010; Legendre and Legendre, 2012).

The biomass time-series of the individual functional groups were log-transformed to facilitate comparison between groups (*as per* Mackas *et al.*, 2001, 2006). Briefly, within each functional group total species biomass was summed per sample before log transformation ($\text{Log}_{10} + 0.001$). Log-transformed functional group biomass was then averaged by month. To account for seasonal differences in zooplankton biomass and to focus on spring months, a climatological mean (1980-2010) was generated using the average of the monthly log-transformed functional group biomass from April- June. Monthly functional group biomass anomalies were then calculated by subtracting the seasonal climatological mean (April-June from 1980-2010) from the corresponding monthly log-transformed functional group biomass values. Thus, annual biomass anomalies represent spring biomass departures from the climatological mean. Note that since anomalies are log-scaled, an anomaly of +1 equates to a tenfold greater biomass than the climatology. Similarly, an anomaly of -1 represents a group specific biomass only 10% of the average climatology, *as per* Galbraith *et al.* (2016).

2.3.5 Statistical Analysis

All statistical analyses were performed within the R statistical framework, version 3.5.1 (R Core Team 2018). To assess yearly long-term trend changes, a non-parametric Spearman's Rho trend test (where rho ranges from -1 to 1) was used to measure the strength of association between time and functional group biomass anomalies, percent total biomass, and abundance using the 'pastecs' package (Grosjean and Ibanez, 2018). Total spring biomass and annual abundance were calculated, and percent contribution was then determined for each functional group. For the trend analysis we used yearly functional group biomass anomalies and percent contribution

of biomass and abundance. Generalized additive models (GAM) were built using the 'mgcv' package (Wood, 2001; Wood *et al.*, 2016) to relate functional group biomass anomalies to local and climatic environmental anomalies (Wood, 2017). GAMs are generalized linear models wherein the linear predictors are the sum of smoothing functions of individual covariates, allowing for non-linear relationships between response and predictor variables. GAMs were fit using a Gaussian identity link function with a thin plate regression spline smoother. Restricted maximum likelihood method (REML) was used as the smoothing parameter estimation method (Wood, 2011). Akaike information criterion (AIC) was used to select model input variables. Both functional group biomass and environmental anomalies were compared on a monthly scale (April, May, and June) for use in GAM analysis. If residuals showed significant evidence of autocorrelation, the GAM model was fit using an autoregressive moving average model (ARMA) in the 'nlme' package (Pinheiro *et al.*, 2018). By including satellite derived chlorophyll into the GAM analysis, the GAM model results reported are for 22 years of the timeseries (1998-2016), as opposed to trend analysis which spans the entire timeseries (1980-2016).

Order/Taxon	Length (mm)	Feeding Type	Trophic Group	Reproduction Mode
Copepod				
<i>Acartia longiremis</i>	1.07 ^(7, 10)	Active Ambush ⁽⁵⁾	Omnivore-Herbivore ⁽⁵⁾	Broadcast spawning ^(5,43)
<i>Acartia tonsa</i>	1.03 ⁽⁷⁾	Active Ambush ⁽⁵⁷⁾	Omnivore-Herbivore ⁽⁵⁾	Broadcast spawning ^(5,43)
<i>Aetideus divergens</i>	1.8 ⁽²⁾	Active Ambush ⁽³⁴⁾	Omnivore ^(4, 6)	Broadcast spawning ^(4,6)
<i>Aetideus pacificus</i>	2.5 ^(2, 10)	Active Ambush ⁽³⁴⁾	Omnivore ^(4, 6)	Broadcast spawning ^(4,6)
<i>Calanus marshallae</i>	3.70 ^(7, 10)	Current ⁽³⁴⁾	Omnivore-Herbivore ⁽¹¹⁾	Broadcast spawning ⁽¹¹⁾
<i>Calanus pacificus</i>	3.00 ^(7, 10)	Current ⁽³⁴⁾	Omnivore-Herbivore ^(11, 13)	Broadcast spawning ⁽¹¹⁾
<i>Centropages abdominalis</i>	1.78 ^(7, 10)	Active Ambush ⁽¹³⁾	Omnivore ⁽¹³⁾	Broadcast spawning ⁽¹³⁾
<i>Calocalanus</i> spp.	1.04 ⁽¹⁰⁾	Current ⁽⁴⁰⁾	Omnivore-Herbivore ⁽⁴⁰⁾	Broadcast spawning ⁽⁴⁰⁾
<i>Clausocalanus</i> spp.	1.15 ⁽¹⁰⁾	Cruise ^(46, 47)	Omnivore-Herbivore ^(67,68)	Egg-brooding sac ^(42, 44)
<i>Ctenocalanus vanus</i>	1.20 ⁽¹⁰⁾	Current ⁽⁴⁰⁾	Herbivore ⁽⁴⁰⁾	Broadcast spawning ^(40, 43)
<i>Eucalanus bungii</i>	7.03 ^(7, 10)	Current ⁽³²⁾	Omnivore-Herbivore ⁽⁵⁾	Broadcast spawning ⁽⁵⁾
<i>Eucalanus californicus</i>	6.45 ^(7, 10)	Current ⁽¹⁷⁾	Omnivore-Herbivore ⁽¹⁷⁾	Broadcast spawning ⁽⁵⁾
<i>Gaetanus simplex</i>	3.3 ^(1, 7)	Current, Active Ambush ^(1, 34)	Omnivore-Carnivore ^(1, 5)	Broadcast spawning ⁽¹⁾
<i>Gaetanus tenuispinus</i>	3.7 ^(1, 7)	Current, Active Ambush ^(1, 34)	Omnivore-Carnivore ^(1, 5)	Broadcast spawning ^(1, 49)
<i>Mesocalanus tenuicornis</i>	2.1 ⁽⁴⁰⁾	Current, Active Ambush ⁽⁴⁰⁾	Omnivore ⁽⁴⁰⁾	Broadcast spawning ⁽⁴⁰⁾
<i>Metridia pacifica</i>	2.89 ^(7, 10)	Cruise ⁽³³⁾	Omnivore ⁽⁵⁾	Broadcast spawning ⁽⁵⁾
<i>Microcalanus pusillus</i>	0.80 ^(7, 10)	Current ⁽³⁶⁾	Omnivore ^(1, 36)	Broadcast spawning ^(1, 36)
<i>Microcalanus pygmaeus</i>	0.86 ^(7, 10)	Current ⁽³⁶⁾	Omnivore ^(1, 36)	Broadcast spawning ^(1, 36)
<i>Neocalanus cristatus</i>	9.23 ^(7, 10)	Current ⁽¹⁵⁾	Omnivore ⁽¹¹⁾	Broadcast spawning ⁽²⁶⁾
<i>Neocalanus flemingeri</i>	5.25 ^(7, 10)	Current ⁽¹⁴⁾	Omnivore ⁽¹¹⁾	Broadcast spawning ⁽²⁶⁾
<i>Neocalanus plumchrus</i>	4.98 ^(7, 10)	Current ⁽¹⁴⁾	Omnivore ⁽¹¹⁾	Broadcast spawning ⁽²⁶⁾

<i>Oithona similis</i>	0.94 ^(7, 10)	Active Ambush ^(12, 28)	Omnivore ^(65, 66)	Egg-brooding sac ⁽²¹⁾
<i>Paracalanus</i> spp.	1.0 ⁽¹⁰⁾	Current ⁽⁴⁰⁾	Omnivore-Herbivore ⁽⁴⁰⁾	Broadcast spawning ⁽⁴⁰⁾
<i>Paraeuchaeta elongata</i>	6.85 ^(7, 10)	Active Ambush ⁽⁴⁵⁾	Carnivore ^(22, 45)	Egg-brooding sac ^(7, 44)
<i>Pseudocalanus mimus</i>	1.52 ^(7, 10)	Current ⁽³⁴⁾	Omnivore-Herbivore ^(5, 69)	Egg-brooding sac ^(5, 43)
<i>Pseudocalanus minutus</i>	1.46 ^(7, 10)	Current ⁽³⁴⁾	Omnivore-Herbivore ^(5, 69)	Egg-brooding sac ^(5, 43)
<i>Pseudocalanus moultoni</i>	1.52 ^(7, 10)	Current ⁽³⁴⁾	Omnivore-Herbivore ^(5, 69)	Egg-brooding sac ^(5, 43)
<i>Pseudocalanus newmani</i>	1.24 ^(7, 10)	Current ⁽³⁴⁾	Omnivore-Herbivore ^(5, 69)	Egg-brooding sac ^(5, 43)
<i>Scaphocalanus brevicornis</i>	2.28 ^(7, 10)	Current ⁽³⁴⁾	Detritivore-Omnivore ⁽⁴⁵⁾	Broadcast spawning ⁽¹⁾
<i>Scaphocalanus magnus</i>	4.61 ^(7, 10)	Current ⁽³⁴⁾	Detritivore-Omnivore ^(1, 45)	Broadcast spawning ^(1, 49)
<i>Scolecithricella minor</i>	1.4 ⁽¹⁾	Current ^(36, 41)	Detritivore-Omnivore ^(36, 41)	Broadcast spawning ⁽¹⁾
Non-Copepod				
Amphipod				
<i>Themisto pacifica</i>	6.5 ^(64, 50, 25)	Active Ambush ⁽³¹⁾	Carnivore ^(25, 31)	Egg brooding ^(64, 50)
Chaetognath				
<i>Eukrohnia hamata</i>	22.5 ⁽¹⁹⁾	Active Ambush ⁽¹⁸⁾	Carnivore ⁽¹⁸⁾	Egg brooding ⁽¹⁶⁾
<i>Parasagitta elegans</i>	26.5 ⁽¹⁹⁾	Active Ambush ⁽¹²⁾	Carnivore ⁽¹⁹⁾	Broadcast spawning ^(1, 51)
Euphausiid				
<i>Euphausia pacifica</i>	20.5 ^(24, 28)	Current ⁽³⁾	Omnivore ⁽³⁾	Broadcast spawning ⁽²⁹⁾
<i>Thysanoessa inspinata</i>	17.0 ⁽³⁰⁾	Current ⁽³⁵⁾	Omnivore ⁽³⁾	Broadcast spawning ⁽²⁹⁾
<i>Thysanoessa spinifera</i>	21.0 ^(1, 31)	Current ⁽³⁵⁾	Omnivore ⁽³⁾	Broadcast spawning ⁽²⁹⁾
Larvacean				
<i>Fritillaria</i> spp.	1.0 ^{(58)T}	Current ⁽⁵⁸⁾	Omnivore-Herbivore ^(58, 59)	Broadcast Spawning ⁽⁵⁸⁾
<i>Oikopleura dioica</i>	1.0 ^{(53, 58, 69, 63)*T}	Current ^(53, 58, 69, 63)	Omnivore-Herbivore ^(53, 58, 69, 63)	Broadcast Spawning ^(53, 58, 69, 63)
<i>Oikopleura labradoriensis</i>	2.4 ^{(58, 60)*T}	Current ^(58, 60)	Omnivore-Herbivore ^(58, 60)	Broadcast Spawning ^(58, 60)
Ostracod				

<i>Conchoecia</i> spp.	2.1 ⁽²⁾	Current ^(1, 48)	Detritivore ^(1, 48)	Broadcast spawning ⁽¹⁾
<i>Discoconchoecia elegans</i>	1.92 ⁽¹⁶⁾	Current ⁽¹⁶⁾	Detritivore ⁽¹⁶⁾	Broadcast spawning ⁽¹⁶⁾
Hydrozoa				
<i>Aegina citrea</i>	20 ^{(60)D}	Passive Ambush ^(37, 60)	Carnivore ^(37, 60)	Broadcast Spawning ^(37, 60)
<i>Aequorea</i> spp.	120 ^{(52, 53, 60)*D}	Cruise ^(52, 53, 60)	Carnivore ^(52, 53, 60)	Broadcast Spawning ^(52, 53, 60)
<i>Aglantha digitale</i>	11.0 ^(8, 9)	Active Ambush ⁽⁸⁾	Carnivore ^(8, 9)	Broadcast spawning ⁽⁸⁾
<i>Clytia gregaria</i>	20 ^{(52)*D}	Cruise ⁽⁵²⁾	Carnivore ⁽⁵²⁾	Broadcast Spawning ⁽⁵²⁾
<i>Dimophyes arctica</i>	10 ^{(1,2)*}	Passive Ambush ⁽²⁾	Carnivore ⁽²⁾	Broadcast spawning ⁽²⁾
<i>Eutonia indicans</i>	35 ^{(2, 52, 55)*D}	Cruise ^(52, 55)	Carnivore ^(52, 55)	Broadcast Spawning ^(52, 55)
<i>Mitrocoma cellularia</i>	90 ^{(52, 55, 60)*D}	Cruise ^(52, 55, 60)	Carnivore ^(52, 55, 60)	Broadcast Spawning ^(52, 55, 60)
<i>Muggiaea atlantica</i>	7 ^{(2)*}	Passive Ambush ^(1, 60, 61)	Carnivore ^(1, 60, 61)	Broadcast Spawning ^(1, 60, 61)
<i>Nanomia bijuga</i>	6 ^{(59)*N}	Passive Ambush ^(61, 62)	Carnivore ^(61, 62)	Broadcast Spawning ^(61, 62)
<i>Sarsia</i> spp.	20 ^{(52, 55, 60)*}	Passive Ambush ^(52, 55, 60)	Carnivore ^(52, 55, 60)	Broadcast Spawning ^(52, 55, 60)
Ctenophora				
<i>Beroe</i> spp.	40 ^{(53, 60)*}	Active Ambush ^(53, 60)	Carnivore ^(53, 60)	Broadcast Spawning ^(53, 60)
<i>Pleurobrachia bachei</i>	8 ^{(52, 53)*}	Passive Ambush ^(52, 53)	Omnivore-Carnivore ^(52, 53)	Broadcast Spawning ^(52, 53)
Thaliacea				
<i>Doliolletta gegenbauri</i>	9 ^{(47, 54)*}	Current ^(47, 54)	Omnivore-Herbivore ^(47, 54)	Alternation of Generations ^(47, 54)

Table 2.2. Functional traits of the 55 selected zooplankton species from the southern shelf area off the west coast of Vancouver Island. References in superscript are listed in Appendix A. Length represents the average adult female/adult body length; * indicates that adult body size/diameter is listed as the max reported in the literature or for WCVI; D denotes size of body diameter, T denotes trunk length (body length, no tail), and N represents nectosome length.

2.4 Results

2.4.1 Environmental Variables

Over the 35-year time series, strong (>1) springtime positive NPGO anomalies occurred in eight years, whereas strong negative anomalies occurred in six years (Figure 2.2a). NPGO anomalies were mostly negative until 1998, where after a shift to nearly all positive anomalies occurred in subsequent years. April-June PDO anomalies were strong for seven years of both positive and negative directions each within the time series (Figure 2.2b). ONI showed strong positive anomalies in six years and also six years of strong negative anomalies (Figure 2.2c). The Southern Oscillation Index (SOI) had both strong positive and negative anomalies for seven years (Figure 2.2d). Spring SST values from Amphitrite Point had strong positive and negative anomalies each present in seven years of the time series (Figure 2.2e). Patterns of SST anomalies mirror those of PDO, with yearly anomalies (either positive or negative) usually matching up, especially after 2005. Spring anomalies of Amphitrite Point sea surface salinity were strongly positive in seven years and negative in six years. Surface salinity anomalies were mostly negative until 1994 (Figure 2.2f). Spring upwelling anomalies had strong positive and negative anomalies each occurring in six of the 35 years (Figure 2.2g). Upwelling anomalies were mostly positive until 1995, after which they increased in variability. Additionally, salinity anomalies follow a similar pattern to upwelling especially after 2005, with both being highly variable. From 1990-1997 and 2014-2016, NPGO anomalies were negative while PDO and SST was usually positive. Similarly, when NPGO was positive in 1998-2004 and 2007-2013, PDO and SST were usually negative.

Figure 2.2. Standardized annual spring (April-June) anomalies of a) North Pacific Gyre Oscillation (NPGO), b) Pacific Decadal Oscillation (PDO), c) Ocean Niño Index (ONI), d) Southern Oscillation Index (SOI), e) Amphitrite Point sea surface temperature (Amp SST), f) Amphitrite Point sea surface salinity (Amp Sal), and g) the Bakun upwelling Index at 48°N 145°W (Upwelling) from 1980-2016. Red line denotes strong positive anomaly threshold and blue strong negative anomaly threshold.

2.4.2 Functional Group Biomass Anomalies, and Percent Biomass and Abundance

Contributions

Species and traits used in the functional group analysis are listed in Table 2.2. Eight groups were identified via cluster analysis. Several clusters (two, three, four, or eight) could be identified depending on which cutting level was chosen (Figure 2.3), with the first level characterized by

feeding type (current and ambush/cruise). The second level separated active and passive ambush feeders from cruise feeders. The third level split functional groups by trophic group, while the fourth level (eight clusters) divided between size classes. Silhouette plots were used as a clustering index and ultimately, eight functional groups were selected as they split the 55 species into ecologically-sensible groups that used all four functional traits (Figure 2.3).

The first group (Detritivores) group contained five species: *Scolecetricella minor*, *Scaphocalanus brevicornis*, *Scaphocalanus magnus*, *Conchoecia* spp., and *Disconchoecia elegans*. (Figure 2.3). Group biomass anomalies displayed no significant linear trend over the time series ($\rho = 0.20$, $p\text{-value} = 0.24$) and had no strong anomalous years (Figure 2.4a). Additionally, percent biomass contribution for Detritivores did not show significant change over time (Figure 2.5a, $\rho = 0.28$, $p\text{-value} = 0.09$) but declined in relative abundance (Figure 2.5b, $\rho = -0.33$, $p\text{-value} = 0.05$).

The Doliolids group contains a single species, *Dolioletta gegenbauri* (Figure 2.3), for which strong positive biomass anomalies only occurred in 2015 and 2016 (Figure 2.4b), significantly increasing over time ($\rho = 0.54$, $p\text{-value} = 0.0007$). Similarly, percent biomass and abundance contribution also increased (Figure 2.5a, $\rho = 0.56$, $p\text{-value} = 0.0004$; Figure 2.5b, $\rho = 0.42$, $p\text{-value} = 0.01$).

Omnivore-Herbivores were the largest group, containing: *Metridia pacifica*, *Microcalanus pusillus*, *Microcalanus pygmaeus*, *Thysanoessa spinifera*, *Euphausia pacifica*, *Thysanoessa inspinata*, *Ctenocalanus vanus*, *Calocalanus* spp., *Paracalanus* spp., *Oikopleura labradorensis*, *Fritillaria*, *Oikopleura dioca*, *Calanus marshallae*, *Calanus pacificus*, *Neocalanus plumchrus*, *Neocalanus cristatus*, *Neocalanus flemingeri*, *Eucalanus bungii*, and *Eucalanus*

californicus, *Clausocalanus* spp., *Pseudocalanus newmani*, *Pseudocalanus moultoni*, *Pseudocalanus mimus*, and *Pseudocalanus minutus* (Figure 2.3). This group had no strong anomalous years throughout the time series and biomass anomalies did not change over time (Figure 2.4c, $\rho = -0.08$, p-value = 0.63). Omnivore-Herbivores biomass contribution did not change throughout the time series (Figure 2.5a, $\rho = 0.13$, p-value = 0.94), although their percent abundance contribution increased (Figure 2.5b, $\rho = 0.61$, p-value < 0.0001).

The fourth group Active Ambush Omnivores contained: *Oithona similis*, *Acartia longiremis*, *Acartia tonsa*, *Mesocalanus tenuicornis*, *Gaetanus simplex*, *Gaetanus tenuicornis*, *Aetideus pacificus*, *Centropages abdominalis*, and *Aetideus divergens* (Figure 2.3). Active Ambush Omnivore biomass anomalies did not change over the time series (Figure 2.4d, $\rho = -0.25$, p-value = 0.15) and had no strong anomaly years. This group showed no change over time in terms of biomass contribution (Figure 2.5a, $\rho = 0.11$, p-value = 0.53), but decreased in percent abundance over time (Figure 2.5b, $\rho = -0.68$, p-value = <0.001).

The fifth group (Egg-Brooding Carnivores) included: *Beroe* spp., *Parasagitta elegans*, *Eukrohnia hamata*, *Paraeuchaeta elongata*, and *Themisto pacifica* (Figure 2.3). The Egg-brooding carnivores also showed no strong anomaly years throughout the time series and did not significantly change over time (Figure 2.4e, $\rho = -0.16$, p-value = 0.36). While percent biomass contribution remained unchanged (Figure 2.5b, $\rho = 0.19$, p-value = 0.25), percent abundance significantly decreased throughout the time series (Figure 2.5b, $\rho = -0.37$, p-value = 0.03).

The Broadcast Carnivores group contained seven species: *Aegina citrea*, *Sarsia* spp., *Pleurobrachia bachei*, *Aglantha digitale*, *Nanomia bijuga*, *Dimophyes arctica*, and *Muggiaea*

atlantica (Figure 2.3). Biomass anomalies for this group were strongly (>1) positive in eight years and negative in three years but did not significantly change over time (Figure 2.4f, $\rho = 0.17$, $p\text{-value} = 0.33$). There was no significant change over time for either percent contribution of biomass and abundance for Broadcast Carnivores (Figure 2.5a; $\rho = -0.03$, $p\text{-value} = 0.86$; Figure 2.5b, $\rho = -0.27$, $p\text{-value} = 0.11$).

The seventh group Cruise Carnivores-A included: *Clytia gregaria*, and *Eutonia indicans* (Figure 2.3). Functional group biomass anomalies for this group showed no significant change over time ($\rho = 0.13$, $p\text{-value} = 0.46$). This group had 10 years of strong positive anomalies and seven years of strong negative anomalies (Figure 2.4g). For Cruise Carnivores-A, both percent biomass and abundance did not change over time (Figure 2.5a; $\rho = -0.08$, $p\text{-value} = 0.62$; Figure 2.5b, $\rho = -0.12$, $p\text{-value} = 0.47$).

The final group (Cruise Carnivores-B) included: *Aequorea* spp., and *Mitrocoma cellularia*, (Figure 2.3). Biomass anomalies for the large cruise feeding carnivores increased throughout the time series ($\rho = 0.76$, $p\text{-value} < 0.0001$), including seven years of strong positive anomalies from 2003-2016 (Figure 2.4h). Additionally, percent biomass and abundance for Cruise Carnivores-B both increased over time (Figure 2.5a, $\rho = 0.69$, $p\text{-value} < 0.0001$; Figure 2.5b, $\rho = 0.78$, $p\text{-value} < 0.0001$).

Figure 2.3. Functional dendrogram obtained from a multiple correspondence analysis (MCA) with a Euclidean distance matrix and Ward's aggregation link. Functional groups one through

eight are shown (top to bottom). Vertical line denotes where the tree was cut to form eight clusters.

Figure 2.4. Annual spring (April-June) functional group biomass anomalies from 1980-2016: a) Detritivores, b) Doliolids, c) Omnivore-Herbivores, d) Active Ambush Omnivores, e) Egg-Brooding Carnivores, f) Broadcast Carnivores, g) Cruise Carnivores-A, and h) Cruise Carnivores-B. Red line denotes strong positive anomaly threshold and blue strong negative anomaly threshold.

Figure 2.5. Percent a) Biomass and b) Abundance contribution of individual functional groups from 1980-2016.

2.4.3 Generalized Additive Model Results

GAM models revealed that seven out of eight functional groups (the exception being the Detritivores) showed significant relationships to environmental variables (Table 2.3 and Appendix B). Amphitrite Point SST and the Southern Oscillation Index were equally important variables, both being significant in three of seven groups. PDO and ONI were significant explanatory variables for two groups, whereas Amphitrite Point salinity and NPGO were each significant for just one group (Table 2.3).

Functional Groups	Adj. r^2	% Deviance	Amphitrite Point Sea Surface Temperature (SST)	Amphitrite Point Surface Salinity (Amp Sal)	North Pacific Gyre Oscillation (NPGO)	Pacific Decadal Oscillation (PDO)	Upwelling	Ocean Niño Index (ONI)	Southern Oscillation Index (SOI)
Detritivores	0.02	6.1		0.12					0.46
Doliolids	0.30	34.5	0.03	0.002					
Omnivore-Herbivores	0.29	47.3	0.02	0.29	0.34		0.33	0.15	
Active Ambush Omnivores	0.21	30.3	0.001		0.14			0.005	0.06
Egg-Brooding Carnivores	0.08	17.8		0.67	0.43	0.12		0.04	0.04
Broadcast Carnivores	0.28	37.8		0.90		0.01	0.28	0.30	0.009
Cruise Carnivores-A	0.36	42.7		0.54		0.0001			0.002
Cruise Carnivores-B	0.17	34.4			0.01	0.06	0.06	0.07	0.12

Table 2.3. Generalized additive model results between functional group biomass anomalies and environmental variables from 1980-2016 with adjusted r^2 value (Adj. r^2), percent deviance explained (% deviance), and the significance of the environmental variables. Significant values are in bold. Variables with blank p-values were not included in the final GAM model for that functional group.

2.5 Discussion

Eight functional groups of mesozooplankton were identified in this study. Amphitrite Point SST and SOI were the most important environmental variables explaining variation in functional group biomass anomalies. Doliolids and Cruise Carnivores-B both increased their percent contributions to biomass and abundance over the time series. In contrast, Detritivores, Active Ambush Omnivores, and Egg-Brooding Carnivores decreased in abundance over time (but not biomass), whereas, Omnivore-Herbivores increased in abundance (but not biomass).

2.5.1 Functional Group Comparison

A functional group approach may be viewed as an intermediate between taxonomic-based assessments and direct measurements of function such as ingestion and secondary production rates (Pomerleau *et al.*, 2015). As such, trait-based approaches can link species with similar ecological roles together with ecosystem functions (*i.e.* productivity).

Copepod-only groups have previously been classified in the WCVI region based primarily on geographic range and bathymetry (Mackas *et al.*, 2004). These included a boreal-shelf group, a subarctic oceanic group, and a southern group; wherein the boreal shelf and subarctic species are endemic to the WCVI and the southern group are usually found within the California Current and offshore. Here, these groups of species belong to two functional groups: Omnivore-Herbivores, and Active Ambush Omnivores, mixing both 'northern' and 'southern' species together. This may explain why there are no strongly positive (>1) or negative (<1) biomass anomalies for these groupings. Even if conditions favor a 'more northern' or 'more southern' assemblage (Mackas and Galbraith, 2002a,b; Mackas *et al.*, 2004), the biomass

anomalies of the group remain close to the climatological average due to these species replacing each other within their group. Thus, species that were previously deemed separate by geography actually fill similar roles within a functional group when conditions change to favor either group of species on the WCVI. These groups may therefore have some functional redundancy that might help mitigate effects of environmental change on a functional level. This is particularly important as both groups (Omnivore-Herbivores and Active Ambush Omnivores) contain some of the most numerically abundant and ecologically important zooplankton species that contribute substantially to the overall biomass of the community (Mackas, 1992; Willette *et al.*, 2001; Mackas *et al.*, 2004; Napp *et al.*, 2005).

Pomerleau *et al.* (2015) classified functional groups in the NE Pacific using a similar set of traits. Here, we expanded the species list to include non-crustaceans and excluded vertical distribution, diel vertical migration, and habitat as traits, as these do not influence the fitness of a species nor describe its function (Litchman *et al.* 2013). Despite these differences the membership of the crustacean groups presented here are comparable to those reported by Pomerleau *et al.* (2015). For example, group membership of the Detritivores group was identical in both studies. Our Active Ambush Omnivores merged two groups from Pomerleau *et al.* (2015), with *Gaetanus* spp. grouping with *Acartia* spp., *Aetideus* spp., *O. similus* and *M. tenuicornis*. The formation of two separate groups, the *Gaetanus* group and *Acartia* group, within Pomerleau *et al.* (2015) may be attributed the inclusion of vertical distribution as a trait, since *Gaetanus* spp. are considered to be mesopelagic and *Acartia* epipelagic. The functional groups established in the present study cluster *P. elegans*, *P. elongata*, *E. hamata* and *T. pacifica* together, but group *A. digitale* and *D. artica* with *P. bachei* and *A. citrea*. This

distinction in grouping is due to their broadcast spawning reproduction mode and the exclusion of vertical distribution and habitat in the trait matrix. Groups five and six from Pomerleau *et al.*, (2015), combined here together to form the Omnivore-Herbivores.

Benedetti *et al.*, (2018) investigated whether Mediterranean copepod functional groups could be characterized by specific environmental niches. The functional groups established here match up well with previously described niche patterns. Carnivorous species such as those within the Broadcast Carnivores, Cruise Carnivores-A and B are associated with warmer, open ocean, and generally less productive areas off WCVI and tend to flourish in years when these types of conditions occur on the southern shelf. In contrast, the Omnivore-Herbivores and the Active Ambush Omnivores groups are usually affiliated with areas of stronger seasonal variation, colder temperatures, and higher chlorophyll *a* concentration (like the current feeding herbivores group in Benedetti *et al.*, 2018). Species within these groups show strong seasonality in abundance/biomass and can reflect changes in the environment by the shifting of group composition from a more 'northern' or 'southern' community assemblage (Mackas and Galbraith, 2002a,b; Mackas *et al.*, 2004). The Doliolids group have capitalized during years that promote their growth and reproduction, rapidly increasing in biomass and abundance in the latter years of the time series that are more associated with warmer, open ocean like conditions. Additionally, the Detritivores may occur over a wider range of conditions and more persistently as they show consistent biomass and abundance throughout the time series. Detritivores are able to maintain their presence off the WCVI regardless of environmental conditions. Conditions favoring Omnivore-Herbivores and Active-Ambush Omnivores should lead to productive ecosystems with enhanced fluxes of energy and nutrients, whereas less

productive years dominated by carnivorous species would have reduced energy fluxes (Benedetti *et al.*, 2018).

2.5.2 Functional Group Ecology

Characteristics of the shelf zooplankton community include a high phytoplankton-based diet with occasional omnivory, whereas the oceanic community characteristics include more carnivory/omnivory (Mackas and Coyle 2005). WCVI shelf biomass is dominated by species within the Omnivore-Herbivores group (*C. marshallae* and *Pseudocalanus* spp.) in May-June before shifting to an Active Ambush Omnivores group species (*A. longiremis*) in July- August. The area along the shelf-break is dominated by species from the Omnivore-Herbivores group (*Neocalanus* spp.) in April-June, which decrease thereafter throughout the summer (Mackas, 1992). Biomass peaks of euphausiid species from the Omnivore-Herbivores group occur May-June and August-September along the shelf (Mackas, 1992). Gelatinous zooplankton biomass which would include members from the Doliolids, Broadcast Carnivores, Cruise Carnivores-A and Cruise Carnivores-B usually peak from May-July, but can dominate during all time periods (Mackas, 1992). In general, for the inner shelf, herbivorous zooplankton biomass increases from February – June, then decreases from July-November. Carnivorous species included in the Egg-Brooding Carnivores group (e.g. such as chaetognaths) decline from April-June, with hydromedusae (Broadcast Carnivores) following later (July – September). Seasonal signals for these areas include summer warming above 50m and strong intrusions of cold, high salinity upwelled water (Mackas, 1992). As such, shelf and shelf-break areas are usually dominated by Omnivore-Herbivores and Active Ambush Omnivores, that thrive in conditions with cooler

temperatures, higher chlorophyll *a* and nutrient concentrations with high phytoplankton biomass. When Omnivore-Herbivores and Active Ambush Omnivores dominate the biomass, we expect food-web dynamics to be dominated by bottom-up processes, and especially when the ‘northern’ species dominate within group biomass. These groups include species which are considered the most numerically abundant and the top contributors to secondary production (Napp *et al.*, 2005).

From summer to fall, groups such as Egg-Brooding Carnivores, Broadcast Carnivores, Cruise Carnivores-A and Cruise Carnivores-B, that flourish in warmer, low chlorophyll, ocean open conditions can dominate the zooplankton biomass. Here we expect food-web dynamics to be driven by top-down processes, as these carnivorous species prey directly on smaller copepods or gelatinous taxa. Additionally, smaller ‘southern’ species within the Omnivore-Herbivores and Active Ambush Omnivores groups may also dominate during warmer conditions. These species contain less lipid than their northern counterparts and are usually associated with the California Current (Mackas *et al.*, 2004). With conditions favoring smaller copepod and larger gelatinous species, a decline in larger calanoid species is possible, which are at a disadvantage under warmer conditions (Barton *et al.*, 2013). Size structure plays an important role in moderating ecosystem functions, where secondary productivity, nutrient recycling, and carbon transfer are weakened when small size classes dominate and boosted when larger crustacean species whose prey include large phytoplankton are dominant (Hébert *et al.*, 2016, 2017). Changes in community size structure may be detectable using the functional group approach as Omnivore-Herbivores had no change in biomass over time but increased in abundance. Increased numbers of smaller southern members of the Omnivore-Herbivores may

drive the change in abundance while maintaining the biomass throughout the time series.

Active Ambush Omnivores also had no change in biomass but decreased in abundance, possibly suggesting that there are fewer larger individuals within this group (i.e. Aetideidae copepods) or as a consequence of increased biomass and abundance of the Cruise Carnivores-B. Species from the Cruise Carnivores-B and Broadcast Carnivores are known to generally consume microzooplankton and are known to prey upon all life stages of *Calanus* spp., as well as adult *Acartia* and *Pseudocalanus* spp (Greene *et al.*, 1986; Purcell and Grover, 1990). Additionally, the Doliolids group also increased in both percent contribution of biomass and abundance, potentially to the detriment of the Omnivore-Herbivores and Active Ambush Omnivores, as they have the ability to efficiently filter very small phytoplankton and other particles (e.g. microzooplankton) including copepod eggs and juveniles from the water column (Deibel, 1982). Strong anomalies of this group, especially in last several years of the time series, may potentially increase direct competition with copepods for food, while simultaneously reducing the abundance of their egg and naupliar stages (Deibel, 1985; Haskell *et al.*, 1999).

2.5.3 Functional Group Responses to the Environment

In the North Atlantic and Southern Ocean, sea surface temperature was found to be the most important variable in defining zooplankton trait-based niches (McGinty *et al.*, 2018). Here, sea surface temperature and PDO were main drivers in variation of biomass anomalies for several groups: Doliolids, Omnivore-Herbivores, Active Ambush Omnivores, Broadcast Carnivores, and Cruise Carnivores-A. Biomass anomaly variation was also significantly explained by the two El Niño indices (ONI and SOI) in four groups: Active Ambush Omnivores, Egg-brooding Carnivores,

Broadcast Carnivores, and Cruise Carnivores-A. For the WCVI, previous studies showed that Strong El Niño events in 1982-1983, 1997-1998, and 2015-2016; as well as anomalous warm water events in 2005 and 2013-2015, have influenced changes in zooplankton community biomass (Mackas and Tsuda, 1999; Mackas *et al.*, 2001, 2004, 2007; Mackas and Galbraith, 2002a; Harrison *et al.*, 2004; Mackas and Coyle, 2005; Patterson *et al.*, 2013; Bond *et al.*, 2015; Tseng *et al.*, 2017).

In 2013, unusually low rates of heat loss and weak winter mixing led to a marine heatwave event (known popularly as ‘the blob’) which persisted in offshore waters west of the WCVI and moved onto the WCVI shelf in 2014 (Bond *et al.*, 2015). Coupled with one of the strongest El Niño events in recent history in 2015-2016 (Tseng *et al.*, 2017), this time period also included blooms of the toxigenic diatom *Pseudo-nitzschia* (McCabe *et al.*, 2016), as well as lower zooplankton abundance and biomass (Batten, 2016). Reduced diatom abundance and diversity along with increased dinoflagellate abundance was also observed during this time (Du and Peterson, 2018). Notable changes in zooplankton community assemblages also occurred off the WCVI in 2015, where the biomass/abundance of ‘northern’ species declined, ‘southern’ species increased and increases in gelatinous species were observed (Galbraith *et al.*, 2016). These gelatinous species have life history strategies that allow them rapidly respond to favourable environmental changes, especially in areas like WCVI where suitable prey are available (Gibson and Paffenhöfer, 2000; Parsons and Lalli, 2002; Lynam *et al.*, 2005; Purcell, 2005; Purcell *et al.*, 2007; Richardson *et al.*, 2009). However, they may not be suitable prey items when compared to the lipid-rich crustacean species that generally dominate the area (e.g. *Thysanoessa* spp., *Eucalanus bungii*, and *Neocalanus* spp.), which are important prey items

for fish, seabirds, and marine mammals in the region (Miller *et al.*, 1984; Hunt *et al.*, 2005; Tsuda *et al.*, 2004; Jahncke *et al.*, 2005). The biomass anomalies of the Doliolids, Broadcast Carnivores, Cruise Carnivores-A, and Cruise Carnivores-B were strongly positive (>1) in 2015 and 2016. In contrast, crustacean-dominated zooplankton functional groups (Omnivore-Herbivores and Active Ambush Omnivores), which contain some of the most numerically abundant zooplankton, displayed only weak negative or positive biomass anomalies in both 2015 and 2016. Similar responses were observed during the 1997-1998 El Niño event, where the WCVI had lower abundance of ‘northern’ shelf-based species and increased abundance of ‘southern’ oceanic species (Mackas and Galbraith, 2002a). However, we observed no strong functional group biomass anomalies for any group during the 1997-1998 El Niño event.

Changes in functional group abundances not observed in biomass anomalies could be due to the anomaly calculation itself, as our calculation is restricted to spring only biomass estimates in which any interannual shifts in biomass peaks would be missed, where changes in seasonal peak biomass is known to be influenced by climate and temperature anomalies (Mackas and Beaugrand 2010). This is similar to the anomaly calculation in Mackas 1992, and Batchelder *et al.*, 2012. Additionally, although fluctuations in species or size composition of the zooplankton community may not alter total biomass significantly, such changes may still be important to higher trophic levels seeking appropriate prey items (Batchelder *et al.*, 2012).

2.6 Conclusion

Local SST and SOI were the main drivers of functional group biomass anomaly variability for the southern shelf region off the WCVI. Biomass anomalies for Doliolids and Cruise Carnivores-B

increased over the time series. Although total zooplankton biomass in the region remained relatively constant from 1980-2016, significant changes in abundance were observed for several groups. In addition, strong anomalies (>1 or >-1) were observed for Doliolids, Broadcast Carnivores, Cruise Carnivores-A, and Cruise Carnivores-B. In contrast, Detritivores, Omnivore-Herbivores, Active Ambush Omnivores and Egg-Brooding Carnivores had biomass anomalies that were “near average” for the entirety of the time series (i.e. not crossing the >1 threshold). Overall, our mesozooplankton functional groups are similar to those reported by Pomerleau et al. (2015). They also fit well into the functional group niches explored in the Mediterranean Sea (Benedetti *et al.*, 2018), and responded similarly to previous taxonomic-based analysis (Mackas, 1992; Mackas *et al.*, 2001) of zooplankton species from the WCVI continental shelf.

Relative to the traditional taxonomic approach, a functional groups approach may help to better understand the environmental drivers affecting zooplankton community composition, while also providing a clearer view of the zooplankton community as a whole (i.e. by reducing the complexity of analyzing many individual species at once). Species and trait combinations may vary by region and the choice of trait types may therefore differ as they reflect organism and ecological functions (Litchman *et al.*, 2013). As such, an added benefit of the functional group approach is that it can be applied retrospectively, allowing for new analyses of already established zooplankton community databases. Nevertheless, the results of our analysis do not negate the usefulness of traditional taxonomic-based analyses. It must be noted that these results are limited to spring observations on the southern-shelf area off WCVI, and that different results may emerge using data from other seasons and/or areas. Therefore, we

suggest that future studies apply a combination of species/region specific and functional group-based analysis for a more comprehensive view of zooplankton community dynamics.

Chapter 3. Drivers of variation in crustacean zooplankton production rates differ across regions off the west coast of Vancouver Island and in the subarctic NE Pacific

Citation:

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3.1 Abstract

The subarctic NE Pacific is comprised of several oceanographic regimes, where regional variability in sea surface temperature (SST), satellite chlorophyll *a* and crustacean zooplankton biomass influence the production rates of crustacean zooplankton. Traditional methods for estimating zooplankton production rates are labor/time intensive and restricted to select copepod species. A practical field alternative is the 'chitobiase method', yielding biomass production rates (BPR) which represent a community-level estimate of somatic production analogous to the moulting rate method. Thus, representing most somatic production, although this method does not include surface growth of pre-overwintering stages (e.g. *Neocalanus* CV). BPR was measured along the west coast of Vancouver Island and in the subarctic NE Pacific during 2005, 2009-2011, and 2015-2018. Generalized additive modeling identified SST and developing crustacean zooplankton biomass as key drivers of BPR variability. BPR varied with the proportion of developing copepod biomass relative to non-copepod crustacean zooplankton biomass. Our analysis indicates that BPR variation is associated with zooplankton community composition, where high zooplankton biomass is not necessarily predictive of high BPR. Specifically, a greater relative biomass of large-bodied, cold-water indicator species and lower biomass of non-copepod crustaceans.

3.2 Introduction

3.2.1 Regional Oceanography and Biology

Our area of study, the northeast Pacific, is comprised of multiple oceanographic regions (Figure 1), which includes a seasonal upwelling zone along the west coast of Vancouver Island (WCVI), a transitional oceanic region characterized by nutrient limitation during summer, and a high nitrate low chlorophyll (HNLC) regime furthest offshore in our area of reference (Boyd and Harrison, 1999; Varela and Harrison, 1999; Whitney *et al.*, 2005; Mackas and Coyle, 2005). The WCVI is a highly productive region that resides in a transition area, where the eastward flowing North Pacific current splits to form both the northward flowing Alaska and southward flowing California current (Freeland, 2006). The latitudinal location of this split and the extent to which local conditions resemble either system varies seasonally and annually (Mackas *et al.*, 2001). A strong sub-surface current seaward of the shelf-break, reverses direction in the spring and fall of each year driven by changes in the large-scale wind field (Freeland *et al.*, 1984). As such, the WCVI transitions between upwelling and downwelling on a seasonal basis, resulting in seasonal differences in temperature, salinity, oxygen and nutrients. During the summer months biological productivity along the southern shelf of Vancouver Island is driven by the Juan de Fuca eddy (Mackas and Sefton, 1982; Freeland, 1988). Spatiotemporal variability of phytoplankton biomass is considerable, but generally higher on-shelf than off-shelf, with inshore peaks in summer and offshore peaks in March/April and October (Mackas and Sefton, 1982; Harris *et al.*, 2009). The Oceanic region within the subarctic NE Pacific is a transition area not influenced by coastal upwelling and which experiences summer nitrate (NO_3) depletion limiting primary productivity (Whitney *et al.*, 1998; Peña and Varela, 2007). Productivity and

phytoplankton biomass are iron-limited and generally lower in the high nitrate low chlorophyll (HNLC) region along Line P where the occasional increase due to nutrient enrichment from mesoscale eddies can occur (Whitney and Robert, 2002; Whitney *et al.*, 2005) and broad-scale events such as volcanic ash deposition (Hamme *et al.*, 2010).

Variation of zooplankton biomass and community composition in the study area is characterized by a gradient from nearshore to open-ocean environments which generally aligns with the oceanographic regimes described above (Mackas and Coyle, 2005). Nearshore/shelf zooplankton communities are not highly diverse and comprised of species which are omnivorous/herbivorous, with narrow vertical migration ranges, small body size, and which have multiple cohorts present (Mackas and Coyle, 2005; Venello *et al.*, 2021). In contrast, the off-shelf to deep-water zooplankton communities in the region are more diverse, and dominated by zooplankton where vertical migration is more common, are larger in body size, and have strongly seasonal reproduction cycles (Mackas and Coyle, 2005). Copepod species in the study area have been classified into geographically separated groups: boreal-shelf, subarctic, and southern, whereby boreal-shelf and 'subarctic' groups dominate in cooler than average and typical years, whereas species from the southern group are more abundant during El Niño years and with anomalous warm water events (Mackas and Galbraith, 2002a; Mackas *et al.*, 2004; Galbraith and Young, 2019).

3.2.2 Zooplankton Production Rate Methods

Production rates can be generally described as mass elaborated per unit time as a function of growth and reproduction. Rate estimates require measures of both biomass and growth rate, usually expressed as $P = B \times g$, where P is production ($\text{mg C m}^{-3} \text{ day}^{-1}$), B is biomass,

and g is growth rate (Kimmerer 1987). Biomass is one of the most commonly reported metrics used in zooplankton studies (e.g. Hays et al. 2005), yet inaccuracies in growth rate determination can result in discrepancies especially for crustacean zooplankton production estimates (Runge and Roff, 2000). For this study, we will define zooplankton production rates as crustacean zooplankton biomass production rates (BPR), which are based on the rate at which crustacean zooplankton produce chitinase activity (CBA) via moulting within the water column. As such, our crustacean zooplankton biomass production rates are a measure of somatic production rates of only moulting crustaceans. This is realized as a change in body size between moults.

Therefore, due to the difficulty in quantifying zooplankton production rates, links to ecosystem functions such as energy transfer and productivity are not well understood, especially with regard to entire crustacean zooplankton communities (Barneche *et al.*, 2021). Past measurements of zooplankton production rates have relied heavily on time consuming, labor-intensive cohort and incubation-based methods (Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991) and egg production rate methods (Runge, 1984; Poulet *et al.*, 1995). However, natural cohort methods are logistically difficult to implement in the field because the approach requires frequent sampling of populations with recognizable stage structure; conditions which are not reliably met for multiple populations in physically dynamic systems (see Kobari *et al.*, 2019 for review).

As an alternative to *in situ* and *ex situ* methods, global empirical models have also been developed. These models are often syntheses of copepod weight-specific growth rates from the laboratory and field, seeking to relate specific growth rate to one or more extrinsic (e.g.

temperature and food availability) and intrinsic (e.g. body size, reproductive mode) factors. Examples include, the Huntley and Lopez (1992) temperature-dependent growth rate model, weight-specific fecundity (Bunker and Hirst, 2004) and somatic growth rate models (Hirst and Lampitt, 1998; Hirst and Bunker, 2003), and the physiological model (Ikeda and Motoda, 1978), under various assumptions of estimating growth rates (Kobari *et al.*, 2019). For the weight-specific growth rate model (Hirst and Lampitt, 1998), adult weight-specific growth rate is assumed to be linear while juvenile growth rate is assumed to be exponential. The Hirst and Bunker (2003) weight-specific growth rate model considers mean chlorophyll *a* concentration in addition to body weight and temperature, while otherwise following the same growth rate assumptions as Hirst and Lampitt (1998). The physiological method (Ikeda and Motoda, 1978) uses respiration rate, assimilation efficiency, gross growth efficiency and a function of body weight and temperature to calculate production. Note that production rates estimated as the product of modeled growth rates and biomass implicitly assume that all individuals in a community are actively growing. However, the generic nature of these models may not always be appropriate for community-level production rate estimates because we cannot expect inter-specific individuals with differing growth requirements to all be growing at the same rate (i.e. Huntley and Lopez, 1992) or at model-defined rates or necessarily growing at all (see Hirst and Sheader, 1997). Model choice depends on desired sensitivity and available information about the zooplankton community. A more sensitive approach may be to apply species-specific and region-specific models (e.g. Liu and Hopcroft, 2006a, 2006b, 2007, 2008) for the subarctic NE Pacific). Note however, that population-level models may not capture processes operating at the community level, as demonstrated by St-Gelais *et al.*, (2017) who found community-level

production rates influenced by additional factors not captured by population-based empirical models for freshwater zooplankton communities. As a result of these various assumptions, empirical models can both over- (Huntley and Lopez, 1992; Hirst and Bunker, 2003) and underestimate (Ikeda and Motoda, 1978; Hirst and Sheader, 1997; Hirst and Lampitt, 1998) copepod production (Avila *et al.*, 2012). This has been described for copepod species in the Gulf of Alaska (Liu and Hopcroft, 2006a, 2006b, 2007, 2008); where over or under-estimation is dependent on the particular model being used for juvenile or adult copepods and the data used for model development that include growth measurements (egg production and somatic growth) for tropical and subtropical species.

More recently, biochemical methods for estimating zooplankton production rates have increased in popularity (Yebra *et al.*, 2017). Nucleic acid production, most commonly applied using RNA concentration and RNA:DNA ratios, has been used to assess zooplankton somatic growth and egg production (e.g. Gorokhova, 2003; Yebra *et al.*, 2011). Additionally, aminoacyl-tRNA synthetases (AARS) assays have been modified as an index of somatic growth in planktonic crustaceans (Yebra and Hernández-León, 2004).

3.2.3 The Chitobiase Method

Substantial progress has been made in the estimation of community-level crustacean zooplankton production rates using the chitobiase method (Oosterhuis *et al.*, 2000; Sastri and Dower, 2006, 2009; Avila *et al.*, 2011, 2012; Sastri *et al.*, 2012; Suchy *et al.*, 2016). Chitobiase is a chitinolytic enzyme used by crustaceans to catalyze the partial recycling of chitin (Roff *et al.*, 1994; Espie and Roff, 1995). Chitobiase is present during the pre-moult phase in the space

between the newly forming exoskeleton and old exoskeleton. At moult, the old exoskeleton is shed and chitobiase is released into the water column, evidenced by an increase in the enzyme concentration coincident to the animal's location (Vrba and Machacek, 1994). The "chitobiase method" assumes that (i) the zooplankton community is in a steady state and (ii) the rate of chitobiase production by molting crustaceans is balanced by its decay by bacteria (Sastri and Roff, 2000; Sastri and Dower, 2006). Additionally, the amount of chitobiase released into the water column has been shown to be proportional to body size and growth increment; a relationship common across a variety of crustacean zooplankton groups (Sastri and Dower, 2009). Therefore, the rate of production of chitobiase in the water column is considered a proxy for the biomass production rate (BPR) of the entire crustacean zooplankton community. Using a simple enzymatic assay, this method is easy to implement in the field and provides a link to ecosystem function, since BPR can be used to estimate energy transfer (and therefore food web response) to environmental change (Sastri *et al.*, 2012; Suchy *et al.*, 2016; Kwong *et al.*, 2020).

The subarctic NE Pacific has a range of oceanographic conditions from the west coast of Vancouver Island and along Line P to Ocean Station Papa (OSP) over-which to assess variation of community-level crustacean biomass production rates (BPR). We expect BPR to vary with variations in temperature, primary productivity, and zooplankton community composition; where BPR from highly productive shelf regions along the WCVI should be higher than those off-shelf and in the HNLC region. Here, we used the chitobiase method to estimate community-level crustacean BPR and explore regional drivers of variation using crustacean zooplankton biomass, satellite chlorophyll *a*, and sea surface temperature. Data were collected in 2005, 2009-2011, and 2015-2018 as part of the La Perouse and Line P oceanographic monitoring

programs that are conducted by Fisheries and Oceans Canada. Surveys take place twice a year for La Perouse (May and September) and three times per year for Line P (February, June, and August).

Figure 3.1. Map of the study area, where coloured rectangles represent the different regions used in this study. Triangles denote stations where crustacean zooplankton production rate samples were collected. All stations where CTD sampling also took place are listed in Appendix C. Contour lines occur at 250m, 500m, 1000m, 1500m, and 2000m, 3000m, and 4000m.

3.3 Methods

3.3.1 Oceanographic Region Designations

Similar to previous regional divisions (Mackas, 1992; Mackas *et al.*, 2001; Mackas and Galbraith, 2002a), we have divided the WCVI into four regions (Figure 3.1): the inner shelf area for both Southern and Northern Vancouver Island (IS_SVI and IS_NVI, respectively), and the Shelf-break/Slope region for Southern and Northern Vancouver Island (SBS_SVI and SBS_NVI, respectively). Coastal stations along Line P within the subarctic NE Pacific are located within the IS_SVI region (P1 and P2) and the SBS_SVI region (P3-P5) off the WCVI. Stations P6-P22 are grouped into the Oceanic region (Figure 3.1), and the subarctic Pacific (P23-P26) including Ocean Station Papa (P26) are located within the HNLC region (Figure 3.1).

3.3.2 Chitobiase Method for Estimating Crustacean Zooplankton Biomass Production Rates

Crustacean zooplankton biomass production rates (BPR) were measured in 2005, 2009-2011, and 2015-2018 (Table 3.2, Figure 3.5). Water samples for chitobiase assays were collected at 6 depths for up to 9 stations during Fisheries and Oceans Canada's La Perouse cruises in May and September in 2005, 2009-2011, 2015-2018 and during Line P cruises in February, June and August in 2005, and 2016 – 2018 (Appendix D, Figure 3.1). Shelf stations usually had a maximum sample depth of 150 m. For stations located in the slope, oceanic, and HNLC regions maximum sample depth was usually 250 m (Appendix D). However, all samples collected in 2005 had a maximum collection depth of 50 m and BPR estimates from 2009-2011 were collected only in September. Chitobiase decay rates were estimated from 500 mL seawater samples screened with 54 µm mesh to remove any crustaceans that might otherwise moult

during the incubations. A 15 mL subsample was filtered (0.22 μm) directly after sampling for each depth to remove any bacteria and used to estimate native *in situ* chitobiase activity (CBA_{nat}). Small sized euphausiids (4-9 individuals) or small-medium copepods (15-30 individuals) were freshly ground in 12 mL of seawater to make a crude chitobiase homogenate that was then filtered (0.22 μm), and then used to “spike” the original 500 mL sample for each depth. This was done to ensure the assay could detect decay rates, as concentrations may be below assay detection if we were to use CBA_{nat} as a starting point (see Sastri and Dower, 2006). A second 15 mL sample was taken just after the addition of the spike (t_0), then every three hours over a 12-hr period (t_3 , t_6 , t_9 , t_{12}). The 15 mL samples were 0.22 μm filtered, covered with parafilm and stored at 4°C until assayed. Depth-specific bulk seawater samples (500 mL) were incubated at sea surface temperature during the 12-hr period using a flow-through seawater system on board the CCGS *John P. Tully*.

Enzyme assays were conducted on board and usually within 24 hours of sample collection. Chitobiase activity (CBA) was measured following Sastri and Dower 2006. Assays were run at 25 °C, started by adding 0.1 mmol of the substrate 4-methylumbelliferyl- β -D-glucosaminide (MBF-NAG; Sigma) to the 0.22 μm filtered seawater samples, and terminated after 60 minutes with the addition of a 2 M NaOH and 0.4 M EDTA solution. The reaction was buffered to pH 6.0 (optimal for copepods) using a 0.15 M citrate-phosphate buffer (McIlvaine, 1921). Chitobiase activity ($\text{nmol MBF liberated L}^{-1} \text{ h}^{-1}$) was estimated by measuring the fluorescence of the liberated MBF using a Turner BioSystems Modulus Fluorometer with a UV-absorbance (365 nm excitation and 450 nm emission). Raw fluorescence was converted to nmol

MBF using a standard curve of known 4-methylumbelliferone concentrations against fluorescence.

Chitobiase activity decay rates were calculated as the slope (k) of the natural logarithm of CBA versus time for each depth (Sastri and Dower, 2006). To account for differences between *in situ* and incubation temperatures, a Q_{10} correction (3.15) was applied to the slope (Sastri and Dower, 2006). The reciprocal of the negative slope ($1/-k$) was used as the average stage duration, or the time (T_{CBA}) taken for moulting animals to produce CBA equivalent to the *in situ* CBA (CBA_{nat}). ΔB represents the sum of all individual growth (biomass produced) and is calculated from CBA_{nat} values using a previously established relationship between CBA and the growth increment of marine copepods ($\log(g_{inc}) = 0.864 \log(CBA_i) - 1.78$; Sastri and Dower, 2006). Daily depth-integrated crustacean zooplankton production rates ($\text{mg C m}^{-2} \text{ d}^{-1}$) were calculated as the biomass production divided by the stage duration ($\Delta B / T_{CBA}$).

3.3.3 Zooplankton Biomass

Zooplankton samples were also collected during the La Perouse and Line P cruises (Figure 3.1). Vertical net hauls using black bongo nets (0.25 m^2 mouth area, 0.23 mm mesh aperture) fitted with a TSK flowmeter were towed from near-bottom to sea surface (when bottom depth was < 250 m) and from 250 m to surface at deeper locations. Samples collected from the bongo net tows were enumerated and identified to species and developmental stage (*as per* Mackas, 1992; Mackas *et al.*, 2001; Mackas and Galbraith, 2002). Briefly, raw counts were transformed to abundance per square meter using a subsampled fraction, volume of water filtered by net, and tow depth. Species and stage-specific length-dry weight relationships were used to convert

abundance to species-specific biomass. Species and stage-specific biomass was converted from mg m^{-3} to mg m^{-2} , using the tow-depth of each vertical net haul. All biomass data originated from a zooplankton database maintained by the Institute of Ocean Sciences, Department of Fisheries and Oceans Canada's (IOS, Sidney, BC, Canada). For crustacean zooplankton biomass and sea surface temperatures, regional averages were calculated using all stations (Appendix C) from a given La Perouse or Line P cruise within a single region for each cruise time period: winter (February), spring (April-June), and late_summer/fall (August and September). Copepod groups designated by geography and bathymetry have previously been established for the NE Pacific (Mackas *et al.*, 2004); these include boreal-shelf, subarctic, and southern groupings; wherein boreal-shelf and subarctic species are endemic to the WCVI and the southern species are usually found within the California Current and offshore (Table 3.1). These groups can help provide insight into community composition relative to oceanographic conditions (Mackas *et al.*, 2004 Galbraith and Young, 2019; Venello *et al.*, 2021) and were used here to link copepod community composition to changes in BPR. The developing crustacean zooplankton biomass used here includes all crustacean zooplankton that can actively develop. This excludes adult (CVI) copepods, CV *Neocalanus spp.*, and any crustacean eggs. We recognize that some boreal-shelf species *Calanus marshallae*, *Calanus pacificus*, and *Eucalanus bungii* can potentially overwinter during stages CIII-CV depending on yearly conditions but they are included as developing here.

Geographic Copepod Group	Species
<i>Boreal-Shelf</i>	<i>Acartia longiremis</i> , <i>Calanus marshallae</i> , <i>Pseudocalanus mimus</i> , <i>Pseudocalanus minutus</i> , <i>Pseudocalanus moultoni</i> , <i>Pseudocalanus newmani</i> ,
<i>Subarctic</i>	<i>Eucalanus bungii</i> , <i>Neocalanus cristatus</i> , <i>Neocalanus flemingeri</i> , <i>Neocalanus plumchrus</i> , <i>Metridia pacifica</i>
<i>Southern</i>	<i>Acartia tonsa</i> , <i>Acartia danae</i> , <i>Calocalanus spp.</i> , <i>Clausocalanus spp.</i> , <i>Eucalanus californicus</i> , <i>Eucalanus hyalinus</i> , <i>Ctenocalanus vanus</i> , <i>Mesocalanus tenuicornis</i> , <i>Metridia pseudopacifica</i> , <i>Paracalanus spp.</i>

Table 3.1. Breakdown of copepod species per group as per Mackas *et al.*, 2004.

3.3.4 Biological and Physical Water Properties

CTD profiles (to 10m off bottom) were conducted using a SeaBird (SBE 911plus) at all stations on the La Perouse and Line P cruises. Sea surface temperature (SST) used here was the 5m depth average of all station CTD profiles within a region for each season (Supplemental Table 2). This data set is maintained by the Institute of Ocean Sciences, Department of Fisheries and Oceans Canada's (IOS, Sidney, BC, Canada). Satellite data (NASA combined surface chlorophyll) were obtained from the 'Spatiotemporal Data and Timeseries Tool kit', which uses both SeaWifs and MODIS-Aqua (Ocean Biology Processing Group, 2020a, 2020b) platforms to provide a monthly cross-calibrated satellite chlorophyll *a* product (O'Brien *et al.*, 2017). This product was then averaged (if needed) to match the cruise time periods used for crustacean zooplankton biomass and SST averages.

3.3.5 Statistical Analysis

All statistical analysis was conducted within the R statistical framework (Version 1.3.1, R Core Team, 2020). Generalized additive models (GAMs) were used to test for non-linear relationships between crustacean biomass production rates (BPR) and biological and physical water properties using the 'mgcv' package (Wood, 2001, 2018), which included sea surface temperature, NASA satellite chlorophyll *a* concentration, and developing crustacean zooplankton biomass. GAMs are generalized additive models wherein the predictors are the sum of smoothing functions of individual covariates, allowing for non-linear relationships between response and predictor variables. GAMs were fit using a Gaussian identity link function with a thin plate regression spline smoother. BPR was log-transformed when necessary to meet residual assumptions of normality. Restricted maximum likelihood method (REML) was used as the smoothing parameter estimation method (Wood, 2011). Akaike information criterion (AIC) was used to select model input variables. GAM smooth plots were created using the 'visreg' package (Breheny and Burchett, 2017). GAM smooth plots show the partial effects of the selected predictor variables on BPR. Partial effect residuals are basic residuals relative to the selected predictor variable.

3.4 Results

3.4.1 Physical and Biological Predictor Variables

Regionally-averaged SST and satellite chlorophyll *a* varied between years and regions (Table 3.2). ‘Warm’ years classified as departures from the climatological mean were observed in 2005, 2010, 2015-2018, where ‘cool’ years are those with normal to below average temperatures (2009 and 2011). For all regions, the warmest average SST was recorded between 2015-2018. Satellite chlorophyll concentrations were highest in the shelf regions, followed by shelf-break/slope regions and then finally the oceanic and HNLC regions (Table 3.2). With the exception of the HNLC region which had high average chlorophyll in 2005, all other areas had maximum satellite chlorophyll concentrations in 2016 and 2017.

Regionally-averaged developing crustacean zooplankton biomass also varied by region, where peak biomass occurred in IS_NVI (Table 3.2). Developing biomass was highest within the shelf regions off the west coast of Vancouver Island (Figure 3.2). In years where BPR was the highest (2009 and 2011), a large portion of the developing biomass was comprised of the Boreal-Shelf copepod group for both shelf and shelf-break/slope areas of Vancouver Island (Figure 3.2). Years with low BPR (2015-2018) had reduced endemic copepod group biomass, increased biomass contributions from the southern copepods, *C. pacificus*, euphausiids, other crustaceans, and other copepods (Figure 3.2). Overall, developing and non-developing crustacean biomass varied between regions (Figure 3.3a), with the highest developing biomass located in both north and south shelf regions (Figure 3.3a). Developing copepod biomass was highest in 2009 and 2011 for IS_SVI, IS_NVI, and SBS_NVI regions over 2015-2018 (Figure 3.3b). In 2015-2018, nearly all regions had a developing biomass dominated by non-copepod

(other) crustaceans (Figure 3.3b). Biomass of CIII, CIV, and CV boreal-shelf copepods was highest in 2009-2011 (Figure 3.4a) when compared to both 2005 and 2015-2018. High biomass of mostly CIII and CIV subarctic copepods was observed in 2005 (Figure 3.4e). In 2015-2018, high biomass of CIV and CV stages for *C. abdominalis* (Figure 3.4b), *C. pacificus* (Figure 3.4c), *Oithona spp.* (Figure 3.4d) and southern copepods (Figure 3.4f) coincided with low BPR (Figure 3.5).

Region	Sea Surface Temperature (°C)	Satellite Chlorophyll <i>a</i> Concentration (mg m ⁻³)	Crustacean Zooplankton Biomass (mg m ⁻²)
IS_SVI	6.7 – 17.7	0.8 – 15.4	93.5 – 7170.5
SBS_SVI	6.7 – 18.2	0.32 – 1.9	201.3 – 6434.8
IS_NVI	7.6 – 16.3	0.4 – 8.8	409.8 – 38552.5
SBS_NVI	8.3 – 18.0	0.36 – 6.1	986.7– 7522.0
Oceanic	5.1 – 18.6	0.18 – 0.85	366.3 – 7254.4
HNLC	5.1 – 16.4	0.17 – 1.02	318.5 – 6746.6

Table 3.2. Range of physical and biological variables for each region observed across all years (2005, 2009-2011, and 2015-2018).

Figure 3.2. Summed developing crustacean biomass (mg m⁻²) of geographic copepod groups: boreal-shelf, subarctic, and southern (Mackas and Galbraith, 2002) as well as *C. abdominalis*, *C. pacificus*, Euphausiid spp., and all other developing copepods and crustaceans for each region and year.

Figure 3.3. Biomass (mg m⁻²) of a) developing vs non-developing crustaceans (adult copepods and *Neocalanus spp.* CV) and b) the composition of the developing biomass (mg m⁻²) as copepods or other crustaceans. Developing biomass excludes adult copepods and *Neocalanus spp.* CV.

Figure 3.4. Stage composition of developing crustacean biomass (mg m⁻²) of geographic copepod groups (Mackas and Galbraith, 2002) as well as several select species: a) boreal-shelf, b) *C. abdominalis*, 'c) *C. pacificus*, d) *Oithona* spp., e) subarctic, and f) southern for each year.

3.4.2 Crustacean Biomass Production Rates

Crustacean zooplankton biomass production rate (BPR) were measured in 2005, 2009-2011, and 2015-2018, where regional BPR ranges varied by year (Figure 3.5a) and region (Figure 3.5b). A stepwise change in BPR was observed during our sampling period (Figure 3.5), strongly mirroring changes in developing copepod and 'other' crustacean zooplankton biomass observed in the same years (Figure 3.2, Figure 3.3b). Overall, BPR was highest in the cool years of 2009 and 2011, and lowest during warmer years of 2015-2018 (Figure 3.5a). BPR was highest

in the shelf regions particularly IS_NVI, followed by shelf-break/slope, with the lowest BPR observed in the oceanic and HNLC regions (Figure 3.5b).

Figure 3.5. Barplot of mean crustacean zooplankton biomass production rates (BPR, $\text{mg C m}^{-2} \text{ d}^{-1}$) by a) year (2005, 2009-2011, and 2015-2018) across all regions, and b) for each region across all years. Standard error bars show mean $\pm$ standard deviation.

3.4.3 Generalized Additive Models

GAMs revealed statistically significant relationships between BPR and various predictor variables for each region. GAM smooth relationships showing the effect of a predictor variable on BPR while the other two variables are held at their mean values are presented for IS_SVI (Figure 3.6a-3.6c), SBS_SVI (Figure 3.7a-3.7c), IS_NVI (Figure 3.8a-3.8c), SBS_NVI (Figure 3.9a-3.9c), Oceanic (Figure 3.10a-3.10c), and HNLC (Figure 3.11a-3.11c) regions. Sea surface temperature was the most important variable in describing variability in BPR, and was statistically significant for three out of six regions (Table 3.4). Developing crustacean

zooplankton biomass followed, significantly explaining variation in BPR in two regions where satellite chlorophyll *a* concentration was significant for one region (Table 3.4). BPR increases with SST until 12-13°C then either levels off or decreases approaching 14-16°C (Figure 3.6a-3.10a), with the exception of the HNLC region where an increase in BPR with temperature is observed (Figure 3.11a). For SBS_NVI, BPR is higher with increasing chlorophyll *a* concentration approaching 9 mg m⁻³ (Figure 3.9b). BPR increases with developing biomass until ~2000 mg m⁻², then decreases until 4000 mg m⁻² after which it increases again for IS_SVI (Figure 3.6c). A significant decrease in BPR with increasing developing biomass occurred for the IS_NVI region, mostly driven by high biomass from 2015 and 2016, where large biomass contributions of non-copepod crustaceans was observed (Figure 3.7c).

Location	Adj. r ²	% Deviance	Sea Surface Temperature (SST, °C)	Satellite Surface Chlorophyll <i>a</i> (mg m ⁻³)	Crustacean Zooplankton Biomass (mg m ⁻²)
IS_SVI	0.71	78.9	0.07	0.06	0.02
SBS_SVI	0.37	45.3	0.001	0.27	0.08
IS_NVI	0.22	33.8	0.16	0.11	0.01
SBS_NVI	0.39	52.4	0.007	0.01	0.29
Oceanic	0.07	16.1	0.07	0.34	0.71
HNLC	0.65	78.4	0.04	0.95	0.07

Table 3.3. Final GAM model results of biomass production rate responses to predictor variables for each region with adjusted r² value (Adj. r²), percent deviance explained (% deviance), and the significance of the environmental variables. Significant values are in bold.

Figure 3.6. IS_SVI GAM smooths for a) sea surface temperature, b) satellite surface chlorophyll *a*, and c) developing crustacean zooplankton biomass. Individual plots show relationship between partial effect residuals and predictor variable when the remaining variables are held at their mean. Gray shaded area represents the 95% confidence interval and are wider where there are fewer data points. Points are colored by sampling year.

Figure 3.7. SBS_SVI GAM smooths for a) sea surface temperature, b) satellite surface chlorophyll a , and c) developing crustacean zooplankton biomass. Individual plots show relationship between partial effect residuals and predictor variable when the remaining variables are held at their mean. Gray shaded area represents the 95% confidence interval and are wider where there are fewer data points. Points are colored by sampling year.

Figure 3.8. IS_NVI GAM smooths for a) sea surface temperature, b) satellite surface chlorophyll a , and c) developing crustacean zooplankton biomass. Individual plots show relationship between partial effect residuals and predictor variable when the remaining variables are held at their mean. Gray shaded area represents the 95% confidence interval and are wider where there are fewer data points. Points are colored by sampling year.

Figure 3.9. SBS_NVI GAM smooths for a) sea surface temperature, b) satellite surface chlorophyll a , and c) developing crustacean zooplankton biomass. Individual plots show relationship between partial effect residuals and predictor variable when the remaining variables are held at their mean. Gray shaded area represents the 95% confidence interval and are wider where there are fewer data points. Points are colored by sampling year.

Figure 3.10. Oceanic GAM smooths for a) sea surface temperature, b) satellite surface chlorophyll a , and c) developing crustacean zooplankton biomass. Individual plots show relationship between partial effect residuals and predictor variable when the remaining variables are held at their mean. Gray shaded area represents the 95% confidence interval and are wider where there are fewer data points. Points are colored by sampling year.

Figure 3.11. HNLC GAM smooths for a) sea surface temperature, b) satellite surface chlorophyll a , and c) developing crustacean zooplankton biomass. Individual plots show relationship between partial effect residuals and predictor variable when the remaining variables are held at their mean. Gray shaded area represents the 95% confidence interval and are wider where there are fewer data points. Points are colored by sampling year.

3.5 Discussion

Sea surface temperature, developing crustacean zooplankton biomass, and satellite chlorophyll a were identified as significant predictors of variability in BPR. Across regions, mean BPR was highest in 2009 and 2011, followed by 2005, and was lowest in 2015-2018. Across years, mean BPR peaked in the IS_NVI region, followed by IS_SVI, then SBS_SVI, SBS_NVI, and was lowest in

the Oceanic and HNLC regions. Developing endemic copepod biomass was also highest in 2009-2011, whereas 2015-2018 had higher biomass contributions of non-copepod developing crustaceans. Overall, biomass of copepod groups was also lower and had more contribution from a variety of crustacean groups in 2015-2018 when compared to earlier years, with larger contributions from *C. pacificus*, southern copepod species, other crustaceans and other copepods in later years.

3.5.1 Ecological Responses to Increased Temperatures

Ecological responses to variations in temperature have been known to manifest as 1) biogeographical shifts, 2) changes in phenology, and 3) size shifts/reductions in body size (Gardner *et al.*, 2011; Garzke *et al.*, 2014). In the subarctic NE Pacific, abundance and northward range extensions of warm-water species were significantly positively correlated with mean annual temperature, where warm ocean conditions lead to range expansions of southern copepod species (Batten and Walne, 2011). These shifts are also apparent within this study, where cool years with high BPR, have higher overall copepod biomass dominated by boreal-shelf and subarctic copepod species. Biogeographical range shifts in the study area are also accompanied by a reduction in body size as well. Increased warming can lead to reductions in body size in addition to shifts in the biogeography of smaller, warm-water marine zooplankton (Garzke *et al.*, 2014). As such, smaller-sized copepods may grow faster under warmer conditions (Ikeda, 1985; Huntley and Lopez, 1992); however, growth rates associated with higher temperatures result in smaller overall adult body size (Kindlmann, Dixon, and Dostalkova, 2001; Lee *et al.*, 2003; Garzke *et al.*, 2014) and as such will have smaller growth increments between moults. Increases in the biomass of southern *spp.* as well as *C. pacificus*

and *Oithona* spp have been observed within our study area from 2015-2018. These species are usually smaller than their endemic counterparts (i.e. subarctic and boreal-shelf species), and since the amount of chitobiase released into the water column is proportional to an individuals' body size (Sastri and Dower, 2006, 2009), these species would release less chitobiase than the bigger subarctic and boreal-shelf copepod species at the time of moult. Thus, reducing the crustacean zooplankton biomass production rates (BPR). Decreased biomass of both subarctic and boreal-shelf species were also observed during these years (2015-2018), which would further reduce the amount of chitobiase released into the water column during moulting. The combination of decreased body-size leading to lower chitobiase released and reductions to large-bodied copepods present a likely cause for the decreased BPR rates in 2015-2018. Furthermore, the years (2009 and 2011) in which BPR was highest, had high biomass contribution of boreal-shelf species, while simultaneously having had the lowest contribution of southern species to biomass overall. As such, those 'cool' years have higher biomass of larger-bodied copepod species which would release more chitobiase in a single moult than warmer years which have decreased larger-bodied species and increased biomass/abundance of smaller-bodied species.

Climatic warming has also been linked to an earlier start to spring and a prolonged summer (Menzel and Fabian, 1999; Thompson and Clark, 2008), leading to shifts zooplankton phenologies where timing of reproduction has been occurring earlier (Hays *et al.*, 2005; Batten and Mackas, 2009; Mackas *et al.*, 2012). *Acartia clausi* populations from northern and southern portions of Europe, had nauplii which grew faster than copepodites with increasing temperature, where development time decreased from ~30-36 days at 10°C to 20-23 days at

15°C and finally to 16-17 days at 18°C (Leandro *et al.*, 2006). Mesocosm studies of Baltic Sea zooplankton, showed copepod nauplii appeared on average 9.2 days faster for every degree Celsius increase in temperature (Sommer *et al.*, 2007). Therefore, it is plausible an earlier start to spring, rapid nauplii development, and longer stage durations of CIV-CV copepodites due to persistent warming may also contribute to lower BPR estimates. This is likely due to the timing of the La Perouse and Line P research cruises, where zooplankton are sampled, which has remained virtually unchanged. As such, these phenological shifts of biomass dominant copepod species may mean that the timing of our sampling for BPR estimates is occurring too late. Therefore, missing most of the nauplii and early copepodite (CI-CIII) development which would frequently and regularly release chitobiase into the water column, leaving a community dominated by copepods with longer stage durations in the CIV and CV stages. As such, measures of post-embryonic development such as median development times (MDT) could be estimated (Klein Breteler *et al.*, 1994) to further resolve stage duration discrepancies.

3.5.2 Increases in Non-Copepod Crustaceans and Gelatinous Zooplankton

Changes in copepod community structure in response to El Niño years (i.e. 1997/98) and anomalous warm water events, such as 2005 and 2013-2015 are well documented (Mackas and Tsuda, 1999; Mackas *et al.*, 2001, 2004, 2007; Mackas and Galbraith, 2002a; Harrison *et al.*, 2004; Mackas and Coyle, 2005; Patterson *et al.*, 2013; Bond *et al.*, 2015; Tseng *et al.*, 2017; Venello *et al.*, 2021). However, recent years (2015-2018) have also shown strong positive biomass anomalies of non-copepod crustaceans and gelatinous zooplankton (Galbraith and Young, 2019; Venello *et al.*, 2021). In an attempt to summarize trends in the relative biomass of

crustacean versus gelatinous zooplankton in the region, Galbraith and Young (2019) developed the “Crunchie:Squishie Index” (CSIndex, Figure 3.12) , where ‘Crunchies’ are all zooplankton with a hard chitinous exoskeleton (e.g. copepods, euphausiids, amphipods and decapods) and ‘Squishies’ are zooplankton with a hydrostatic skeleton (e.g. hydromedusae, salps, doliolids, and ctenophores). Although informal in terms of classification terminology, the CSIndex does reflect longstanding ideas about energy flow in marine webs, insofar as gelatinous zooplankton are widely held to be of lower nutritional quality for higher trophic levels relative to lipid-rich crustacean zooplankton (Mianzan *et al.*, 2001; Parsons and Lalli, 2002). The CSIndex provides a high-level snapshot of zooplankton community structure to which food web implications can be implied. In fact, distributions of zooplankton based on water and carbon content were divided between those considered gelatinous and those non-gelatinous, where non-gelatinous species usually had higher carbon content (Kiørbe, 2013). That said, the CSIndex does have potential caveats especially with regard to catchability and preservability differences between crustacean and gelatinous zooplankton species. For instance, plankton net biases may overwhelmingly catch crustacean zooplankton while damaging gelatinous zooplankton beyond identification, which may have led to undersampling of gelatinous species throughout the timeseries.

Coupled with decreased developing copepod biomass, increased biomass of crustaceans such as euphausiids, amphipods and decapods may have also contributed to lower BPR in 2015-2018. *Euphausia pacifica* had strong positive biomass anomalies from 2015 -2018 in both Southern and Northern regions of Vancouver Island, as did *Thysanoessa spinifera* in 2015 and 2016 (Galbraith and Young, 2019). Euphausiids have long intermolt periods of between several days and two weeks (Shaw *et al.*, 2009), with potentially zero or negative growth periods. In

fact, negative growth occurs all year round in *E. pacifica* off the Oregon coast, related to poor feeding conditions in the winter and primary energy allocation to reproduction rather than somatic growth in the summer (Shaw *et al.*, 2010). Therefore, in regions like IS_SVI during 2015 where euphausiid biomass was above its long-term average, high crustacean biomass would not necessarily equate to high crustacean productivity (Suchy *et al.*, 2016). This would be due in large part to the fact that these types of individuals are not regularly releasing chitinase into the water column when compared to developing copepodites. Therefore, growth rate assumptions made by global empirical models which are copepod-specific and assume similar growth rates between different copepod species, may be inaccurate when communities aren't dominated by the models "average species" (Hirst and Shearer, 1997). This may be especially true of highly diverse zooplankton communities, as all members are unlikely to be growing at the same rate (Hirst and Shearer, 1997). Additionally, the relationship between biomass and BPR is different between regions, highlighting the roles of community composition and regional oceanographic conditions in shaping BPR.

'Squishie' biomass anomalies were strongly positive in 2015-2018 for both southern and northern shelf regions (Figure 9). In fact, doliolid numbers were the highest recorded off the WCVI to date (Galbraith *et al.*, 2016), and showed strong positive biomass anomalies in 2015 and 2016 (Venello *et al.*, 2021), which did not occur in any of the other years for which we have BPR measurements. This has the potential to increase competition between crustacean and gelatinous zooplankton species, which may be further detrimental to crustacean development (Sommer and Stibor, 2002; Sullivan and Kremer, 2012). However, the vertical distribution of crustacean and gelatinous zooplankton may also differ (Greer *et al.*, 2020) and the availability

of prey items may be different within those depth layers (Walters *et al.*, 2019). Furthermore, direct predation of copepods and euphausiid eggs/nauplii by gelatinous zooplankton also reduce the number of growing crustaceans within the community (Purcell, 1981; Deibel, 1982; Sullivan and Kremer, 2012) and therefore limiting the release of chitinase into the water column. This has been documented *in situ* for marine copepod species, where increased ocean temperatures lead to increases in mortality rates and predation (Hirst and Kiorboe, 2002).

Figure 3.12. Recreated with permission from Galbraith and Young, 2019; the Crunchie-Squishie Index shows biomass anomalies of each group type for 1995-2018. Orange bars show ‘Crunchie’ biomass anomalies and blue bars represent the ‘Squishie’.

3.5.3 Consequences for Higher Trophic Levels

The differences in BPR observed here may also have food web implications. Decreases in BPR and endemic (boreal-shelf and subarctic) copepod biomass in 2015-2018 may indicate a less productive system. While the southern copepod species may fill similar functional roles as the endemic copepod species (Pomerleau *et al.*, 2015; Venello *et al.*, 2021), they are usually smaller

in size and contain less lipid than their boreal-shelf and subarctic counterparts (Mackas *et al.*, 2004). Conditions that favor these southern copepod species can also favor large gelatinous species (Barton *et al.*, 2013), which occurred in 2015-2018 but not in 2005, perhaps a reason why BPR was higher in 2005 relative to the more recent warm years. Historically, in warm years when southern copepods have positive biomass anomalies, commercially and ecologically important fish and bird species have also been negatively impacted (Schweigert *et al.*, 2010; Bertram *et al.*, 2017; Hipfner *et al.*, 2020; Perry *et al.*, 2021). Diet and productivity of Cassin's auklets was affected during the two strongest El Niño events (1998 and 2016), where mean body mass of nesting auklets was determined to be higher in 'cool' years and was highest overall on a diet strictly comprised of copepods (specifically *N. cristatus*) followed by a copepod plus euphausiid diet, and lastly lowest mean body mass occurred on diets comprised of larval fish (Hipfner *et al.*, 2020). During 'the blob' in particular, a mass mortality of Cassin's auklets occurred dying of starvation due to shifts in zooplankton composition, where lipid-poor zooplankton was the dominant predictor of carcass abundance (Jones *et al.*, 2018). Climate models have also predicted reduced carrying capacity for predators in the North Pacific due to increased ocean warming induced declines of zooplankton biomass and abundance (Woodworth-Jeffcoats *et al.*, 2017).

While, 'other' crustacean zooplankton such as euphausiids provide another source of food for higher trophic levels (*see* Hipfner *et al.*, 2020; Perry *et al.*, 2021), they may not be as beneficial for growing seabirds and other predators. For example, growth rates of Cassin's Auklets, were highest when nesting birds consumed a diet primarily composed of subarctic copepods, specifically lipid-rich *Neocalanus cristatus*, followed by a copepod plus euphausiid

diet, and had the slowest growth when feeding mostly on larval fish (Hipfner *et al.*, 2020).

Additionally, as zooplankton community composition changes, predators may have no choice but to utilize smaller copepods, other crustaceans and gelatinous zooplankton as an additional food source as a subsistence food since lipid-rich copepod prey would be limited (Mianzan *et al.*, 2001; Parsons and Lalli, 2002; Lüsken *et al.*, 2021).

3.6 Conclusions

The data presented here constitute the largest and longest set of “routine” *in situ* estimates of community-level crustacean zooplankton production rates. Lower BPR estimates can be tied to changes in zooplankton community composition, which fluctuates in the NE Pacific with warm and cool ocean conditions and have been more pronounced following the anomalous warm water event of 2013-2015. The highest crustacean zooplankton biomass production rates that we recorded occurred in the ‘cool’ years of 2009-2011, followed by lower rates in the ‘warm’ year of 2005, and the lowest observed rates in the ‘warm’ years of 2015-2018. Developing copepod biomass differed between these years; most notably reductions overall developing copepod biomass and especially for boreal-shelf developing copepod biomass in 2015-2018 as well as increased biomass of smaller species such as the southern, *C.pacificus*, and *Oithona spp.* groups. Coupled with increased biomass contribution of ‘other’ crustacean zooplankton and gelatinous zooplankton, this may account for the low BPR values observed since 2015.

These changes in zooplankton community structure may reflect potential future scenarios of community response to environmental variability (such as increases in sea surface temperatures) that alter productivity and energy transfer. Therefore, this historically highly

productive region that is both ecologically and economically important, will feel the consequences in terms of energy available for higher trophic levels in the future. Where decreases in lipid-rich, protein-rich, developing copepod biomass may be especially problematic for larval and juvenile fish species. Additionally, the replacement of crustacean zooplankton with gelatinous species as a food source could affect the flow of energy to higher trophic levels. For instance, increases in gelatinous zooplankton biomass increase carbon export to the deep ocean via fecal pellets and carcasses, possibly making the system more efficient in terms of carbon sequestration (Lebrato *et al.*, 2013; Steinberg and Landry, 2017). On the other hand, reductions in the faster sinking crustacean zooplankton fecal pellets, could potentially inhibit another pathway of carbon sequestration as well.

Chapter 4. TTE and community composition

4.1 Abstract

Trophic transfer efficiency (TTE) is the proportion of energy passed from one trophic level to another. As such, TTE is a critical component shaping marine ecosystems where small variations in TTE can propagate upwards impacting the amount of food available for higher trophic levels. Long-assumed to be an average of 10%, TTE can be highly variable across oceanographic regimes. Consequently, identifying the factors driving TTE is important in more accurately anticipating potential changes within marine ecosystems and to fisheries production. Here, TTE measurements are presented from the west coast of Vancouver Island and the subarctic northeast Pacific from 2015-2018 with TTE ranging from 0.1 – 35%. Additionally, zooplankton diversity and community composition were assessed as factors driving variation in TTE. The abundance-based diversity metrics functional dispersion, functional divergences, and species evenness as well as mixed layer depth were significant predictors of TTE across the study area. Zooplankton community composition was also significantly different between high TTE (above 10% average) and low TTE (below 10% average). This difference was driven by Omnivore-Herbivores and Active Ambush Omnivores from a functional trait perspective and by boreal-shelf, *Oithona spp.*, and southern copepod groups from a geographic-taxonomic point of view.

4.2 Introduction

Trophic transfer efficiency (TTE) is recognized as both a high-order measure of ecosystem function and a central tenet of ecology (Lindeman, 1942; Dickman *et al.*, 2008; Tanaka and

Mano, 2012). Typically, TTE between contiguous trophic levels is assumed to be 10% in both terrestrial and aquatic ecosystems (Semper, 1881; Lindeman, 1942; Gaedke and Straile 1994; Pauly and Christensen, 1995). However, TTE estimates can vary greatly, especially between phytoplankton and zooplankton ranging from <1% - 35% (e.g. Cushing 1973; Jennings *et al.* 2002; Bradford-Grieve *et al.* 2003; Trebilco *et al.*, 2013; Suchy *et al.* 2016) and potentially up to 50% in both freshwater and marine systems (Anderson *et al.*, 2009). TTE has been shown to vary over specific time periods (Libralato *et al.*, 2004) as well as vary depending on species composition, where some species are more efficient than others (Straile, 1997). Since the consequences of TTE can compound through ecosystems any variation in TTE can have profound effects on food availability for top predators (Eddy *et al.*, 2021). As such, an assumption of 10% efficiency in marine ecosystems (Gaedke and Straile 1994; Pauly and Christensen, 1995) can be either under or over-estimating energy transfer within these systems. In fact, fish production can potentially vary by more than two orders of magnitude when TTE ranges from 4% to 27% across coastal, oceanic, and upwelling zones (Eddy *et al.*, 2021). However, despite the known importance of TTE estimates it remains a large source of uncertainty in our understanding of marine ecosystem functioning, where variation in TTE and the processes that control TTE need to be further resolved (Eddy *et al.*, 2021).

TTE was originally defined as “*the efficiency of productivity of any (trophic) level relative to the productivity of any previous level*”, where productivity was defined as being the general rate of production (Lindeman, 1942). Studies of TTE in freshwater ecosystems have been successful in exploring different facets of energy transfer using direct measurements (e.g. Dickman *et al.*, 2008; Gladyshev *et al.*, 2011; Peace *et al.*, 2015; Barneche *et al.*, 2021), whereas

researchers in marine ecosystems have mostly utilized size-spectra and modeling techniques (e.g. Parsons and Chen, 1994; Berglund *et al.*, 2007; Blanchard *et al.*, 2011; Woodson and Litvin, 2015; Maureaud *et al.*, 2017) with a few exceptions (Jennings *et al.*, 2002; Anjusha *et al.*, 2013). For example, by utilizing spatial overlap data between predators and prey to get a proxy for trophic transfer efficiency (Greer and Woodson, 2016). However, despite its longstanding history, TTE estimates in marine ecosystems have only rarely been based on rates of production (Priyadarshi *et al.*, 2019) and are more commonly derived from ratios of biomass between successive trophic levels (e.g. Gaedke and Straile 1994; Jennings *et al.*, 2002; San Martin *et al.*, 2006; García-Comas *et al.*, 2016). This is particularly true for those with interest in economically important fish stocks, which has led to various attempts to directly correlate global estimates of primary production with global fish production (Parsons and Chen, 1994; Pauly and Christensen, 1995; Sommer *et al.*, 2002) and within the subarctic NE Pacific (Ware and Thomson, 2005).

The continued reliance on biomass ratios is largely due to the difficulties in estimating secondary production rates, especially in marine systems. Although community-level rates of primary production rates have been measured *in situ* for nearly 70 years (Steeman-Neilson, 1952), with progress allowing for routine field measures of primary production rates (*i.e.* O_2/Ar ; Kaiser *et al.*, 2005; Hamme *et al.*, 2012; Varela *et al.*, 2016; Izett *et al.*, 2018; Giesbrecht *et al.*, 2019; Giesbrecht and Varela, 2021), comparable *in situ* estimates of production rates by crustacean zooplankton communities remain scarce (Sastri *et al.* 2012, Suchy *et al.* 2016). Furthermore, most zooplankton growth-rate estimation methods are measured at the population-level and are generally species- or stage-specific. These include cohort and

incubation-based methods (Kimmerer and Mckinnon, 1987; Peterson *et al.*, 1991) and egg production rate methods (Runge, 1984; Poulet *et al.*, 1995). Additionally, global empirical models have also been developed to estimate copepod growth rates including the temperature-dependent growth rate model (Huntley and Lopez, 1992), weight-specific fecundity (Bunker and Hirst, 2004) and growth models (Hirst and Lampitt, 1998; Hirst and Bunker, 2003) all operating under various assumptions. In contrast, community-level estimates of zooplankton production analogous to primary production rate estimates are largely absent from the literature. More recently, biochemical approaches to estimating zooplankton production rates have grown in popularity (Yebra *et al.*, 2017).

Additionally, substantial progress has been made in the estimation of community-level crustacean zooplankton production rates using the chitobiase method (Oosterhuis *et al.*, 2000; Sastri and Roff 2000; Sastri and Dower 2006, 2009; Avila *et al.*, 2011, 2012; Sastri *et al.*, 2012; Suchy *et al.*, 2016). Unlike biomass ratios and empirical production rate models (i.e. Huntley and Lopez, 1992; Hirst and Lampitt, 1998; Hirst and Bunker, 2003; Bunker and Hirst, 2004), which make the assumption that all individuals within a specific size spectrum or a select species within a community are growing at the same rate, the chitobiase method captures production rates for all developing crustaceans including nauplii and juveniles as well as late-stage individuals that may have longer inter-moult periods (Hirst and Sheader, 1997; Trebilco *et al.*, 2013; Suchy *et al.*, 2016). Crustacean zooplankton biomass production rates (BPR hereafter) estimated by the chitobiase method for freshwater planktonic communities, showed that these *community-level* production rates were correlated to the same factors known to affect *population-level* production rates, such as temperature and total biomass (St-Gelais *et al.*,

2017). Additionally, community-level BPR estimates using the chitobiase method were also driven by lake morphometry and catchment properties, which were not captured using an empirical model that estimated population-level production rates (St-Gelais *et al.*, 2017). In fact, high crustacean zooplankton biomass does not always equate to high production rates, especially as community composition changes between oceanographic regimes (Venello *et al.*, 2021b (Chapter 3)). Biomass-based TTE estimates can also be affected by net sampling biases - which typically under-sample smaller copepods, nauplii, and eggs (Hopcroft *et al.*, 2001; Turner, 2004). In contrast, a community-level chitobiase production rate estimate incorporates production from these members of the community without the need for net sampling.

As a ratio of the production rates within contiguous trophic levels, TTE may also be affected by factors that affect production rates within a trophic level. These include the metabolic/energetic characteristics of species within a community (i.e. that affect energy flow per unit biomass) and the relative biomass and abundance of species at each trophic level (Tanaka and Mano, 2012). The first factor includes functional traits which can include feeding strategies, physiological, and life-history traits; while the second represents species-specific responses (i.e. evidenced via changes in abundance and biomass) to ecological and environmental interactions. As such, changes to diversity within a community may alter its ability to efficiently transfer energy (Hooper *et al.*, 2005; Tanaka and Mano, 2012; Valdivia *et al.*, 2016).

Traditionally, biodiversity studies have focused largely on the number of species present (species richness, S), as well as the distribution of abundance or biomass across species (species evenness, J') within a community (Smith and Wilson, 1996; Gaston, 2000; Hamilton, 2005).

Other well-known diversity indices also include the Simpson index (Simpson, 1949), which represents the probability that two randomly chosen individuals will belong to the same species, as well as the Shannon diversity index (H') which represents both the number and evenness of species present within a community (Shannon, 1948). Although calculating taxonomic diversity remains a well-established way of assessing patterns in biodiversity, additional knowledge regarding the biology and ecology of the individual species that are present within a given system may provide deeper insight into high-level ecosystem processes and functions, such as TTE (McGill *et al.*, 2006). This may be accomplished by using species functional traits to quantify functional diversity (FD) (Chapin *et al.*, 2000; Naeem *et al.*, 2002) and functional group diversity (Tilman, 2001; Pomerleau *et al.*, 2015; Benedetti *et al.*, 2015, 2018, Venello *et al.*, 2021a).

The functional diversity of a community is defined as “the value and range of organismal traits that influence their performance and ecosystem functioning” (Díaz and Cabido, 2001), where traits can be defined as the morphological, physiological, and behavioral characteristics that define the role of a given species within the ecosystem, as well as the ecological niche that a given species occupies (Litchman *et al.*, 2013). Functional traits can represent different critical ecological functions, and can affect key ecosystem processes such as productivity and energy transfer (Hébert *et al.*, 2017). As such, functional diversity has been shown to have a greater influence on ecosystem functions such as productivity rather than species (taxonomic) diversity (Hooper and Dukes, 2004; Hooper *et al.*, 2005; Schittko *et al.*, 2014).

Functional diversity indices include functional richness ($FRic$), functional evenness ($FEve$), functional divergence ($FDiv$) (Mason *et al.*, 2005; Villéger *et al.*, 2008) as well as

functional dispersion (*FDis*) (Laliberté and Legendre, 2010). *FRic* is analogous to *S*, representing the amount of niche space occupied by a species, independent of its abundance (Mason *et al.*, 2005). *FEve* is comparable to J' and represents the evenness of the distribution of abundance in niche space (Mason *et al.*, 2005). *FDiv* is the distribution of species abundance in niche space (Mason *et al.*, 2005), whose taxonomic analogue is the Shannon diversity index (H'). Note that *FDiv* can vary independently of *FRic* and *FEve*, where high a *FDiv* indicates a community where the most abundant species occur at the extremities of the functional character range (Mason *et al.*, 2005). *FDis* represents the estimated mean distance of all species to the weighted centroid of the community in trait space (Laliberté and Legendre, 2010). Similar to *FDis*, Rao 's quadratic entropy (*Rao Q*, Rao, 1982), also represents the spread of species abundance in trait space. Importantly, *FDis* and *Rao Q* are unaffected by species richness, can utilize any number or type of trait, and considers the relative abundances of species (Laliberté and Legendre, 2010, Stuart-Smith *et al.*, 2013). Nonetheless, FD indices can still be sensitive to trait choice, with *FRic* being most sensitive when the traits of rare species are not considered (Pakeman, 2014; Lefcheck *et al.*, 2015).

Functional diversity has been commonly used to relate community composition to ecosystem function in terrestrial and freshwater ecosystems (Diaz and Cabido, 2001; Barnett *et al.*, 2007; Roscher *et al.*, 2013; Russell *et al.*, 2014; Schmitz *et al.*, 2015; Russo *et al.*, 2016; Hébert *et al.*, 2017). For marine zooplankton, however, the use of functional diversity has been limited to descriptions of functional traits within a community (Kiorboe, 2011; Barton *et al.*, 2013; Litchman *et al.*, 2013; Hébert *et al.*, 2016), to establish functional groups (Pomerleau *et al.*, 2015; Benedetti *et al.*, 2015, 2018; Venello *et al.*, 2021a), or to compare of taxonomic *versus*

functional diversity metrics (Pomerleau *et al.*, 2015). Links between functional diversity and ecosystem functions, such as productivity and energy transfer within marine ecosystems have not been directly addressed (Eddy *et al.*, 2021). Since functional diversity can have greater influence over ecosystem functions (i.e. when compared to taxonomic diversity), and since changes in community diversity may alter energy transfer, links between the functional diversity and ecosystem functions are needed to further resolve variation in energy transfer. This becomes increasingly important when zooplankton community composition changes as a response to climate change.

One such area is the subarctic northeast (NE) Pacific, which is driven by strong-bottom up control between phytoplankton and zooplankton (Ware and Thomson, 2005) and is characterized by considerable variation in copepod and zooplankton diversity, where differences manifest between regional oceanographic regimes and in response to climate variability (Mackas, 1994; Mackas and Galbraith, 2002; Mackas *et al.*, 2004, Venello *et al.*, 2021a, b (Chapter 3)). Such shifts in zooplankton diversity may also affect higher trophic levels, since changes in the dominant copepod assemblages (Mackas and Galbraith, 2002; Mackas *et al.*, 2004) and increases in non-crustacean and gelatinous zooplankton (Venello *et al.*, 2021 a,b (Chapter 3)), may impact production rates and alter the energy pathways of the entire ecosystem.

One notable shift in zooplankton composition in the NE Pacific occurred during the anomalous warm water event of 2014/2015 (colloquially known as “The Blob”), and from which community composition conditions have yet to fully return to normal (Bond *et al.*, 2015; Galbraith and Young, 2019; Venello *et al.*, 2021 a, b (Chapter 3)). During that event, gelatinous

zooplankton biomass in the region increased 10-fold in 2015 and the doliolid, *Dolioletta gegenbauri* as well as pyrosome, *Pyrosoma atlanticum* was observed at the highest biomass levels in 30 years (Galbraith and Young, 2019; Venello *et al.*, 2021a). Thus, in order to properly assess ecosystem function responses to shifts in zooplankton community composition due to environmental variability, rate-based estimates of TTE should be linked to both taxonomic and functional diversity.

In this study, community-level crustacean zooplankton biomass production rates and net community production rates were used to estimate TTE across the NE Pacific from 2015-2018. Broad-scale links between TTE and zooplankton community composition were established using both geographic-taxonomic copepods groups (Mackas and Galbraith, 2002; Mackas *et al.*, 2004) and functional trait groups (Venello *et al.*, 2021a). Additionally, taxonomic and functional diversity metrics were used to explore the possible links between biodiversity and ecosystem function (TTE) within the NE Pacific.

4.3 Methods

4.3.1 Study Area

Please refer to the introduction in data chapter 2, “*Drivers of variation in crustacean zooplankton production rates differ across regions off the west coast of Vancouver Island and in the subarctic NE Pacific*”. The study area for the west coast of Vancouver Island and the NE Pacific (Figure 4.1) are explained in greater detail there. Additional station sampling information is provided in Appendices C and D.

Figure 4.1. Map of the study area. Triangles denote stations where crustacean zooplankton production rate and net community production rate samples were collected as well as zooplankton abundance both along the west coast of Vancouver Island (top panel) and along Line P (lower panel) in the NE Pacific. Reference contour lines are 250m, 500m, 1000m, 1500m, and 2000m, 3000m, and 4000m. Appendices C and D provides station sampling information.

4.3.2 Trophic Transfer Efficiency (TTE)

Trophic transfer efficiency (TTE) was calculated as the ratio of crustacean zooplankton biomass production rates (BPR, $\text{mg C m}^{-2} \text{d}^{-1}$) as estimated by the chitobiase method (Sastri and Roff, 2000; Sastri and Dower, 2006) and net community production (NCP, $\text{mg C m}^{-2} \text{d}^{-1}$) as derived from underway O_2/Ar mass spectrometry (Izett *et al.*, 2018; Izett and Tortell, 2020). NCP represents a balance between primary production and both auto- and heterotrophic

community respiration (Izett *et al.*, 2018). Crustacean zooplankton BPR and NCP were estimated at the stations shown in Figure 4.1 between 2015-2018.

Crustacean zooplankton BPR was estimated using a simple ship-board enzymatic assay, where the decay rate of the crustacean moulting enzyme chitinase in the water column was used to estimate crustacean zooplankton production rates (see Sastri and Dower, 2009; Suchy *et al.*, 2016; Venello *et al.*, 2021b *in review* (Thesis Chapter 3)). Briefly, net community production was estimated from underway $\Delta\text{O}_2/\text{Ar}$ or $\Delta\text{O}_2/\text{N}_2$ measurements and corrected for vertical mixing fluxes of O_2 using discrete N_2O measurements (Izett *et al.*, 2018; Izett and Tortell, 2020). Continuous O_2/Ar and O_2/N_2 measurements were conducted on seawater that was pumped into the main laboratory (from a nominal intake depth of 5 m) using membrane inlet mass spectrometry (Tortell, 2005) and an O_2 Optode / Gas Tension Device (GTD) system (see Izett and Tortell, 2020), where the optode O_2 data was calibrated using discrete samples. Individual TTE estimates greater than 35% were deemed artefacts and not included in the analysis (Gladyshev *et al.*, 2011; Suchy *et al.*, 2016).

4.3.3 Zooplankton Abundance

Zooplankton samples were also collected during Fisheries and Oceans Canada's La Perouse program (May and September) and the Line P (February, June, August) monitoring cruises in May and September from 2015-2018 (Figure 1). Vertical net hauls were conducted with black bongo nets (0.25 m² mouth area, 0.23 mm mesh aperture) fitted with a TSK flowmeter from near-bottom to sea surface (when bottom depth was < 250 m) on the continental shelf and upper slope and from 250 m to surface at deeper locations and off the shelf. Samples collected from the bongo net tows were enumerated and identified to species and developmental stage

(as per Mackas, 1992; Mackas *et al.*, 2001; Mackas and Galbraith, 2002). Briefly, raw counts were transformed to abundance per square meter using a subsampled fraction, volume of water, and tow depth. Abundance data were extracted from the zooplankton database maintained by the Institute of Ocean Sciences (Sidney, BC, Canada).

4.3.4 Zooplankton Functional and Taxonomic Diversity

Four functional diversity indices and four analogous taxonomic diversity indices were calculated from all available stations sampled during the La Perouse and Line P oceanographic monitoring surveys during 2015-2018. These included functional richness (*FRic*), functional evenness (*FEve*), functional dispersion (*FDIs*), and functional divergence (*FDiv*), as well as species richness (*S*), species evenness (*J'*), Shannon diversity index (*H'*), and Simpson diversity index (*D*). All indices were calculated using the *FD* and *Vegan* packages (Laliberté and Shipley, 2011; Oksanen *et al.*, 2013) within the R statistical framework (R Core Development Team, 2021).

Diversity indices used in this analysis for each cruise season (February, May/June, and August/September) were averaged across stations within each region during 2015-2018. The traits that were used for the functional diversity calculations were previously used to establish functional groups for the inner shelf region of southern Vancouver Island (Chapter 2 - Venello *et al.*, 2021a). In all, 55 crustacean and gelatinous mesozooplankton species were divided into eight functional groups using four functional traits: (i) size class of average body length or max body size/diameter, (ii) feeding type (ambush, cruise, current, or mixed), (iii) trophic group (carnivore, detritivore, omnivore, or herbivore), and (iv) reproductive mode (alternation of generations, broadcast spawners, egg-brooding, or egg-brooding sac). The resulting functional groups described by Venello *et al.* (2021a) were: Detritivores, Doliolids, Omnivore-Herbivores,

Active Ambush Omnivores, Egg-Brooding Carnivores, Broadcast Carnivores, Cruise Carnivores-A, and Cruise Carnivores-B. (Table 4.1).

To examine patterns within specific zooplankton groups in each region, the relative abundance contributions of functional groups (Table 4.1; Venello *et al.*, 2021a) and geographically-based taxonomic copepod groups, hereafter referred to as ‘geographic-taxonomic’ groups (Mackas and Galbraith, 2002) are also presented here. On the basis of geography and bathymetry, Mackas and Galbraith (2002) defined copepod groups for the subarctic NE Pacific; including a ‘boreal-shelf’, ‘subarctic’, and ‘southern’ groupings; wherein the boreal-shelf and subarctic species are endemic to the WCVI and the southern group species are usually found within the California Current and offshore (Table 4.2). Additionally, a ‘gelatinous’ group as well as *Calanus pacificus*, *Centropages abdominalis* and *Oithona* spp. were also included with the copepod groupings (Table 4.2).

Functional Group	Species
Detritivores	<i>Scolecithricella minor</i> , <i>Scaphocalanus brevicornis</i> , <i>Scaphocalanus magnus</i> , <i>Conchoecia</i> spp., and <i>Disconchoecia elegans</i> .
Doliolids	<i>Dolioletta gegenbauri</i>
Omnivore-Herbivores	<i>Metridia pacifica</i> , <i>Microcalanus pusillus</i> , <i>Microcalanus pygmaeus</i> , <i>Thysanoessa spinifera</i> , <i>Euphausia pacifica</i> , <i>Thysanoessa inspinata</i> , <i>Ctenocalanus vanus</i> , <i>Calocalanus</i> spp., <i>Paracalanus</i> spp., <i>Oikopleura labradorensis</i> , <i>Fritillaria</i> , <i>Oikopleura dioca</i> , <i>Calanus marshallae</i> , <i>Calanus pacificus</i> , <i>Neocalanus plumchrus</i> , <i>Neocalanus cristatus</i> , <i>Neocalanus flemingeri</i> , <i>Eucalanus bungii</i> , and <i>Eucalanus californicus</i> , <i>Clausocalanus</i> spp.,

	<i>Pseudocalanus newmani</i> , <i>Pseudocalanus moultoni</i> , <i>Pseudocalanus mimus</i> , and <i>Pseudocalanus minutus</i>
Active Ambush Omnivores	<i>Oithona similis</i> , <i>Acartia longiremis</i> , <i>Acartia tonsa</i> , <i>Mesocalanus tenuicornis</i> , <i>Gaetanus simplex</i> , <i>Gaetanus tenuicornis</i> , <i>Aetideus pacificus</i> , <i>Centropages abdominalis</i> , and <i>Aetideus divergens</i>
Egg-Brooding Carnivores	<i>Beroe</i> spp., <i>Parasagitta elegans</i> , <i>Eukrohnia hamata</i> , <i>Paraeuchaeta elongata</i> , and <i>Themisto pacifica</i>
Broadcast Carnivores	<i>Aegina citrea</i> , <i>Sarsia</i> spp., <i>Pleurobrachia bachei</i> , <i>Aglantha digitale</i> , <i>Nanomia bijuga</i> , <i>Dimophyes arctica</i> , and <i>Muggiaea atlantica</i>
Cruise-Carnivores A	<i>Clytia gregaria</i> , and <i>Eutonia indicans</i>
Cruise-Carnivores B	<i>Aequorea</i> spp., and <i>Mitrocoma cellularia</i>

Table 4.1. Functional group designations and associated species from Venello et al., 2021a.

Geographic-taxonomic Group	Species
Boreal-Shelf	<i>Acartia longiremis</i> , <i>Calanus marshallae</i> , <i>Pseudocalanus mimus</i> , <i>Pseudocalanus minutus</i> , <i>Pseudocalanus moultoni</i> , <i>Pseudocalanus newmani</i> ,
Subarctic	<i>Eucalanus bungii</i> , <i>Neocalanus cristatus</i> , <i>Neocalanus flemingeri</i> , <i>Neocalanus plumchrus</i> , <i>Metridia pacifica</i>
Southern	<i>Acartia tonsa</i> , <i>Acartia danae</i> , <i>Calocalanus</i> spp., <i>Clausocalanus</i> spp., <i>Eucalanus californicus</i> , <i>Eucalanus hyalinus</i> , <i>Ctenocalanus vanus</i> , <i>Mesocalanus tenuicornis</i> , <i>Metridia pseudopacifica</i> , <i>Paracalanus</i> spp.

<i>Oithona</i> spp.	<i>Oithona atlantica</i> , <i>Oithona setigera</i> , <i>Oithona similis</i>
<i>Gelatinous</i>	<i>Aegina citrea</i> , <i>Aequorea</i> spp., <i>Aglantha digitale</i> , <i>Beroe</i> spp., <i>Clytia gregaria</i> , <i>Dimophyes arctica</i> , <i>Dolioletta gegenbauri</i> , <i>Eutonia indicans</i> , <i>Mitrocoma cellularia</i> , <i>Muggiaea atlantica</i> , <i>Nanomia bijuga</i> , <i>Pleurobrachia bachei</i> , <i>Sarsia</i> spp.
<i>Calanus pacificus</i>	<i>Calanus pacificus</i>
<i>Centropages abdominalis</i>	<i>Centropages abdominalis</i>

Table 4.2. Geographic-taxonomic group designations and associated species.

4.3.5 Statistical Analysis

All statistical analyses were conducted within the R statistical framework (Version 1.3.1, R Core Team, 2020). Data points were pooled across all regions as there were not enough TTE estimates to allow a regional (i.e. between-region) analysis. Generalized additive models (GAMs) were used to test for non-linear relationships between TTE and functional and taxonomic diversity indices, as well as average mixed layer depth temperature (MLD) using the *mgcv* package (Wood, 2001, 2018). MLD was used to account for any potential temperature influences on TTE and was calculated using a density threshold criterion, where there is a density difference of 0.125 kg/m³ from the average density in the upper 5 m (R Izett, UBC pers. comm.). The base of the mixed layer was therefore defined as the depth at which the density first exceeds the average 5m density by 0.125 kg/m³ (Kara *et al.*, 2000). *FRic* and species richness were found to be highly correlated (Spearman's rho = 0.9), as were species evenness and both the Shannon and Simpson diversity indices (Spearman's rho = 0.9). As such pairs of correlated variables were not included together within GAMs, using backward selection

techniques GAMs were built by removing either correlated variable and using the Akaike information criterion (AIC) to select final model input variables.

GAMs are generalized additive models wherein the predictors are the sum of the smoothing functions of individual covariates, allowing for non-linear relationships between response and predictor variables. GAMs were fit using a Gaussian identity link function with a thin plate regression spline smoother. The restricted maximum likelihood method (REML) was used as the smoothing parameter estimation method (Wood, 2011). GAM smooth plots were created using the *visreg* package (Breheny and Burchett, 2017) to show the partial effects of the selected predictor variables on TTE, which are basic residuals relative to the selected predictor variable.

All multivariate analyses were conducted using the *vegan* package (Oksanen *et al.*, 2013) within the R statistical framework. A K-means clustering approach was used to establish three TTE clusters (low, mid, and high) using the *NBClust* package, where the number of k-means TTE group clusters was determined using the silhouette method (Charrad *et al.*, 2014). TTE values in the low, medium, and high clusters ranged from 0.15-7.9%, 9.36-20.0%, and 21.8-34.7% (Table 4.3). A permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) was conducted to assess significant differences in community composition among TTE clusters. Non-metric multi-dimensional scaling (NMDS) based on a Bray-Curtis dissimilarity matrix (Clarke, 1993) was used to visualize community composition data in 2-dimensional space. Finally, a similarity percentages analysis (SIMPER, Clarke, 1993) was to compare the percent contribution of both functional and geographic-taxonomic groups to the community composition between different TTE clusters.

4.4 Results

TTE Cluster	Range (%)	Mean (%)
Low (n = 21)	0.15 - 7.9	3.9
Mid (n = 24)	9.36 - 20.0	14.1
High (n = 9)	21.8 – 34.7	27.7

Table 4.3. TTE clusters established by Kmeans clustering, including the range of values within each group and the group mean.

4.4.1 Trophic Transfer Efficiency (TTE) and Diversity Indices

TTE estimated using crustacean biomass production rates (BPR) and net community production (NCP) was highly variable across the study area, ranging from nearly 0% to 35% (Table 4.3, 4.4 and Figure 4.2). Mean annual TTE fell below the oft-cited average value of 10% (Pauly and Christensen, 1995) in 2015 and 2018, and above 10% in 2016, 2017 (Table 4.4, Figure 4.2).

Diversity indices were also highly variable across the study area (Table 4.5, Appendix E).

Maximum functional and species richness and functional divergence occurred in 2015 and 2016 (Table 4.5, Appendix E). Functional evenness, dispersion and species evenness, Shannon diversity and Simpson diversity indices peaked in 2016 (Table 4.5, Appendix E). Minimum mixed layer depth (MLD) temperature occurred in 2016 and 2017 (8.8 °C, Table 4.5, Appendix E), whereas maximum MLD temperature also occurred in 2016 (15.8 °C, Table 4.5, Appendix E).

Year	TTE (%)	Mean TTE
2015	0.33 – 31.7	6.0
2016	0.15 – 28.5	14.0

2017	2.5 – 34.7	15.0
2018	2.6 – 7.5	5.1

Table 4.4. Range of TTE values per year as well as annual mean TTE. TTE estimates >35% (n= 14) were excluded as artefacts *as per* Gladyshev *et al.*, 2011 and Suchy *et al.*, 2016.

Figure 4.2. Barplots of mean TTE derived from NCP and BPR estimates (in $\text{mg C m}^{-2} \text{d}^{-1}$) per year. Standard error bars show mean $\pm$ standard deviation. TTE estimates > 35% (n = 14) were excluded as artefacts, *as per* Gladyshev *et al.*, 2011 and Suchy *et al.*, 2016.

Year	Predictor Variable	Range
2015	<i>FRic</i>	0.037 - 0.097
	<i>FEve</i>	0.105 - 0.539
	<i>FDis</i>	0.060 - 0.291
	<i>FDiv</i>	0.779 - 0.991
	Species Richness	15 - 39
	Species Evenness	0.182 - 0.813
	Shannon Diversity	0.572 - 2.584
	Simpson Diversity	0.187 - 0.902
	MLD Temperature (°C)	11.5 - 13.4
2016	<i>FRic</i>	0.053 - 0.097
	<i>FEve</i>	0.108 - 0.538
	<i>FDis</i>	0.059 - 0.283
	<i>FDiv</i>	0.725 - 0.973
	Species Richness	18 - 39
	Species Evenness	0.164 - 0.868
	Shannon Diversity	0.498 - 2.873
	Simpson Diversity	0.157 - 0.930
	MLD Temperature (°C)	8.8 - 15.8
2017	<i>FRic</i>	0.027 - 0.097
	<i>FEve</i>	0.111 - 0.571
	<i>FDis</i>	0.104 - 0.316
	<i>FDiv</i>	0.681 - 0.983
	Species Richness	12 - 37
	Species Evenness	0.329 - 0.827
	Shannon Diversity	0.998 - 2.599
	Simpson Diversity	0.437 - 0.903
	MLD Temperature (°C)	8.8 - 15.5
2018	<i>FRic</i>	0.036 - 0.090
	<i>FEve</i>	0.142 - 0.466
	<i>FDis</i>	0.085 - 0.235
	<i>FDiv</i>	0.761 - 0.992
	Species Richness	13 - 30
	Species Evenness	0.364 - 0.675
	Shannon Diversity	1.105 - 2.228
	Simpson Diversity	0.474 - 0.863
	MLD Temperature (°C)	13.0 - 15.4

Table 4.5. Annual range of values for diversity metrics and mixed layer depth (MLD) temperature across the study area.

4.4.2 Zooplankton Community Composition

Both functional and geographic-taxonomic group abundances varied considerably between years (Figure 4.3 and Figure 4.4). The Omnivore-Herbivore functional group comprised <50% of the total group abundance in 2015 and 2017, while contributing over 50% in 2016 and 2018 (Figure 4.3). *Dolioletta gegenbauri* contributed ~15% in 2015 and 2017 (Figure 4.3). 2015-2017 also showed small contributions from the Broadcast Carnivore, Egg-Brooding Carnivore, and Detritivore functional groups (Figure 4.3). In 2018, the majority of the community was comprised of Active Ambush Omnivores and Omnivore-Herbivores (Figure 4.3). For the geographic-taxonomic groups, community abundance in 2015-2017 showed small contributions from the subarctic, *Calanus pacificus*, and *Calanus abdominalis* groups; with larger contributions from the southern, gelatinous, and *Oithona* groups (Figure 4.4). In 2018, the boreal-shelf group comprised more than 50% of the total group abundance, with smaller contributions from the *Oithona* and southern groups (Figure 4.4).

Figure 4.3. Annual percent abundance contributions of functional groups (Venello *et al.*, 2021a; Table 1).

Figure 4.4. Annual percent abundance contributions of geographic-taxonomic groups as well as *C. pacificus*, *C. abdominalis*, *Oithona spp.*, and all gelatinous species used in the FG analysis.

4.4.3 Linking Diversity Metrics to Variability in TTE

Results from GAMs with the best fit included two functional and one taxonomic diversity metric along with average mixed layer depth (MLD) temperature (Table 4.6). Species Evenness, functional divergence (*FDiv*), MLD temperature, and functional dispersion (*FDis*) collectively explained 41% of variation in TTE (Table 4.6, Figure 4.5a-4.5d). TTE decreased with increased species evenness and *FDiv* (Figure 4.5a and 4.5b). In contrast, TTE showed a sigmoidal relationship with MLD temperature, wherein higher TTE values occurred at <10 °C and between

13-14°C, and lower TTE occurred at ~12°C and >14°C (Figure 4.5c). Finally, *FDis* and TTE showed a U-shaped relationship, where high TTE occurred at both low and high functional dispersion but lower TTE occurred at mid-range *FDis* (Figure 4.5d). Also of note is that for *FDiv*, MLD temperature, and *FDis*, the TTE estimates from 2015 were consistently the lowest values reported (Figures 4.5b, 4.5c, and 4.5d).

	adj. r^2	% Deviance	Predictor Variables	p-value
TTE	0.41	49.4	Species Evenness	0.003
			<i>FDiv</i>	0.04
			MLD Temperature	0.02
			<i>FDis</i>	0.0005

Table 4.6. GAM model results showing species evenness, functional divergence (*FDiv*), mixed layer depth (MLD) temperature, and functional dispersion (*FDis*) as significant in explaining variation in trophic transfer efficiency (TTE) with adjusted r^2 value (Adj. r^2), percent deviance explained (% deviance), and the significance of the diversity variables. Significant values are in bold.

Figure 4.5. GAM smooths for the relationship of TTE to a) species evenness, b) functional divergence (*FDiv*), c) mixed layer depth (MLD, °C) temperature, and d) functional dispersion (*FDis*). Individual plots show relationships between partial effect residuals of TTE and the predictor variable when the remaining predictor variables are held at their mean. Gray shaded area represents the 95% confidence interval. The color of the points represents sampling year.

4.4.4 Zooplankton Community Composition and TTE

Representation of zooplankton community composition in 2D space via NMDS shows a gradient of TTE for both the functional groups approach and geographic-taxonomic group abundance (Figure 4.6a and 4.6b, respectively). Stress values for both NMDS plots were <0.2 and therefore provide an acceptable solution between the two axes (Clarke, 1993). Community composition differed significantly between high and low TTE clusters using both the functional groups approach and the geographic-taxonomic group approach (Table 4.7). The largest difference in community composition (72%) occurred between high and low TTE clusters for functional group abundance, followed by geographic-taxonomic group abundance, where high and low TTE cluster communities were 68% different from each other (Table 4.7).

Functional Group Abundance	High-Low (72%)	0.12	0.02*
	High-Mid (60%)	0.05	0.5
	Low-Mid (66%)	0.07	0.07
Geographic-taxonomic Group Abundance	High-Low (68%)	0.09	0.04*
	High-Mid (61%)	0.04	0.8
	Low-Mid (58%)	0.04	0.4

Table 4.7. Pairwise PERMANOVA results between TTE cluster and either functional and geographic-taxonomic group abundance. Significant differences are in bold.

Figure 4.6. NMDS plot of community composition by TTE cluster for a) functional and b) geographic-taxonomic group abundance.

SIMPER analysis identified the particular functional and geographic-taxonomic groups that were responsible for ~80% of the difference between the high and low TTE communities (Table 4.8). For functional group abundance the Omnivore-Herbivore and Active Ambush Omnivore groups were responsible for most of the difference between high and low TTE communities (Table 4.8). Marginally significant differences between low and mid TTE communities were also driven mostly by the Omnivore-Herbivore and Active Ambush Omnivore groups (Table 4.8). For the geographic-taxonomic group abundances, boreal-shelf, *Oithona* spp., and southern groups drove the differences between high and low TTE communities (Table 4.8).

	Difference between TTE clusters	Zooplankton Groups	Cumulative contribution of most influential groups
Functional Group Abundance	High-Low (72%)	Omnivore Herbivores	0.49
		Active Ambush Omnivores	0.82
	Low-Mid (66%)	Omnivore Herbivores	0.53
		Active Ambush Omnivores	0.82
Geographic-taxonomic Group Abundance	High-Low (68%)	Boreal-Shelf	0.37
		<i>Oithona</i> spp.	0.59
		Southern	0.80

Table 4.8. SIMPER analysis of both functional and geographic-taxonomic group community composition and differences between TTE clusters. Zooplankton groups listed account for ~80% of variation between high and low TTE communities.

4.5 Discussion

Functional dispersion (*FDis*) and divergence (*FDiv*) as well as species evenness (*J'*), and mixed layer depth temperature were identified as significant explanatory variables of TTE across the study. Mean TTE was higher than the oft-assumed 10% average (Gaedke and Straile 1994; Pauly and Christensen 1995) in 2016 and 2017, with annual means of 14% and 15% respectively, whereas mean TTE in 2015 and 2018 was below 10%. Additionally, zooplankton community composition was significantly different between high and low TTE clusters, driven primarily by differences in the abundance of Omnivore-Herbivores and Active Ambush Omnivores from the functional trait perspective and by the abundances of boreal-shelf, *Oithona* spp., and southern copepods from a geographic-taxonomic one.

It has been suggested that species and functional richness are likely less important than the spread of species/trait abundances within a community (Hillebrand *et al.*, 2008; Soininen *et al.*, 2012 and refs within; Boersma *et al.*, 2016; Valdivia *et al.*, 2016). The results presented here

further corroborate these ideas, as the abundances of specific groups define low and high TTE communities and abundance-based metrics $FDis$, $FDiv$, and J' were determined to be the main drivers of TTE variation. Environmental filtering caused by stressors such as temperature may not be strong enough to eliminate species and functional roles completely (Boersma *et al.*, 2016; Valdivia *et al.*, 2016). All species/trait combinations may still be present within a community but environmental changes, such as an increase in temperature, will likely alter the number of individuals present within particular functional trait combinations (i.e. functional dispersion/divergence) (Boersma *et al.*, 2016; Valdivia *et al.*, 2016). In fact, this has been observed for the west coast of Vancouver Island and within the subarctic northeast Pacific, where copepod group abundance and biomass fluctuate with 'warm' and 'cool' years (Mackas and Galbraith, 2002).

4.5.1 Temperature Structures Marine Communities

Since temperature plays a fundamental role in structuring marine biodiversity (Tittensor *et al.*, 2010), it is expected that changes to ecosystem functions, such as energy transfer, are due partly to shifts in species/community assemblages as a response to ocean warming (Tittensor *et al.*, 2010; du Pontavice *et al.*, 2020). In fact, decreases in TTE have been linked to rising temperatures across a range of marine and freshwater ecosystems (du Pontavice *et al.*, 2020; Barneche *et al.*, 2021). In a mesocosm experiment, increased warming reduced energy flow from herbivores to carnivores as well as the efficiency of energy transfer between primary producers and detritus to herbivores and detritivores, respectively (Ullah *et al.*, 2018). Similarly, Goldenberg *et al.*, (2017) determined that warming stalls secondary productivity and causes

trophic inefficiency between adjacent levels. Additionally, a warming of 4°C has been shown to decrease TTE by 56% in freshwater ecosystems, with an overall decrease in both phytoplankton and zooplankton biomass (Barneche *et al.*, 2021).

It is well known that temperature changes correspond to shifts in copepod community composition in the NE subarctic Pacific, where decreases in endemic species and increases in southern species generally occur during warm years and with the opposite occurring in ‘normal’ or cool years (Peterson *et al.*, 2002; Mackas and Galbraith 2002; Mackas *et al.*, 2004). However, neither group of species completely replaces the other but, rather, each alters in relative abundance and biomass (Mackas and Galbraith 2002; Mackas *et al.*, 2004; Venello *et al.*, 2021a). The specific groups that are known to fluctuate most under such circumstances (Omnivore-Herbivores, Active Ambush Omnivores, boreal-shelf, and southern) are the same groups that were responsible for ~80% of the variation between the high and low TTE communities found here. Despite established links between temperature and differences in community composition (Mackas and Galbraith 2002; Mackas *et al.*, 2004; Galbraith and Young, 2019; Venello *et al.*, 2021a) little work has been done to explicitly address links between diversity metrics and ecosystem function (i.e. energy transfer), especially for marine zooplankton.

4.5.2 Ecological Context of Functional Diversity Metrics

Functional diversity (FD) is a multifaceted approach to quantifying community structure and new tools to assess FD have highlighted its importance as a fundamental driver of ecosystem functioning (Hooper *et al.*, 2005). *FD_{is}* is a measure of functional similarity amid the dominant members of a community (Villéger *et al.*, 2010) and has been considered a metric of ‘net’ FD

representing the remaining variation in the relationship between FD and species richness (Devictor *et al.*, 2010). *FDiv* is a measure of variation in species functions and the position of their abundances in trait space (Mason *et al.*, 2005; Schleuter *et al.*, 2010; Villéger *et al.*, 2010). Communities with both high *FDIs* and *FDiv* can have high degrees of niche differentiation, leading to a more efficient use of resources and higher productivity with less prey overlap (Mason *et al.*, 2005; Petchey and Gaston, 2006; Villéger *et al.*, 2010). Within this study, communities with both high and low *FDIs* had higher TTE; however, a decrease in TTE was observed with higher *FDiv*.

The results presented here show efficient energy transfer between phytoplankton and zooplankton when the zooplankton community is either most functionally similar or dissimilar (both low and high *FDIs*). Communities with high *FDIs* may have a greater tolerance to environmental stressors due to a greater diversity of trait combinations (Hooper *et al.*, 2005; Gusmao *et al.*, 2016; Cooke *et al.*, 2019 and references therein). This may serve to enhance ecosystem stability by increasing the ability to buffer against environmental changes, where variation in functional trait representation increases the odds that some species will respond favorably to changes in climate (Diaz and Cabido, 2001; Cooke *et al.*, 2019). However, high *FDIs* communities may also be sensitive to species loss as there is low functional redundancy within such communities (Wiedmann *et al.*, 2014). High functional dispersion can also enable non-endemic species with differing trait combinations to increase in abundance through niche heterogeneity (Mason *et al.*, 2005; Mason *et al.*, 2008; Wiedmann *et al.*, 2014). High functional dispersion among zooplankton in the subarctic NE Pacific may represent communities during ‘warm’ water years and within the coastal upwelling regions of the study area (Mackas and

Galbraith, 2002; Peterson, 2009; Galbraith and Young, 2019; Venello et al., 2021), where converging water masses may increase niche differentiation. Typically, endemic copepod species in the region are omnivorous-herbivorous. With increased temperatures the abundance/biomass of gelatinous and carnivorous zooplankton expand, increasing the degree of the omnivorous/carnivorous niche within the community.

In contrast, low *FDis* communities may indicate a zooplankton assemblage with a lower abundance of unique trait combinations, a greater degree of niche overlap, and/or a reduction in niche space filled by the community as a whole (Gerisch *et al.*, 2012; Gusmao *et al.*, 2016, Josué *et al.*, 2019). Therefore, low *FDis* communities may have a limited capacity to adapt to environmental changes as they are comprised of many species which are functionally redundant and occupy similar functional roles (Wiedmann *et al.*, 2014). Additionally, low *FDis* would also be less sensitive to species loss due to this redundancy.

In the present study, a low *FDis*, high TTE community is best represented by zooplankton species that fall within two functional groups: Omnivore-Herbivores and Active Ambush Omnivores. Members of these groups can fill the same functional role, replacing each other in abundance depending on 'warm' or 'cool/normal' years (Venello *et al.*, 2021a). This niche overlap or reduction in niche space could also occur within the Oceanic and high nutrient low chlorophyll (HNLC) conditions in the study area, where species need to have common functional features (Wiedmann *et al.*, 2014) that allow them to use non-traditional energy pathways (i.e. the microbial loop) and non-diatom phytoplankton prey (Boyd and Harrison, 1999; Harrison *et al.*, 2004; Harris *et al.*, 2009). The ability to tolerate a variable diet may be essential in a changing environment especially as changes to phytoplankton quality and

availability may affect zooplankton functional diversity (Chapin *et al.*, 2000). In a Brazilian Lake ecosystem, phytoplankton composition was significantly related to zooplankton traits and *FDis* where eutrophication led to changes in the composition of zooplankton traits, effectively filtering out zooplankton that could not utilize cyanobacteria as a prey source (Josué *et al.*, 2019).

Additionally, oligotrophic and/or nutrient limited regions can be very efficient at transferring energy. For example, oligotrophic regions, in the Atlantic Ocean were found to be fairly efficient at transferring energy (San Martin *et al.*, 2006) as they show higher stability and a tighter coupling between phytoplankton and zooplankton via grazing (Calbet, 2001). Similarly, the sub-antarctic Southern Plateau region of New Zealand, where primary production is low and there is high activity of the microbial loop with a long-chain food web, experiences average transfer efficiencies of 23% (Bradford-Grieve *et al.*, 2003). Conversely, high variability in productivity off the west coast of Vancouver Island (Boyd and Harrison, 1999; Harrison *et al.*, 2004; Harris *et al.*, 2009; Venello *et al.*, 2021b), could also lead to weakly structured food webs with fast inefficient biomass transfers (Odum, 1969). The combination of high spatio-temporal variability in production and advective diffusion of zooplankton results in weak coupling between primary producers and consumers which lowers TTE (San Martin *et al.*, 2006; du Pontavice *et al.*, 2020). Moreover, phytoplankton blooms in productive areas, such as the west coast of Vancouver Island, may not be strongly controlled by consumers, thereby allowing excess particles to sink out of the surface waters, which would also contribute to lower transfer efficiency (Cushing, 1971, 1973; Parsons, 1988; San Martin *et al.*, 2016). In fact, TTE has been broadly predicted to decrease in coastal upwelling areas under future warming scenarios-

including increased eutrophication, acidification, stratification, and changes to community composition (Calbet *et al.*, 2014; du Pontavice *et al.*, 2020).

4.5.3 Implications for Higher Trophic Levels

Lower transfer efficiency can occur when species abundances increase at the edges of trait space, *i.e.* the abundance of the most different trait combinations increase (*FDiv*) (Schleuter *et al.*, 2014). For example, ‘The Blob’ a warm water mass within the subarctic NE Pacific, (Bond *et al.*, 2015; Tseng *et al.*, 2017) in 2014/2015 was characterized by large increases in the abundance and biomass of the doliolid *Dolioletta gegenbauri*, a warm-water oceanic species that is usually rare in the region, as well as other gelatinous zooplankton (Galbraith and Young, 2019; Venello *et al.*, 2021a). As highly efficient filter feeders, doliolids have the ability to rapidly clear the water column of phytoplankton, thereby potentially redirecting the flow of energy within the subarctic NE Pacific to phytoplankton-gelatinous zooplankton. This could provide an alternate energy pathway that may not be fully utilized in a system that is usually dominated by phytoplankton-crustacean zooplankton trophic interactions (Gibson and Paffenhöfer, 2000; Parsons and Lalli, 2002; Lynam *et al.*, 2005; Purcell, 2005; Purcell *et al.*, 2007; Richardson *et al.*, 2009). High functional dispersion/divergence and the subsequent changes to community composition could also have significant implications for higher trophic levels, despite highly efficient energy transfer when TTE is above the assumed average of 10%. For instance, shifts from a high abundance of crustacean zooplankton species to more gelatinous/carnivorous species may reduce the prey quantity and quality for ecologically and economically important fish and seabird species that typically consume crustacean zooplankton (Miller *et al.*, 1984;

Hunt *et al.*, 2005; Tsuda *et al.*, 2004; Jahncke *et al.*, 2005). In addition, a warmer environment will likely favor smaller, faster growing copepod species (i.e. southern and carnivorous species) which may potentially decrease the efficiency of biomass transfer due to higher metabolic rate requirements that lead to higher respiration losses (Palomares and Pauly, 1998; Heilmayer *et al.*, 2004; Pörtner *et al.*, 2012; Barneche and Allen, 2018). Additionally, these southern species may be considered a less desirable prey source as they are usually less lipid-rich than subarctic and boreal-shelf counterparts (Tsuda *et al.*, 2004; Yamada *et al.*, 2016). Therefore, increases in the abundance of non-endemic copepod and gelatinous zooplankton species may increase the functional diversity of the community while simultaneously decreasing the efficiency with which energy is transferred. This may not be reflected in the TTE estimates presented here as they are restricted to chitobiase-based estimates of crustacean zooplankton production rates, which only include moulting crustacean zooplankton. Therefore, non-moulting crustacean developmental stages as well as production by gelatinous zooplankton production should be included in TTE moving forward, and especially in areas heavily influenced by climate change. These community members could be accounted for by using approaches such as RNA:DNA ratios as an index of somatic growth and egg production (Gorokhova, 2003; Yebra *et al.*, 2011) or aminoacyl-tRNA synthetases (AARS) assays as another somatic growth index (Yebra and Hernández-León, 2004) in conjunction with chitobiase production rates.

4.6 Conclusion

With more frequent and persistent anomalous warm water events occurring in the NE Pacific (Chandler *et al.*, 2016, 2017), continued warming may start to act as an environmental filter,

selecting for species whose functional traits will allow them to be successful under more severe warming scenarios in the future (Leibold *et al.*, 2004; Valdivia *et al.*, 2016;). Such changes to community assemblages may or may not result in negative responses in TTE since, as shown here, zooplankton communities in the NE Pacific can be both functionally similar or dissimilar while still efficiently transferring energy. This result corroborates findings along a productivity gradient in the Atlantic Ocean, where productive waters were no more efficient at transferring energy than were oligotrophic regions, making TTE invariable with increases in regional productivity (San Martin *et al.*, 2006). However, a more functionally dissimilar zooplankton community within the subarctic NE Pacific may impact higher trophic levels that rely on certain prey types, since decreases in abundance of endemic copepod species may be detrimental to ecologically and economically important fish, sea-bird and mammal species.

Increases in the abundance of gelatinous zooplankton and non-endemic crustacean zooplankton may alter this traditional energy pathway (i.e. phytoplankton-lipid-rich crustacean zooplankton-fish), by either storing less energy in crustacean zooplankton (less lipid rich) or sequestering it within gelatinous animals which appear to have few predators. Despite potential changes to traditional energy pathways when $FDis/FDiv$ is high, the subarctic NE Pacific is efficient in transferring energy from phytoplankton to crustacean zooplankton when the zooplankton community is both functionally similar and dissimilar. However, more energy may move to higher trophic levels when the community is most similar, comprised of mostly of endemic copepod species.

Chapter 5. Conclusions

5.1 Research Summary and Significance

The main objectives of this thesis were to assess regional variability in crustacean zooplankton production rates (BPR), link changes in zooplankton community composition and diversity to ecosystem function (i.e. production rates and energy transfer), and identify drivers of variation in BPR, functional group biomass, and trophic transfer efficiency (TTE). By utilizing the Institute for Ocean Sciences zooplankton database, collecting routine estimates of crustacean zooplankton production rates, and using those to estimate energy transfer, this thesis has tested some of the key assumptions that are often made in zooplankton ecological studies.

Results from Chapter 2 showed functional differences in the zooplankton community composition over time, where increasing temperatures and more frequent marine heat waves have combined to alter the zooplankton community. Marine heat waves have occurred repeatedly in the years since the most recent anomalous warm water event (“The Blob”) in 2014/2015 (State of the Pacific Ocean Meeting, 2020), seemingly preventing zooplankton community composition to return to its pre-blob state. Changes to community composition not only alter the functional roles of zooplankton (Figure 2.4) but also impact ecosystem functions such as production rates (Figure 3.5) and energy transfer (Figure 4.2).

Chapter 3 represents one of the first attempts to quantify drivers of regional variability in community-level estimates of crustacean zooplankton production rates for marine ecosystems. These community-level estimates have differing regional responses to sea surface temperature, satellite chlorophyll *a* concentration, and developing crustacean zooplankton biomass (Table 3.2, Table 3.4, Figures 3.6-3.11). Most notable within this chapter is the

implication that a high biomass of developing crustaceans doesn't necessarily equate to high crustacean zooplankton biomass production rates. This is especially true for communities with either a low proportion of developing copepod biomass with more late-stage members (CIV and CV) or a higher proportion of developing biomass of 'other' crustaceans that will have longer inter-moult periods and will release chitobiase less frequently. Zooplankton community composition in years during and since "The Blob" consisted of low endemic copepod biomass (especially from the subarctic taxonomic group), an increased biomass of smaller copepod species - leading to low BPR. In contrast, the "pre-blob years" were characterized by higher production rates, higher developing copepod biomass and a community composition that was dominated by subarctic and boreal-shelf copepods. Copepod groups have responded to differing temperature regimes in the past (Mackas and Galbraith, 2002a; Mackas *et al.*, 2004; Galbraith and Young, 2019); however, recent conditions from "The Blob" have also altered biomass contribution from gelatinous zooplankton (Figure 2.4). However, Chapter 3 highlights negative effects of these shifts in community composition on crustacean zooplankton production rates and potentially negative impacts to higher trophic levels.

Lastly, Chapter 4 used community-level crustacean production rates and net community production rates to estimate trophic transfer efficiencies (TTE) within the region. This study is one of the first to link a widely-accepted measure of ecosystem function (TTE) to biodiversity for marine zooplankton. Functional and taxonomic diversity indices such as species evenness, functional dispersion, and functional divergence, as well mixed layer depth, explained significant variation in TTE (Table 4.6). TTE declined with increased species evenness and functional divergence. However, TTE was high at both low and high functional dispersion.

Therefore, these abundance-based diversity indices (species evenness, functional dispersion, and functional divergence) may hold greater explanatory power than measures of richness (taxonomic or functional) in understanding how marine ecosystems function.

To date there is still a need to more fully resolve the processes that control TTE, especially since slight variations in TTE can propagate through ecosystems and have large effects on food availability for higher trophic levels (Eddy *et al.*, 2021). In fact, several of the outstanding points highlighted by Eddy *et al.*, (2021) as future directions have been explored within this thesis, these include 1) new data acquisition methods to improve transfer efficiency estimates, 2) spatiotemporal variation in TTE for different species and functional groups and factors explaining this variation, and 3) TTE response to changes in species distributions and the processes needed to more fully resolve TTE within ecosystem models. Therefore, one of the main contributions this thesis makes to the current literature is the use of routine rate-based estimates of TTE made by empirical measurements and the attempt to understand processes controlling TTE variation in the subarctic NE Pacific by 1) using chitobiase based crustacean zooplankton production rates and net community production rates to estimate TTE, 2) attempting to understand spatiotemporal variability in TTE, and 3) making linkages between zooplankton diversity and community composition (from both a functional and geographic-taxonomic perspective) and TTE. Understanding the spatial and temporal variability in TTE is crucial and knowing under what conditions TTE changes (above or below the assumed 10% average) is important. Especially as slight shifts in TTE can lead to large differences in the abundance of top predators (Jennings and Collingridge, 2015; Stock *et al.*, 2017; Moore *et al.*, 2018; Eddy *et al.*, 2021). Chapter 4 also highlights how changes in

community composition can affect ecosystem function. In terms of community composition, 'high' TTE communities were found to be significantly different from those with 'low' TTE, driven primarily by differences in the abundance of Omnivore-Herbivores and Active Ambush Omnivores (Table 4.7, Figure 4.6). These functional groups included all of the copepod groups (subarctic, boreal-shelf, southern, *C. abdominalis*, *C. pacificus* and *Oithona spp.*) as well as some 'other' crustaceans from Chapter 3, further highlighting how changes in composition can alter ecosystem function. As such, the reorganizing of zooplankton communities as a response to ocean warming and/or reoccurring marine heat waves has the potential to transform how the subarctic NE Pacific marine ecosystem functions, creating a potential "new normal" in which the zooplankton community is dominated by small, carnivorous copepods and gelatinous zooplankton as opposed to the endemic large, lipid-rich subarctic/boreal copepod species. The presence of euphausiid species may represent an alternative pathway for some marine species, but may constitute a second-class prey item to others, such as nesting seabirds (Hipfner *et al.*, 2020). These changes may propagate upward to higher trophic levels resulting in reduced amounts of quality prey items which in turn may be detrimental to the growth and survival of upper level organisms.

5.2 Challenging Ecological Assumptions

Routine estimates of community-level measures of ecosystem function can help to challenge long-standing ecological assumptions and to more accurately assess the structure and function of marine zooplankton communities. Traditional zooplankton production rate methods are time-consuming, labor intensive and are limited to a species/population-specific point of view

(Runge, 1984; Kimmerer and Mckinnon, 1987; Peterson *et al.*, 1991; Poulet *et al.*, 1995).

Empirical production rate models also assume an ‘average’ global growth rate based on a select size range of copepod species and are not a measure of ‘community-level’ production rates, *per se* (Huntley and Lopez, 1992 etc). These models are then applied using bulk biomass estimates, where traditional sampling techniques used to assess zooplankton abundance and biomass can be biased, excluding smaller copepod species and early developmental stages to the detriment of both biomass and biomass-based production estimates (Gallienne & Robins 2001).

Therefore, when community composition does not reflect this size range of copepods (CIII and below), or has an increased biomass of non-copepod crustaceans or CIV, CV copepods, global models may overestimate productivity (Suchy *et al.*, 2016, Kwong *et al.*, 2020).

The chitobiase approach used in this thesis captures the production of all actively developing members of crustacean zooplankton communities and works independently of net-based biomass estimates. As such, the chitobiase-based crustacean zooplankton production rates presented here challenge the assumption of ‘high biomass = high productivity’ especially as zooplankton community composition changes with ocean warming. This result emphasizes the idea that not every individual within a zooplankton community is developing at the same rate, both between and among species (Hirst and Sheader, 1997). While expanding the ability to assess zooplankton production rates, the chitobiase approach is not without its limitations, being restricted to actively developing crustaceans which excludes pre-adult copepods packing on lipids for overwintering as well as egg production. Crustacean zooplankton eggs are chitinous and may therefore release some chitobiase during hatching, however this is still unproven. Furthermore, chitobiase production rate estimates do not include non-crustacean

zooplankton, which may have been an issue during “The Blob” years as well as into the future if these conditions keep occurring. Finally, increases in euphausiids and non-copepod crustaceans (i.e. which may moult less frequently than early developing stages of copepods) could contribute to chitobiase production rates at differing timescales.

Additionally, the relative ease of use of the chitobiase method allows for crustacean zooplankton production rates to be estimated over a range of oceanographic conditions and in conjunction with community-level primary production methods to estimate ecosystem functions such as TTE. The TTE estimates presented here show a range in variability (0.1 - 35%) similar to previous work (e.g. Cushing 1973; Jennings *et al.* 2002; Bradford-Grieve *et al.* 2003; Trebilco *et al.*, 2013; Suchy *et al.* 2016). Mean annual TTE was below the oft-assumed 10% average (Semper, 1881; Lindeman, 1942; Gaedke and Straile 1994; Pauly and Christensen, 1995) in 2015 and 2018 (6 and 5% respectively), while above the 10% average in 2016 and 2017 (14 and 15% respectively). Therefore, an assumption of 10% efficiency under those annual conditions would be both an over- and underestimation of transfer efficiency.

Lastly, despite long-standing assumptions of the importance of richness (either species or functional) to changes in ecosystem function (Hooper *et al.*, 2005), diversity indices that include species/trait abundances, such as species evenness and functional dispersion, were significant predictors of TTE in the subarctic NE Pacific. This supports the growing evidence (Hillebrand *et al.*, 2008; Soininen *et al.*, 2012 and references therein; Boersma *et al.*, 2016; Valdivia *et al.*, 2016) that highlights the importance in the spread of abundance of species and traits rather than the absolute number of species/traits to ecosystem function. This is reflected in the relationship between TTE and *FDis*, where changes in the abundance of species with the

more extreme trait combinations can facilitate high TTE. Finally, this work also addresses the need for an increased use of functional diversity metrics in addition to traditional taxonomic indices, since functional dispersion and divergence were two of the significant explanatory variables for the differences in TTE presented in Chapter 4 (Table 4.6, Figure 4.5). For terrestrial ecosystems, functional indices (over taxonomic indices) have been shown to better explain variation in ecosystem function (Hooper and Dukes, 2004; Hooper *et al.*, 2005; Schittko *et al.*, 2014), but these studies are lacking in marine ecosystems, and especially for zooplankton.

5.3 Future Applications

The functional trait approach can provide further insight into the functioning of marine ecosystems, and one key benefit of this approach is that it can be used retroactively on already existing data sets. As such, taxonomic time series of species abundance can be used to reassess communities using functional traits. However, traits for some species may be hard to find, and trait selection will be based on the research question being asked balanced by available data. Despite these few drawbacks, future research should include both a taxonomic as well as functional perspective when it comes to zooplankton community composition within marine ecosystems. Additionally, phytoplankton community composition may also play a role in lowering transfer efficiencies, as it can act as a surrogate for food quality in which the TTE from phytoplankton to herbivores can depend on plant nutrient stoichiometry (Dickman *et al.* 2008, Peace 2015). Additionally, food quality not quantity was shown to affect crustacean zooplankton production rates (Koski and Breteler, 2003; Koski *et al.*, 2006; Jónasdóttir *et al.*, 2009; Suchy *et al.*, 2013). As such, phytoplankton taxonomy data should be collected and

analyzed in conjunction with BPR, TTE, and zooplankton community composition, as changes in the community composition of primary producers can have consequences for higher trophic levels and may reduce/facilitate energy transfer (Dickman *et al.*, 2008; Peace *et al.*, 2015).

A rather novel application for the routine use of the community-level estimates of crustacean zooplankton production rates, TTE estimates as well as the functional group approach presented here is the potentiality to better parameterize marine ecosystem models and hopefully better predict fisheries yields by better representing zooplankton dynamics within these models. In the past there have been issues regarding realistic representations of zooplankton within size-spectra and marine ecosystem models (such as end-to-end models), where including the functional characteristics of zooplankton have improved model performance (Heneghan *et al.*, 2016). Additionally, Jennings and Collingridge (2015), suggested that discrepancies between modeled and observed mesopelagic fish biomass over large spatial scales (Irigoien *et al.*, 2014) was due to the poor resolution of energy transfer in lower trophic levels. Therefore, even if a spatial or temporal average of TTE is 10%, it is critical to know the range of variation in energy transfer surrounding that average. This would help to highlight the regions and/or times of year energy transfer is above or below 10% and what species are facilitating or inhibiting the transfer of energy in marine ecosystems. Furthermore, by quantifying and identifying the drivers of spatiotemporal variation in BPR and TTE as well as identifying zooplankton functional groups, this thesis provides model metrics that can be more realistically represented. Accurately depicting zooplankton functional roles and better parameterizing production rates as well as energy transfer is of increasing importance as ocean

warming and more frequent occurrence of marine heatwaves are likely altering marine ecosystem function by changing zooplankton community composition.

Recent work has shown that filtered chitobiase samples remain stable for several weeks after sampling date if kept refrigerated (L. Hubbert, unpublished data). Therefore, we have the ability to increase the number of sampling stations as chitobiase assays can happen post-cruise as well as onboard. This development also increases the ability to get samples from anywhere as a dedicated chitobiase analyst does not need to be onboard. Sampling and storage can happen like many other water samples. As such, one suggestion for future work would be to assess BPR over finer spatial scales. This would help determine the degree of spatial variability in crustacean zooplankton production rates by establishing a ‘productivity’ sampling line within each of the oceanographic regimes found within the subarctic NE Pacific. This would help to further refine the spatial resolution and potentially allow for larger separation between sampling stations and therefore allow for chitobiase measurements to be made over large spatial scales. This spatial variability has been quantified for zooplankton community composition off the WCVI previously (Mackas, 1984); however, with a changing ocean climate, perhaps an update of spatial variability in zooplankton community composition including BPR measurements is necessary. Additionally, better resolving BPR over temporal time scales is also important especially as ocean warming can alter growth rates and phenologies of crustacean zooplankton species (Hays *et al.*, 2005; Leandro *et al.*, 2006; Sommer *et al.*, 2007; Batten and Mackas, 2009; Mackas *et al.*, 2012). Therefore, a Lagrangian “drift study” approach where BPR is sampled repeatedly over days possibly weeks to sample the same patch of water would be beneficial to further understand how BPR changes over time.

Additionally, future research should focus on further refining the trophic linkages within pelagic food-webs in the subarctic NE Pacific. Beyond increased productivity sampling, a more complete view of food-web interactions especially within a changing ecosystem are needed. In conjunction with chitinase BPR and primary productivity sampling, additional analyses such as fatty acid, total lipid, and isotopic markers are needed to tease apart interactions between species and trophic levels. By combining these methods, we can estimate variation in productivity, TTE, and see which species/functional groups are driving energy flow/storage within the subarctic NE Pacific. In Chapter 4, I identified functional and geographic-taxonomic groups driving community composition differences between high and low TTE. The next step would be to select a number of animals from these groups to conduct lipid and fatty acid analysis on, as storage type and amount differences may affect energy flow within the subarctic NE Pacific. This is particularly important when comparing southern *versus* boreal-shelf and subarctic copepod group species as well as crustacean *versus* gelatinous zooplankton. Southern copepod species have been considered less lipid-rich than their northern subarctic NE Pacific counterparts (Tsuda *et al.*, 2004; Yamada *et al.*, 2016). A recent study has highlighted that many gelatinous zooplankton species do not have the same weight-specific energy content when compared to crustacean zooplankton species, with the exception of some Gastropoda and Tunicata species (Lüskow *et al.*, 2021). In fact, Kiørbe (2013) found a bimodal distribution of zooplankton body composition where most zooplankton fall into a gelatinous or non-gelatinous category with respect to differences in water and carbon content. Therefore, additional comparisons of lipid storage type and amount would help better resolve their viability as an appropriate prey source for higher trophic levels, since past studies have indicated they usually

contain less lipids than crustacean zooplankton (Ju *et al.*, 2004; Kruse *et al.*, 2010) as well as lower energy content (Lüskow *et al.*, 2021) and carbon (Kiørbe, 2013). Fatty acid analysis for zooplankton species along the WCVI have been restricted to a single species, *Calanus marshallae* (Bevan, 2015), whereas several crustacean zooplankton species from neighboring Strait of Georgia have been examined previously (El-Sabaawi *et al.*, 2009, 2010; Costalago *et al.*, 2020). Although recent work has attempted to expand fatty acid, and total lipid analysis to more crustacean zooplankton species as well as chaetognaths (Stevens *et al.*, *in review*), lipid analysis for other gelatinous zooplankton species is still needed. Chapter 2 and 3 have shown increased abundance and biomass of gelatinous zooplankton off the WCVI (possibly to the detriment of crustacean zooplankton) since 2015, including such taxa in any fatty acid, lipid or isotopic analysis is critical moving forward so we can assess their role in our ecosystem. Finally, incorporating additional biochemical production rate methods such as AARS would allow for estimations of non-crustacean production rates as well. This would help to provide a more complete picture of all secondary production rates not just for crustacean zooplankton, especially if increases in gelatinous zooplankton continue.

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Appendices

Appendix A: References for Species Trait Information Listed in Table 2.2 for Chapter 2

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Appendix B: Generalized Additive Model (GAM) Smooths Between Functional Group Biomass Anomalies and Significant Variables for Chapter 2

Appendix C: List of Stations Within a Region Used to Average SST and Crustacean Zooplankton Biomass for Chapter 3

Region Stations	Latitude (°N)	Longitude (°W)
IS_SVI		
P1	48.575	-125.5
P2*	48.6	-126
A2*	48.378333	-126.06333
B5*	48.676667	-125.77083
B7*	48.533333	-125.59167
B8*	48.575	-125.5
C1	48.482167	-125.255
C2*	48.436667	-125.155
C3*	48.390833	-125.34667
D1*	48.9725	-125.7842
D2*	48.8860	-125.9500
E1*	48.5283	-125.0633
E2	49.0717	-126.0750
E4	48.528333	-125.06333
LB01	48.673333	-124.99133
LB02	48.65	-125.04
LB03	48.622	-125.093
LB04	48.5945	-125.14533
LB05	48.566667	-125.2
LB06	48.536333	-125.2585
LB07	48.478	-125.36833
LB08*	48.421667	-125.4775
LB09	48.366667	-125.58
LB10	48.3095	-125.68917
LC01	48.840667	-125.46217
LC02	48.811333	-125.51583
LC03	48.7825	-125.57067
LC04*	48.723833	-125.68
LC05*	48.665667	-125.79
LC06*	48.607667	-125.9
LC07	48.549333	-126.00833
LC08/A1*	48.490833	-126.11833
LD01	49.002	-125.73
LD02	48.973	-125.784
LD03	48.944	-125.84
LD04	48.886	-125.95
LD05	48.828	-126.06
LD06	48.77	-126.17

LD07	48.711	-126.28
LG01	49.341667	-126.58333
LG02*	49.311667	-126.635
LG03	49.25	-126.72833
LG04*	49.188333	-126.82333
LG05	49.123333	-126.92167
SBS_SVI		
P3	48.625	-126.33333
P4*	48.65	-126.66667
P5	48.6916667	-127.16667
LB11	48.253333	-125.79583
LB12	48.215333	-125.865
LB13	48.176667	-125.93533
LB14	48.141333	-126
LB15	48.072667	-126.141
LB16	48.008833	-126.28333
LC09*	48.432333	-126.22833
LC10	48.373333	-126.33667
LC11	48.315833	-126.445
LC12/A4*	48.25	-126.66667
LD08	48.653	-126.39
LD09	48.595	-126.5
LD10	48.537	-126.61
LD11*	48.479	-126.716
LG06	49.058333	-127.02
LG07*	48.99	-127.12
LG08	48.921667	-127.22167
LG09*	48.853333	-127.32333
IS_NVI		
LJ01	49.738333	-127.04167
LJ02*	49.71	-127.08833
LJ03	49.651667	-127.185
LJ04*	49.591667	-127.28167
LBP1	50.08	-127.88
LBP2*	50.066667	-127.90333
LBP3*	50.053333	-127.92167
CS03*	50.76	-129.33333
CS04	50.82	-129.21667
CS05*	50.933333	-129
CS06*	51	-128.86333
CS07*	51.075	-128.73333
CS08*	51.141667	-128.6
CS09*	51.208333	-128.46667
CS10*	51.275	-128.33333

SBS_NVI		
	LJ05	49.527667
	LJ06*	49.465
	LJ07	49.400833
	LJ08*	49.335167
	LJ09	49.267833
	LBP4	50.023333
	LBP5*	50
	LBP6*	49.936667
	LBP7*	49.873333
	LBP8*	49.81
	LBP9*	49.7500
	CS00*	50.461
	CS01*	50.581667
	CS02*	50.688333
	LQ03	50.661833
	JI22*	50.663667
Oceanic		
	P6	48.7433333
	P7	48.7766667
	P8*	48.8166667
	P9	48.8566667
	P10	48.8933333
	P11	48.9333333
	P12*	48.97
	P13	49.1233333
	P14	49.1233333
	P15	49.2
	P16*	49.2833333
	P17	49.35
	P18	49.4333333
	P19	49.5
	P20*	49.5666667
	P21	49.6333333
	P22	49.7
HNLC		
	P23	49.7666667
	P24	49.8366667
	P25	50
	P35	50
	P26*	50

SST from CTD profiles were collected at all listed stations. * denotes all stations where zooplankton samples were collected. **Bold-italic** font note stations where BPR was also estimated.

Appendix D: Chitobiase Station Sampling Information for Chapter 3

Cruise and Stations	Region	Sample Depths (m)
<i>La Perouse May 2005</i>		
LC04	IS_SVI	5, 10, 25, 50
LC09	SBS_SVI	5, 10, 25, 50
LG02	IS_SVI	5, 10, 25, 50
LG09	SBS_SVI	5, 10, 25, 50
CS07	IS_NVI	5, 10, 25, 50
CS01	SBS_NVI	5, 10, 25, 50
<i>Line P June and August 2005</i>		
P4	SBS_SVI	5, 10, 25, 50
P12	Oceanic	5, 10, 25, 50
P20	Oceanic	5, 10, 25, 50
P26	HNLC	5, 10, 25, 50
<i>La Perouse September 2005</i>		
LC04	IS_SVI	5, 10, 25, 50
LC09	SBS_SVI	5, 10, 25, 50
LG02	IS_SVI	5, 10, 25, 50
LG09	SBS_SVI	5, 10, 25, 50
CS07	IS_NVI	5, 10, 25, 50
CS01	SBS_NVI	5, 10, 25, 50
<i>La Perouse September 2009</i>		
LC04	IS_SVI	5, 15, 25, 50, 75, 100
LC09	SBS_SVI	5, 15, 25, 75, 150, 250
CS07	IS_NVI	5, 10, 25, 50
CS01	SBS_NVI	5, 15, 25, 75, 150, 250
<i>La Perouse September 2010</i>		
LC04	IS_SVI	5, 15, 25, 50, 75, 100
LC09	SBS_SVI	5, 15, 25, 75, 150, 250
LG02	IS_SVI	5, 15, 25, 50, 75, 90
LG09	SBS_SVI	5, 15, 25, 75, 150, 250
CS07	IS_NVI	5, 10, 25, 50
CS01	SBS_NVI	5, 15, 25, 75, 150, 250
<i>La Perouse September 2011</i>		
LC04	IS_SVI	5, 15, 25, 50, 75, 100
LC09	SBS_SVI	5, 15, 25, 75, 150, 250
LG02	IS_SVI	5, 15, 25, 50, 75, 90
LG09	SBS_SVI	5, 15, 25, 75, 150, 250
CS07	IS_NVI	5, 10, 25, 50
CS01	SBS_NVI	5, 15, 25, 75, 150, 250
<i>La Perouse May 2015</i>		
LB08	IS_SVI	5, 10, 20, 50, 100, 134
LC04	IS_SVI	5, 10, 20, 50, 150
LC09	SBS_SVI	5, 10, 20, 50, 150, 250
LD11	SBS_SVI	5, 10, 20, 50, 150, 250
LG02	IS_SVI	5, 10, 20, 50, 90
LBP3	IS_NVI	5, 10, 20, 50, 150
CS09	IS_NVI	5, 10, 20, 50, 150, 175
CS02	SBS_NVI	5, 10, 20, 50, 150, 250

<i>La Perouse September 2015</i>		
LB08	IS_SVI	5, 10, 20, 50, 150
LC04	IS_SVI	5, 10, 20, 50, 150
LC09	SBS_SVI	5, 10, 20, 50, 150, 250
LG02	IS_SVI	5, 10, 20, 50, 90
LG09	SBS_SVI	5, 10, 20, 50, 150, 250
LBP3	IS_NVI	5, 10, 20, 50, 150
CS09	IS_NVI	5, 10, 20, 50, 150
CS02	SBS_NVI	5, 10, 20, 50, 150, 250
<i>Line P February, June, and August 2016</i>		
P2	IS_SVI	5, 10, 20, 50, 75, 100
P4	SBS_SVI	5, 10, 20, 50, 150, 250
P8	Oceanic	5, 10, 20, 50, 150, 250
P12	Oceanic	5, 10, 20, 50, 150, 250
P16	Oceanic	5, 10, 20, 50, 150, 250
P20	Oceanic	5, 10, 20, 50, 150, 250
P26	HNLC	5, 10, 20, 50, 150, 250
<i>La Perouse May 2016</i>		
LB08	IS_SVI	5, 10, 20, 50, 75, 100
LC04	IS_SVI	5, 10, 20, 50, 100, 150
LC09	SBS_SVI	5, 10, 20, 50, 150, 250
LG02	IS_SVI	5, 10, 20, 50, 75, 90
LG09	SBS_SVI	5, 10, 20, 50, 150, 250
LBP3	IS_NVI	5, 10, 20, 50, 100, 150
LBP8	SBS_NVI	5, 10, 20, 50, 150, 250
CS09	IS_NVI	5, 10, 20, 50, 100, 150
CS02	SBS_NVI	5, 10, 20, 50, 150, 250
<i>La Perouse September 2016</i>		
LB08	IS_SVI	5, 10, 20, 50, 75, 100
LC04	IS_SVI	5, 10, 20, 50, 100, 150
LC09	SBS_SVI	5, 10, 20, 50, 150, 250
LD09	SBS_SVI	5, 10, 20, 50, 150, 250
LG02	IS_SVI	5, 10, 20, 50, 75, 90
LG09	SBS_SVI	5, 10, 20, 50, 150, 250
LBP3	IS_NVI	5, 10, 20, 50, 100, 150
LBP8	SBS_NVI	5, 10, 20, 50, 150, 250
CS09	IS_NVI	5, 10, 20, 50, 100, 150
CS02	SBS_NVI	5, 10, 20, 50, 150, 250
<i>Line P February, June, and August 2017</i>		
P2	IS_SVI	5, 10, 20, 50, 75, 100
P4	SBS_SVI	5, 10, 20, 50, 150, 250
P8	Oceanic	5, 10, 20, 50, 150, 250
P12	Oceanic	5, 10, 20, 50, 150, 250
P16	Oceanic	5, 10, 20, 50, 150, 250
P20	Oceanic	5, 10, 20, 50, 150, 250
P26	HNLC	5, 10, 20, 50, 150, 250
<i>La Perouse May and September 2017</i>		
LB08	IS_SVI	5, 10, 20, 50, 75, 100
LC04	IS_SVI	5, 10, 20, 50, 100, 150
LC09	SBS_SVI	5, 10, 20, 50, 150, 250

LG02	IS_SVI	5, 10, 20, 50, 75, 90
LG09	SBS_SVI	5, 10, 20, 50, 150, 250
LBP3	IS_NVI	5, 10, 20, 50, 100, 150
LBP8	SBS_NVI	5, 10, 20, 50, 150, 250
CS09	IS_NVI	5, 10, 20, 50, 100, 150
CS02	SBS_NVI	5, 10, 20, 50, 150, 250
<i>Line P February, June, and September 2018</i>		
P2	IS_SVI	5, 10, 20, 50, 75, 100
P4	SBS_SVI	5, 10, 20, 50, 150, 250
P8	Oceanic	5, 10, 20, 50, 150, 250
P12	Oceanic	5, 10, 20, 50, 150, 250
P16	Oceanic	5, 10, 20, 50, 150, 250
P20	Oceanic	5, 10, 20, 50, 150, 250
P26	HNLC	5, 10, 20, 50, 150, 250
<i>La Perouse May and September 2018</i>		
LB08	IS_SVI	5, 10, 20, 50, 75, 100
LC04	IS_SVI	5, 10, 20, 50, 100, 150
LC09	SBS_SVI	5, 10, 20, 50, 150, 250
LG02	IS_SVI	5, 10, 20, 50, 75, 90
LG09	SBS_SVI	5, 10, 20, 50, 150, 250
LBP3	IS_NVI	5, 10, 20, 50, 100, 150
LBP8	SBS_NVI	5, 10, 20, 50, 150, 250
CS09	IS_NVI	5, 10, 20, 50, 100, 150
CS02	SBS_NVI	5, 10, 20, 50, 150, 250

Appendix E: Barplots (mean $\pm$ se) of Taxonomic and Functional Diversity Indices During Each Sampling Year for Chapter 4