ABSTRACT

Title of Thesis:	ENERGY DENSITY OF AMPELISCID AMPHIPOD POPULATIONS PREYED UPON BY GRAY WHALES IN THE NORTHERN BERING AND CHUKCHI SEAS
	Brian Patrick Marx, Master of Science: Marine, Estuarine, & Environmental Sciences, 2025
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The shallow and highly productive waters of the northern Bering and Chukchi Seas in the Pacific sector of the Arctic are able to support numerous upper trophic level predators, including benthic feeders such as the gray whale (*Eschrichtius robustus*). The Eastern North Pacific population, currently the largest population of the species, migrates thousands of kilometers from calving lagoons in Baja California, Mexico to Arctic foraging grounds to feed on numerous kinds of marine invertebrates. Historically, their primary source of food has been benthic ampeliscid amphipods (Family Ampeliscidae), which can form large, dense mats of tubes in sandy sediments on the seafloor. However, several studies have noted a decline in the biomass of these amphipods since the 1980s, particularly in the Chirikov Basin just south of Bering Strait, where they are the most abundant. Concurrently with this trend, gray whales have experienced two major Unusual Mortality Events (1999-2000 and 2019-2023), as defined by NOAA; observations of emaciated whales during these events have called into question the quality and

availability of benthic amphipods as prey for gray whales and their ability to support the gray whale population. To address these questions, the caloric contents of several of the most abundant benthic amphipod genera in this region were measured and compared to similar measurements published in studies going back as far as 1978. As part of this study, a conversion factor between frozen and formalin-preserved amphipod specimens was developed and applied to a time series of amphipod abundance and biomass (1970-2019) to better quantify how energy density of benthic amphipod communities has changed over time. The energetic content of these amphipods has not changed significantly from historical values, but the amount of biomass per square meter of seafloor available has declined drastically. For ampeliscid amphipods in the Chirikov Basin, the maximum mean energy density was 347.08 kJ m^{-2} in 1984; the minimum mean energy density was 31.07 kJ m^{-2} in 2010, a 90% decline over 26 years. These findings suggest that, while benthic amphipods are still a high-quality food source, the extensive and dense sources of energy they once provided are no longer available. In response, gray whales are venturing further north in search of prey, bypassing formerly sufficient foraging grounds.

Two supplementary (S) files of data sets are included with this thesis project, along with descriptions of each of the variables used in the dataset. File S1 consists of all the caloric measurements made for Chapter 2. File S2 is the compiled time series synthesized for Chapter 3. Some variables in the time series dataset (S2) are calculated from values in the Chapter 2 caloric data.

ENERGY DENSITY OF AMPELISCID AMPHIPOD POPULATIONS PREYED UPON BY GRAY WHALES IN THE NORTHERN BERING AND CHUKCHI SEAS

by

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data, contact Alynne Bayard (bayard@umces.edu) with the Grebmeier-Cooper Lab, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Sciences.

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File S2: The compiled time series synthesized and summarized in Chapter 3. Some variables in this file are calculated from values in File S1.

Chapter 1: Introduction

Introduction

Arctic Marine Ecosystems

Marine ecosystems of the Arctic Ocean and its surrounding marginal seas have been experiencing global climate change at an accelerated rate in recent decades (Perovich et al., 2007; Screen & Simmonds, 2010). Increasing global temperatures, driven by increasing levels of CO_2 and other radiative gases in the atmosphere, are contributing to warming of the Arctic at 2-4 times the global rate (Screen & Simmonds, 2010), shrinkage of sea ice extent, the loss of multi-year ice and ice thickness, earlier sea ice melt in spring, and later sea ice formation in autumn (Arrigo & van Dijken, 2015; Comiso et al., 2011). Warming air and sea temperatures and the loss of sea ice are also contributing to the ice-albedo feedback loop; as high-albedo ice cover is lost to darker, open ocean, less solar radiation is reflected back into the atmosphere. This heat is instead being absorbed by the oceans, increasing heat fluxes and driving further loss of sea ice (Manabe & Stouffer, 1980; Perovich et al., 2007). Pelagic and benthic ecosystems in the Arctic Ocean and surrounding marginal seas are tightly linked to sea ice dynamics and are therefore highly vulnerable to ongoing environmental changes (Cooper et al., 2012; Grebmeier et al., 2015; Pisareva et al., 2015). Indeed, the structure and function of these ecosystems are drastically changing in response to observed environmental changes (Grebmeier, 2012; Kędra et al., 2015; Mueter et al., 2021).

The high proportion of shallow continental shelves around the margins of the Arctic Ocean, extreme seasonal weather variations, low year-round temperatures, permanent and seasonal sea ice coverage, and a large supply of freshwater from surrounding rivers and melting sea ice are distinctive features of Arctic marine ecosystems (Hollowed et al., 2013). Many endemic Arctic species have adapted to these conditions and are specialists in cold-water life, meaning they are dependent on ice-associated ecosystems and their seasonal cycles (Hollowed et al., 2013; Tu et al., 2015). Warming temperatures and the drastic loss of sea ice, driven by global climate change, have been described as the primary "footprints", or signals, observed in Arctic marine ecosystems. Consequences of these signals include shifts in biogeographical ranges, alterations to community production and stock size, changes in community compositions, phenological shifts, and physiological and behavioral changes (Brandt et al., 2023). These primary footprints have also developed into secondary effects, such as alterations to diets, restructuring of competitive relationships, and a changing pathogen load in Arctic waters (Brandt et al., 2023). Changes have been noted at all trophic levels and are driving the restructuring of food webs in these vulnerable ecosystems (Kędra et al., 2015; Mueter et al., 2021; Olsen et al., 2019).

Trophic interactions and food webs

Shallow marginal seas overlying the continental shelves and surrounding the deep Arctic Ocean basin are home to highly productive benthic communities, particularly in the Pacific sector (Feng et al., 2021; Grebmeier et al., 2006a). Benthic production in the northern Bering and Chukchi Seas supports numerous upper trophic-level predators, small-scale commercial and artisanal fishing, and subsistence harvests for small coastal communities in Russia and Alaska

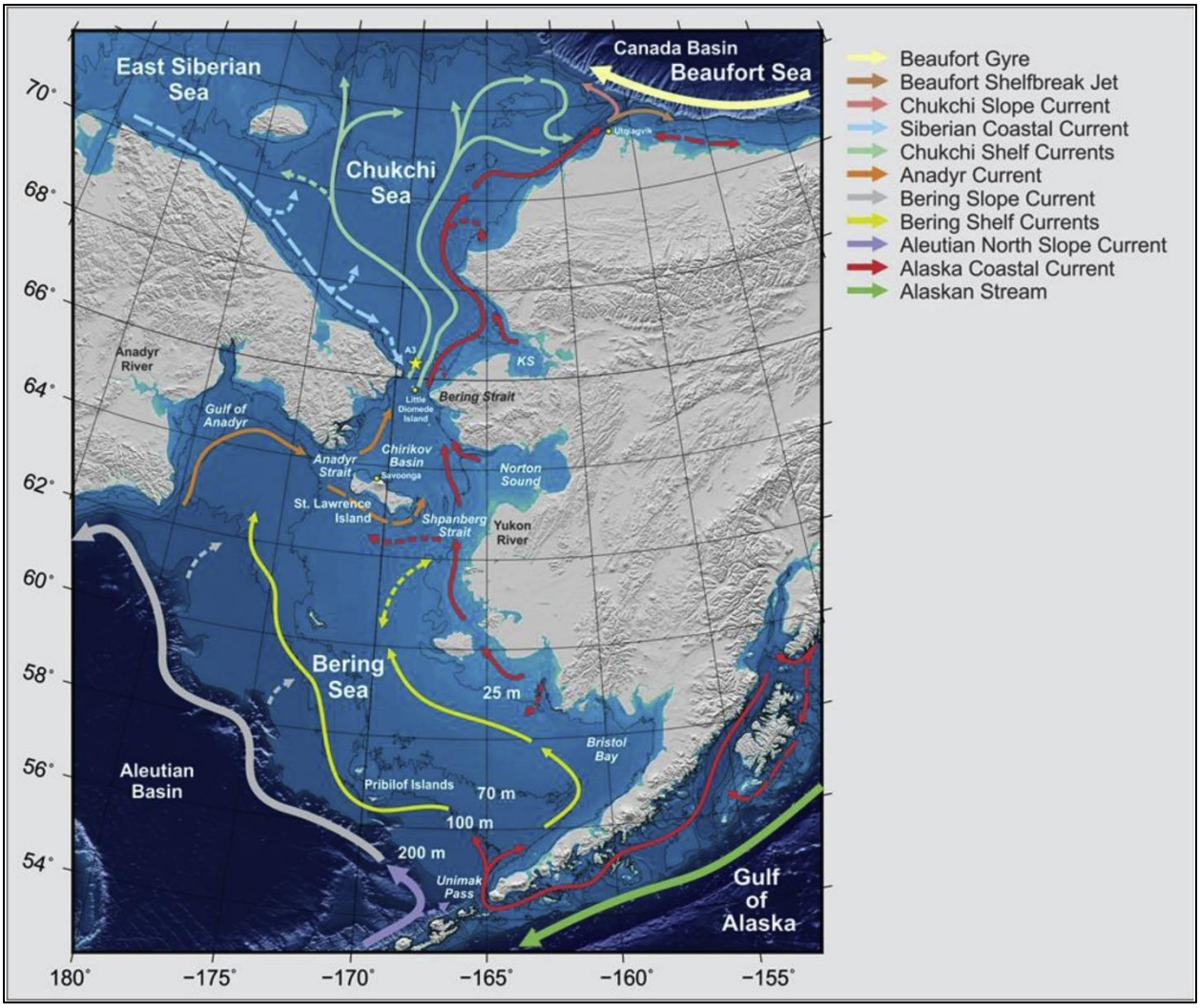

Figure 1.1: Location map of the Pacific Arctic region with water body and place names. Persistent currents are shown with solid arrows; intermittent or poorly known flows are denoted with dashed arrows. Bering Strait mooring A3 is marked with a yellow star. Abbreviation KS denotes Kotzebue Sound. Depth isopleths are contoured with thin black lines at 25, 70, 100 and 200 m. (Figure 1 in Danielson et al., 2020)

(Danielson et al., 2020). These productive benthic communities, in turn, are supported by organic carbon supplied by ice-associated and seasonal primary production through tightly linked benthic-pelagic coupling (Tu et al., 2015; Wilt et al., 2014). Nutrient-rich Pacific water advected north via the Anadyr Current fuels blooms of primary production, particularly in the northern Bering Sea, in between St. Lawrence Island and Bering Strait, and in the southern Chukchi Sea, in the waters north of Bering Strait (Cooper & Grebmeier, 2022; Frey et al., 2023) (Figure 1.1).

This tight coupling fuels hotspots of high benthic biomass, where hydrographic and sediment conditions are favorable; these hotspots are prime foraging grounds for a variety of benthic-feeding predators, such as diving sea ducks, walrus, fish, seals, and gray whales (Denisenko et al., 2015; Grebmeier et al., 2006b). The characteristically short length of many Arctic marine food chains keeps transfer efficiency relatively high, supporting large populations of endemic and seasonal predators (Grebmeier, 2012; Iken et al., 2010). However, in tandem with ecosystems around the globe, Arctic marine ecological structure in the Pacific influenced sector has been undergoing changes across trophic levels in response to anthropogenic climate change (Duarte et al., 2012; Kędra et al., 2015).

One of the more concerning changes is the disruption and restructuring of benthic-pelagic coupling in the shallow seas of the Pacific sector, such as the northern Bering and Chukchi shelves (Grebmeier, 2012). Historically, primary production in Arctic waters has been comprised mostly of lipid-rich diatoms and small- to medium-sized flagellates growing along the ice edge (Duarte et al., 2012; Giesbrecht et al., 2019); the larger, heavier diatoms sink relatively quickly, exporting large amounts of lipid-rich organic matter to the seafloor before zooplankton have a chance to graze heavily on the bloom (Duarte et al., 2012; Iken et al., 2010). As sea ice extent contracts northward, warmer open waters left behind are more favorable to smaller phytoplankton, such as dinoflagellates and coccolithophores (Giesbrecht et al., 2019). These smaller cells sink much more slowly than diatoms and larger, heavier phytoplankton, so they stay in the water column longer where they are processed by microbes and grazed upon by zooplankton (Duarte et al., 2012). The longer this organic carbon stays in pelagic trophic pathways, the lower the quality of food that is finally available to the benthos (Kędra et al., 2015). A shift from a benthic-dominated system to a pelagic-dominated system is one of several

contributing factors to declining benthic biomass in several hotspots throughout the Pacific sector, with consequences for upper trophic levels (Grebmeier, 2012; Tu et al., 2015). For example, a decline in dominant clam populations in the northern Bering Sea has been tied to a decline in spectacled eider populations (Grebmeier, 2012).

Another concerning trend in Arctic marine ecosystems in response to anthropogenic climate change is borealization, the shift of subarctic and temperate species northward into regions where they are not endemic, due to warming temperatures (Fossheim et al., 2015; Mueter et al., 2021). As Arctic species decline in biomass and abundance in response to environmental changes, warming waters allow a variety of organisms to travel further northward, potentially filling ecological niches left vacant (Ershova et al., 2015; Fossheim et al., 2015). Throughout the Arctic, this has been documented at most trophic levels, including plankton, invertebrates, fish, and marine mammals (Ershova et al., 2015; Fossheim et al., 2015; Hauser et al., 2018; Mueter et al., 2021). The introduction of new species to an area can create competition for resources, especially when the newcomers are generalists competing with endemic Arctic specialists (Bluhm & Gradinger, 2008; Fossheim et al., 2015; Hollowed et al., 2013). Species shifting northward can also bring along new pathogens and parasites, or the introduced species may become invasive in certain circumstances if they are able to establish reproductive populations (Chan et al., 2018). As ecosystems and food webs change and restructure in response to environmental changes, it is critical to understand how trophic pathways are functioning and how much energy is moving along these pathways (Kędra et al., 2015).

Ecosystem monitoring in the Pacific Arctic: Pacific Distributed Biological Observatory

Detecting and understanding the various changes that marine ecosystems are undergoing in the Pacific Arctic sector has been made possible by continuous, annual sampling efforts from

various projects and institutions (Grebmeier et al., 2010). The synthesis of data from these various sources provides a time series of environmental and ecological data spanning decades, and in 2010, the Distributed Biological Observatory (DBO) was formally established to provide a framework to facilitate standardized sampling at established time series stations and transects (Grebmeier et al., 2019). The DBO has been functioning to bring together various international and national projects and data sources under one umbrella to facilitate the collection and sharing of resources and data (Grebmeier et al., 2019). This collaboration has provided evidence for the effects of climate change on ecosystems in the Pacific Arctic and the consequences it has for upper trophic level predators and the Indigenous and local communities that depend on resources from this region (Moore & Grebmeier, 2018).

The DBO was instrumental in providing the rationale and resources for this thesis project. Marine mammal observation and monitoring are key components for understanding ecosystem health and functioning in the Pacific Arctic (Moore et al., 2022; Reeves et al., 2014). The gray whale, *Eschrichtius robustus*, Lilljeborg, 1861, is a baleen whale native to the Pacific Ocean that feeds primarily on benthic crustaceans, and the shallow waters overlying the continental shelves in the northern Bering and Chukchi Seas are considered their primary foraging grounds (Brower et al., 2017). Abundance estimates have been made for the largest population of gray whales, which migrates along the western coasts of North America, since the 1960s (Eguchi et al., 2024), and marine mammal observers aboard DBO-funded cruises contribute to these estimates. Two major Unusual Mortality Events (UME), as defined by NOAA Fisheries, have been declared in recent decades (1999-2000 and 2019-2024), prompting concern over the health of gray whales and potential problems with food quality and/or quantity (Raverty et al., 2024). Since gray whales are primarily benthic feeders (Nerini & Oliver, 1983), the benthic biomass and

abundance sampling carried out by the DBO in known gray whale foraging grounds has become critical to investigating the causes behind the recent UMEs (Stewart et al., 2023). Benthic amphipods that occur in dense aggregations in the Pacific Arctic, particularly those in the family Ampeliscidae, are known to be a primary prey item for gray whales that migrate to northern foraging grounds in the northern Bering and Chukchi Seas (Bluhm & Gradinger, 2008; Nerini & Oliver, 1983).

Objectives

The objectives of this study can be summarized as having three main goals. First, this study intended to quantify the caloric content of several of the dominant benthic amphipod genera present in benthic biomass hotspots identified and monitored by the Distributed Biological Observatory in the Pacific Arctic, especially those identified as gray whale foraging habitat. Second, this study sought to develop a caloric conversion factor between amphipods that have been preserved in formalin (the standard method for preserving invertebrate field collections at sea) and those that have been frozen, approximating a "fresh" sample. Third, this conversion factor will be applied to a decades-long time series of formalin-preserved amphipod wet weight (g wet wt. m^{-2}) so that energy density per m^2 can be approximated as if the samples were collected fresh and frozen for each of the DBO regions where these taxa are dominant in the benthos. This time series of energy density per m^2 of these amphipods, which are a crucial prey source for gray whales, will presumably provide evidence for whether or not food and nutritional stress has contributed to recent gray whale UMEs.

Statement of Hypotheses & Thesis Structure

The following hypotheses were formulated in order to investigate the questions posed by this study:

Hypothesis 2.1: Preservation method does not cause a significant difference in the energy content of amphipods in the genus *Ampelisca*.

> *Alternative Hypothesis*: There is a significant difference in the energy content between frozen and formalin-preserved samples of amphipods in the genus *Ampelisca*, reflecting the abundant carbon atoms present in formalin that could contribute to apparent energy density.

Hypothesis 2.2: There is no significant seasonal difference in the energy content of amphipods belonging to the genus *Ampelisca* in the Pacific Arctic Region.

> *Alternative Hypothesis*: There is a significant difference between the energy content of amphipods in the genus *Ampelisca* collected in the summer and fall seasons, due to seasonal reproductive cycles, food quality, and food availability.

Hypothesis 2.3: There are no significant geographic differences in the energy content of amphipods in the genus *Ampelisca* collected in different DBO regions.

> *Alternative Hypothesis*: Amphipods in the genus *Ampelisca* collected in different DBO regions have significantly different energy content due to varying environmental conditions and food quality/quantity in each region.

This thesis is organized into four individual chapters. This section, Chapter 1, introduces the background behind the study, the rationale for conducting the study, and the hypotheses that were tested in the following chapters. Chapter 2 presents the caloric measurements for the samples collected and tests hypotheses 2.1-2.3 using nonparametric comparisons. Chapter 3

describes the conversion factor that was developed to compare between frozen and formalin-preserved samples, which is then applied to the time series of amphipod wet weight, the end goal being to quantify the energy density of samples collected since 1970. Finally, Chapter 4 provides a conclusion section, including unresolved questions and potential next steps to follow this study.

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Chapter 2: Caloric measurements & analysis

Introduction

Value of caloric studies

The caloric content, or energy density, of prey or a community of prey can provide valuable insights into trophic transfers through food webs, the nutritional quality of food that a predator is consuming, and the impacts of predation on a prey population (Percy & Fife, 1981; Lawson et al., 1998). The caloric content of an organism is determined by its biochemical makeup; for example, lipids and carbohydrates tend to be more energetically dense than other compounds, such as proteins (Paine, 1973; Percy, 1979). An organism's biochemical makeup is in turn determined by many contributing factors, such as physiology, reproductive cycles, diet, competitive and parasitic interactions, and numerous other environmental variables (Paine, 1973; Wilt et al., 2014). Furthermore, caloric content can vary intra- and interspecifically, temporally, and spatially (Hildebrand et al., 2021; Lawson et al., 1998; Wacasey & Atkinson, 1987). Some organisms experience seasonal fluctuations in caloric content due to ongoing nutritional and reproductive cycles, while others maintain relatively stable caloric content throughout the year (Hildebrand et al., 2021; Percy, 1979; Tyler, 1973). Some organisms exhibit a positive relationship between body size and energy content (Lawson et al., 1998; Szaniawska & Wołowicz, 1986), a trend that could impact trophic interactions as rising global temperatures select for smaller body sizes (Daufresne et al., 2009). Investigating patterns and trends associated with the energy content of a prey item can provide insights into the health of associated

predators, from the individual to the population level (Tu et al., 2015). Within a food web, knowing the energy content of a prey item can inform estimates of how much energy is transferred to higher trophic levels (Szaniawska & Wołowicz, 1986; Tu et al., 2015). As climate change shifts biogeographical ranges, alters physiology, introduces new species, drives other species to extinction, and restructures interactions within ecosystems, understanding the quality and quantity of food available is critical to understanding the health of changing ecosystems (Daufresne et al., 2009; Kędra et al., 2015; Tu et al., 2015).

Relevance to gray whales

The gray whale, *Eschrichtius robustus*, Lilljeborg, 1861, is a baleen whale currently native to the Pacific Ocean (Brower et al., 2017). The Eastern North Pacific (ENP) population inhabits waters along the western coast of North America and is the larger of the two main populations, the other being the Western North Pacific (WNP) population, which inhabits waters along the coasts of east Asia, from the Sea of Okhotsk to southern China (NOAA Fisheries, 2024). The ENP population makes one of the longest mammalian migrations on Earth, from calving lagoons in Baja California, Mexico to summer foraging grounds in the northern Bering and Chukchi Seas, traveling as far as 14,000 miles (approximately 22,000 km) round-trip (NOAA Fisheries, 2024; Pike, 1962). A small sub-group of the ENP, referred to as the Pacific Coast Feeding Group, only migrates as far north as the Pacific Northwest, Vancouver Island, and southeastern Alaska, where they forage in shallow bays along the coast (Calambokidis et al., 2017). Being opportunistic foragers, gray whales will also stop to forage along their migration route if an adequate food source is encountered, either on the seafloor or in the water column (Bluhm et al., 2007; Moore et al., 2003). Throughout their migration, they encounter a myriad of obstacles and dangers in a rapidly changing world: increased maritime traffic from commercial

shipping, oil and gas exploration and development, tourism, increasing levels of anthropogenic noise, and increased exposure to more powerful storms (Reeves et al., 2014). Gray whales' preference for shallow coastal waters only increases their exposure to human activities and the disturbances they cause (Villegas-Amtmann et al., 2015). In addition to these growing stressors, there is also concern around the quality and quantity of food prey available while foraging (Moore et al., 2003; Stewart et al., 2023). Within the past couple decades, there have been two major Unusual Mortality Events (UME) declared by the US National Oceanic and Atmospheric Administration (NOAA); these mass stranding events, one from 1999-2000 and the second from 2019-2023, raised concern over food quality and availability due to the high number of observations of emaciated and starving whales (Stewart et al., 2023; Raverty et al., 2024).

Gray whales employ a unique feeding strategy for baleen whales. They are primarily benthic foragers, diving down to the seafloor, suctioning up sediment through the sides of their mouths, and filtering this sediment through their baleen, trapping the benthic organisms that live within the sediments (Moore et al., 2003; Nerini & Oliver, 1983). Gray whales are opportunistic foragers, switching prey types if an adequate food source is encountered, either from the sediments or in the water column (Moore et al., 2003). However, they have historically relied on dense patches of benthic ampeliscid amphipods (Family Ampeliscidae) located in the northern Bering Sea, particularly in the Chirikov Basin, based on sightings and dietary analysis (Nerini et al., 1980; Moore et al., 2003). This 40,000 km^2 basin just south of Bering Strait is supplied with nutrient-rich water carried northward by the Anadyr Current, fueling high levels of primary production (Coyle et al., 2007) (Figure 1.1). Organic carbon produced by this primary production led to the development of extensive mats of ampeliscid amphipod tubes, numbering as many as 40,000 individuals per square meter (Supplementary File S2). Gray whales gathered in this

region in large numbers as late as the 1980s yet have mostly abandoned these once busy foraging grounds in recent years (Bluhm et al., 2007; Moore et al., 2022). In the same time span, ampeliscid amphipod biomass in the Chirikov Basin has dropped dramatically (Coyle et al., 2007; Chapter 3, this study). While there are certainly multiple contributing factors to the recent UMEs, the fading of this once prime foraging ground is suspected of playing a major role (Moore et al., 2003; Moore et al., 2022).

The occurrence of two major UMEs, only a couple decades apart, is unusual for a long-lived cetacean such as the gray whale (Stewart et al., 2023). Major mortality events occur regularly for marine mammals for a variety of reasons, ranging from disease to pollution to negative human interactions, and are an indicator of ocean health (NOAA Fisheries, 2025). Gray whales regularly face dangers such as anthropogenic noise, harmful algal blooms, toxic spills, pollutants, predation by orcas, subsistence harvesting, and overlaps with an increasing volume of traffic within shipping lanes, so when a major mortality event occurs, it is critical to understand what has tipped the scales (Raverty et al., 2024). Observations of emaciated whales with diminished body condition during both events suggested causes relating to food quantity and quality (Moore et al., 2001; Raverty et al., 2024). Moreover, the observations are no doubt underreported, since emaciated whales that perish at sea are more likely to sink, due to severe blubber loss (Raverty et al., 2024). Furthermore, the population size of ENP gray whales was estimated to be approximately 29,960 in 2015/2016 (Eguchi et al., 2024), while their carrying capacity is estimated to be around 25,000 (Raverty et al., 2024). These observations, along with major contractions of ampeliscid amphipod populations in the Pacific Arctic and the poleward shift of gray whale foraging locations, have supported the food stress hypothesis (Stewart et al., 2023).

Benthic amphipod populations in the Pacific Arctic

Ampeliscid amphipods, primarily of the genus *Ampelisca*, are well-documented as a preferred prey item for gray whales in the Pacific Arctic (Bluhm et al., 2007; Coyle et al., 2007). These benthic, tube-building crustaceans form dense mats in sandy sediments where there is a strong supply of rich organic matter to the benthos (Highsmith & Coyle, 1992). Some of the most productive amphipod communities in the world are ampeliscid amphipod beds in the Pacific Arctic (Highsmith & Coyle, 1990). In recent decades, these ampeliscid amphipod beds have been shrinking, even disappearing; this trend has been particularly noticeable in the Chirikov Basin, once a primary foraging ground for migrating gray whales (Coyle et al., 2007; Grebmeier, 2012; Kędra & Grebmeier, 2021; Moore et al., 2022). The loss of these ampeliscid amphipod beds has dramatically reduced the standing stock of their benthic biomass in this region and has driven gray whales farther north into the Chukchi and Beaufort Seas in increasing numbers in search of food (Grebmeier et al., 2006b; Moore et al., 2022).

The decline in ampeliscid amphipod biomass has been well-documented over the past several decades (Coyle et al., 2007; Grebmeier, 2012, Grebmeier et al., 2018; Kędra & Grebmeier, 2021; Moore et al., 2022). However, only a few studies have investigated the energy density of these organisms in this particular region, these being Stoker (1978), Hondolero et al. (2012), and Wilt et al. (2014). These studies have measured caloric content for a wide variety of benthic invertebrates instead of focusing on one particular taxon; therefore, sample sizes are often quite small for some invertebrates, as small as n=1 in some cases. Caloric studies on marine invertebrates are also often conducted on formalin-preserved specimens, since this is a common method for preservation of samples collected at sea. Therefore, this study focuses some additional attention on this topic by measuring the energy density of several of the dominant

benthic amphipod genera found in the Pacific Arctic Region (PAR), particularly the genus *Ampelisca* (Family Ampeliscidae), which is an important component of the gray whale diet. Furthermore, energy density was measured for both frozen (to approximate a "fresh" sample) and formalin-preserved samples for comparison and to establish a conversion between the two in order to look at past formalin-preserved samples in a time series effort, which is explained further in Chapter 3.

Methods

Sample collections

Amphipods were collected in 2023 as part of benthic macrofaunal sampling aboard two research cruises occupying stations in the Distributed Biological Observatory (DBO) in the PAR. The first cruise occurred from July 7-27, 2023, aboard the Canadian Coast Guard Ship *Sir Wilfrid Laurier* (SWL23), and the second cruise occurred from September 10 through October 4, 2023, aboard the RV *Sikuliaq* (SKQ23). Collections were undertaken at stations where amphipods are dominant in the benthos, based on prior studies, and where there was sufficient biomass available to collect for later caloric analyses (Figure 2.1). Collections focused on four of the dominant amphipod families found in this region: Ampeliscidae, Melitidae, Pontoporeiidae, and Isaeidae. Four DBO regions were sampled for this study: DBO2 in the Chirikov Basin south of Bering Strait, DBO3 in the southern Chukchi Sea just north of Bering Strait, DBO4 in the northeastern Chukchi Sea off the coast of Wainwright, Alaska, and DBO5 in the northeastern Chukchi Sea offshore from Utqiaġvik, Alaska. DBO1, which is located to the southwest of St. Lawrence Island, is also a highly productive benthic hotspot, but this transect was not sampled due to low biomass of amphipods that occurs here.

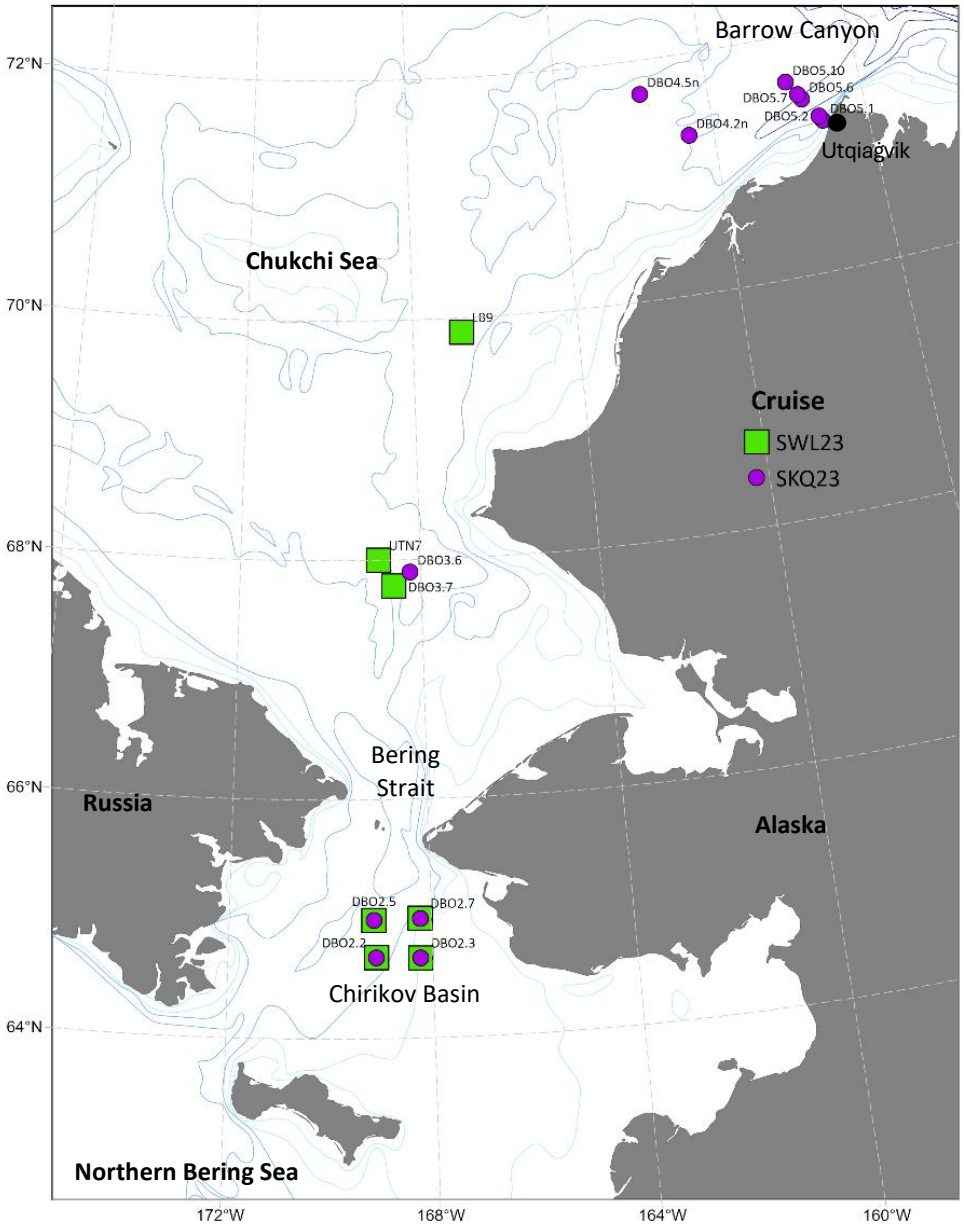

Figure 2.1: Stations sampled during 2023 for caloric analysis in this study. Stations are labelled as being sampled during SWL23 (July, green squares), during SKQ23 (Sept-Oct, purple circles), or both.

Benthic infaunal macroinvertebrates were sampled during SWL23 and SKQ23 using a weighted 0.1 m^2 van Veen grab and sieved through a 1-mm screen using seawater; amphipods were subsampled from one of the grabs after it was rinsed and transferred to a sorting tray filled with seawater. During SKQ23, additional amphipods were subsampled from the benthic epifauna collected during beam trawling with a 10 ft. (3.05 m) modified plumb staff beam trawl after they

were identified, counted, and weighed for biomass and abundance measurements; these were also kept in seawater until preservation and storage. Following preliminary identification to the lowest taxa possible and counting immediately after sampling, the amphipods were either packaged in Whirl-Pak bags and frozen in a -20° freezer or packaged in plastic containers filled with a 10% buffered seawater and formalin mixture for preservation. All samples were returned to and processed at the Chesapeake Biological Laboratory in Solomons, Maryland.

Caloric measurements

Sample processing occurred within 7 months of collection; frozen samples were kept in a -20° freezer at the Chesapeake Biological Laboratory, and formalin-preserved samples were stored with other formalin-preserved samples in sealed buckets. Following a final identification to genus, all of the collected amphipods were rinsed with deionized water, counted, and weighed before being patted dry and placed in a 60°C drying oven until a constant mass was achieved; several of the largest samples were weighed periodically, assuming they would take the longest to dry. Samples were removed singly for caloric analysis, leaving the remaining samples in the drying oven to prevent as little moisture as possible from being reabsorbed by the samples. Dried samples were ground into a fine powder using a mortar and pestle before being compressed into pellets using a Parr Instruments (Moline, Illinois, USA) pellet press and weighed. The nominal target weight for dried pellets was 0.200 g but varied based upon the amount of sample available; the mean weight of dried pellets before combustion (± one standard deviation) was 0.214±0.053 g. Sample pellets were combusted in oxygen within a Model 1109 semi-micro bomb using a Model 6200 isoperibol bomb calorimeter with an attached Model 6510 water handling system, both from Parr Instruments. The water handling system dispensed controlled volumes of water to fill the calorimeter bucket and maintain temperature, thereby increasing the precision and

reliability of calorimetry operations. The energetic equivalency of the semi-microbomb was calculated using repeated firings of 0.2 g benzoic acid (C_6H_5COOH) standards as advised by the manufacturer; a total of 24 standards were run over the course of 123 sample measurements. Corrections were applied following combustion to account for unburned fuse wire and any ash remaining after combustion.

Statistics

Summary statistics for variables in this study were calculated, including the means and standard deviations of samples by taxa, preservation method, cruise, and DBO region. Due to the skewed distribution of the data, unequal sample sizes, and uneven variability, nonparametric Kruskal Wallis rank sum tests and pairwise comparisons using Wilcoxon rank sum tests were used to quantify patterns in the data for the genus *Ampelisca*. Results of all statistical tests conducted are interpreted at the 95% confidence level. All statistical analysis was conducted using the base R programming language (v.4.2.3; R Core Team, 2023) in RStudio (v.2023.12.1); data was prepared for analysis using the tidyverse package (v.2.0.0; Wickham et al., 2019), and plots were created using the ggplot2 (v.3.4.4; Wickham, 2016) and patchwork (v.1.2.0; Pedersen, 2024) packages. Boxplots were generated using the sample mean (center line inside the box), the 25^{th} and 75^{th} percentiles (bottom and top lines of the box), the range of values (whiskers), and any outliers identified by ggplot2 (solid circles). Each individual data point was also plotted over the boxplot (open circles) using a jitter function to spread the points apart so that they would be better visible.

Results

Caloric results

A total of 123 caloric measurements were made on sample collections of the four most commonly collected amphipod families in this region: Ampeliscidae, Melitidae, Pontoporeiidae, and Isaeidae. Caloric values from genera within the family Ampeliscidae, *Ampelisca*, *Byblis*, and *Haploops*, were estimated. Caloric values from the three other amphipod families are represented by one genus each: *Melita* from Melitidae, *Pontoporeia* from Pontoporeiidae, and *Protomedeia* from Isaeidae. The means and standard deviations for each genus were determined for each preservation method (Table 2.1 & Figure 2.2), cruise (Table 2.2), and DBO region (Table 2.3).

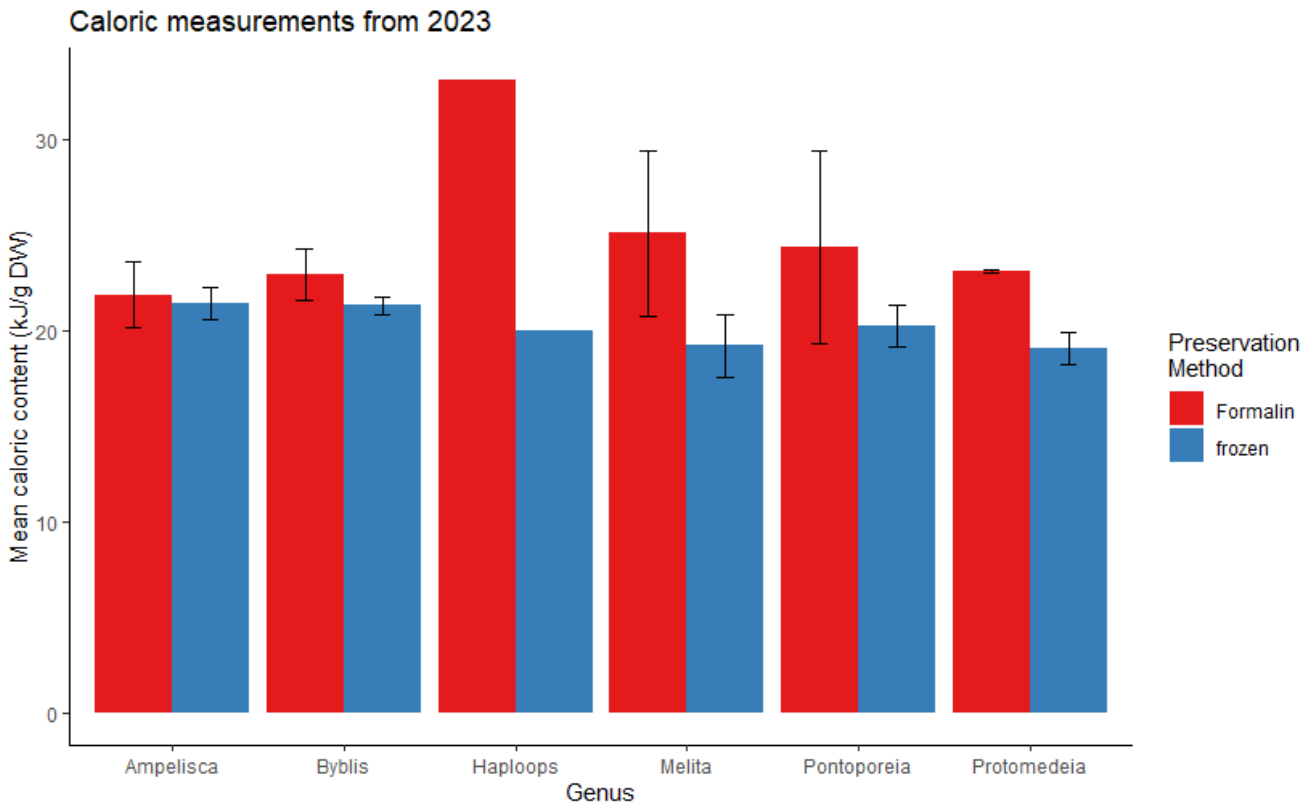

Figure 2.2: Caloric measurements in kJ g^{-1} DW (Dry Weight) for each genus collected in this study, separated by preservation method, and including ± one standard deviation where applicable.

Table 2.1: Mean energy content measurements for the six genera measured in this study in kJ/g DW (Dry Weight) for both preservation methods used (frozen, formalin). Standard deviations are included, where applicable. All measurements that means and standard deviations are calculated from are in Supplementary File S1.

Family	Genus	Preservation Method	Sample Size (n=)	Mean energy content (kJ/g DW)	Std. deviation (±kJ/g DW)
Ampeliscidae	*Ampelisca*	frozen	49	21.47	0.87
		formalin	43	21.91	1.73
	Byblis	frozen	5	21.34	0.45
		formalin	6	22.98	1.32
	Haploops	frozen	1	20.04	NA
		formalin	1	33.15	NA
Isaeidae	*Protomedeia*	frozen	7	19.08	0.83
		formalin	2	23.11	0.08
Melitidae	*Melita*	frozen	2	19.24	1.62
		formalin	2	25.12	4.36
Pontoporeiidae	*Pontoporeia*	frozen	3	20.28	1.11
		formalin	2	24.40	5.08
All	All	frozen	67	21.08	1.18
		formalin	56	22.28	1.99

Table 2.2: Mean energy content measurements for the six genera measured in this study in kJ/g DW (Dry Weight) for both cruises/seasons (SWL23/July; SKQ23/Sept-Oct). Standard deviations are included, where applicable. Full data provided in Supplementary File S1.

Family	Genus	Cruise	Sample size (n=)	Mean energy content (kJ/g DW)	Std. deviation (±kJ/g DW)
Ampeliscidae	*Ampelisca*	SWL23 (July)	19	20.96	0.62
		SKQ23 (Sept-Oct)	73	21.86	1.43
	Byblis	SWL23 (July)	3	21.83	0.24
		SKQ23 (Sept-Oct)	8	22.39	1.51
	Haploops	SWL23 (July)	0	NA	NA
		SKQ23 (Sept-Oct)	2	26.60	9.27
Isaeidae	*Protomedeia*	SWL23 (July)	4	19.54	0.85
		SKQ23 (Sept-Oct)	5	20.32	2.54
Melitidae	*Melita*	SWL23 (July)	2	20.06	2.79
		SKQ23 (Sept-Oct)	2	24.29	5.53
Pontoporeiidae	*Pontoporeia*	SWL23 (July)	3	20.03	0.68
		SKQ23 (Sept-Oct)	2	24.78	4.54
All	All	SWL23 (July)	31	20.72	1.01
		SKQ23 (Sept-Oct)	92	22.04	2.13

Table 2.3: Mean energy content measurements for the six genera measured in this study in kJ/g DW (Dry Weight) for the four DBO regions sampled from (DBO2/Chirikov Basin; DBO3/Southern Chukchi Sea; DBO4/Wainwright; DBO5/Barrow Canyon). Standard deviations are included, where applicable. Full data provided in Supplementary File S1.

Family	Genus	DBO Region	Sample size (n=)	Mean energy content (kJ/g DW)	Std. deviation (±kJ/g DW)
Ampeliscidae	*Ampelisca*	DBO2	34	21.01	0.70
		DBO3	NA	NA	NA
		DBO4	24	23.01	0.72
		DBO5	34	21.40	1.54
	Byblis	DBO2	7	22.04	0.99
		DBO3	NA	NA	NA
		DBO4	NA	NA	NA
		DBO5	4	22.58	1.85
	Haploops	DBO2	NA	NA	NA
		DBO3	NA	NA	NA
		DBO4	1	33.15	NA
		DBO5	1	20.04	NA
Isaeidae	*Protomedeia*	DBO2	8	19.91	2.04
		DBO3	1	20.48	NA
		DBO4	NA	NA	NA
		DBO5	NA	NA	NA
Melitidae	*Melita*	DBO2	NA	NA	NA
		DBO3	2	20.06	2.79
		DBO4	NA	NA	NA
		DBO5	2	24.29	5.53
Pontoporeiidae	*Pontoporeia*	DBO2	1	21.57	NA
		DBO3	4	22.02	4.02
		DBO4	NA	NA	NA
		DBO5	NA	NA	NA
All	All	DBO2	50	20.99	1.18
		DBO3	7	21.24	3.21
		DBO4	25	23.41	2.15
		DBO5	41	21.62	1.88

Caloric density measurements of all amphipod samples (n = 123) range from 18.09 - 33.15 kJ g^{-1} Dry Weight (DW), with mean and median values of 21.71 kJ g^{-1} DW and 21.47 kJ g^{-1} DW, respectively. Energy density values for each genus, separated by preservation method, are listed in Table 2.1 and compared in Figure 2.2. The mean energy content for the most abundant family Ampeliscidae (n = 105), which includes the genera *Ampelisca*, *Byblis*, and *Haploops*, was 21.43±0.85 (SD) kJ g^{-1} DW for frozen samples (n = 55) and 22.27±2.31 kJ g^{-1} DW for formalin-preserved samples (n = 50). For the most abundant genus, *Ampelisca* (n = 92), the mean energy content for frozen samples was 21.47±0.87 kJ g^{-1} DW (n = 49), and the mean energy content for formalin-preserved samples was 21.91±1.73 kJ g^{-1} DW (n = 43) (Table 2.1). The full data set is available in Supplementary File S1.

Comparisons among measurements for the genus *Ampelisca*

Kruskal-Wallis rank sum tests were used to compare caloric measurements between preservation methods, between cruises, and among regions for the genus *Ampelisca* (Table 2.4), since this genus is the most abundant in the region and comprises approximately 75% of the caloric measurements made (n = 92). The mean energy content for formalin-preserved amphipods in the genus *Ampelisca*, 21.91±1.73 kJ g^{-1} DW (Dry Weight), is slightly higher but

Table 2.4: Results of the Kruskal-Wallis rank sum tests performed for samples in the genus *Ampelisca* to look for significant differences in preservation method, cruise/season, and DBO region.

Taxa	Variable	chi-squared	p-value
Ampelisca	Preservation Method (frozen vs. formalin)	1.637	0.20
	Cruise/Season (SWL23/July vs. SKQ23/Sept-Oct)	7.061	0.0079
	DBO Region (DBO2 vs. DBO4 vs. DBO5)	37.746	6.36E-09

not significantly different to the mean value for frozen samples, 21.47±0.87 kJ g^{-1} DW (Table 2.1, Figure 2.3A). A significant difference was detected between cruises (chi^2 = 7.061, p-value = 0.0079) (Table 2.4); the mean caloric values measured for the July cruise (SWL23) and September cruise (SKQ23) were 20.96±0.62 and 21.86±1.43 kJ g^{-1} DW, respectively (Table 2.2). Measurements from SKQ23 are higher than measurements from SWL23 (Figure 2.3B). A Kruskal-Wallis rank sum test determined that there was a significant relationship between energy content of *Ampelisca* and the DBO region in which they were collected; this is explored further in the next section.

Pairwise comparisons using the Wilcoxon rank sum test indicated a potential spatial pattern among measurements for the genus *Ampelisca* (Table 2.5). Comparisons were only made

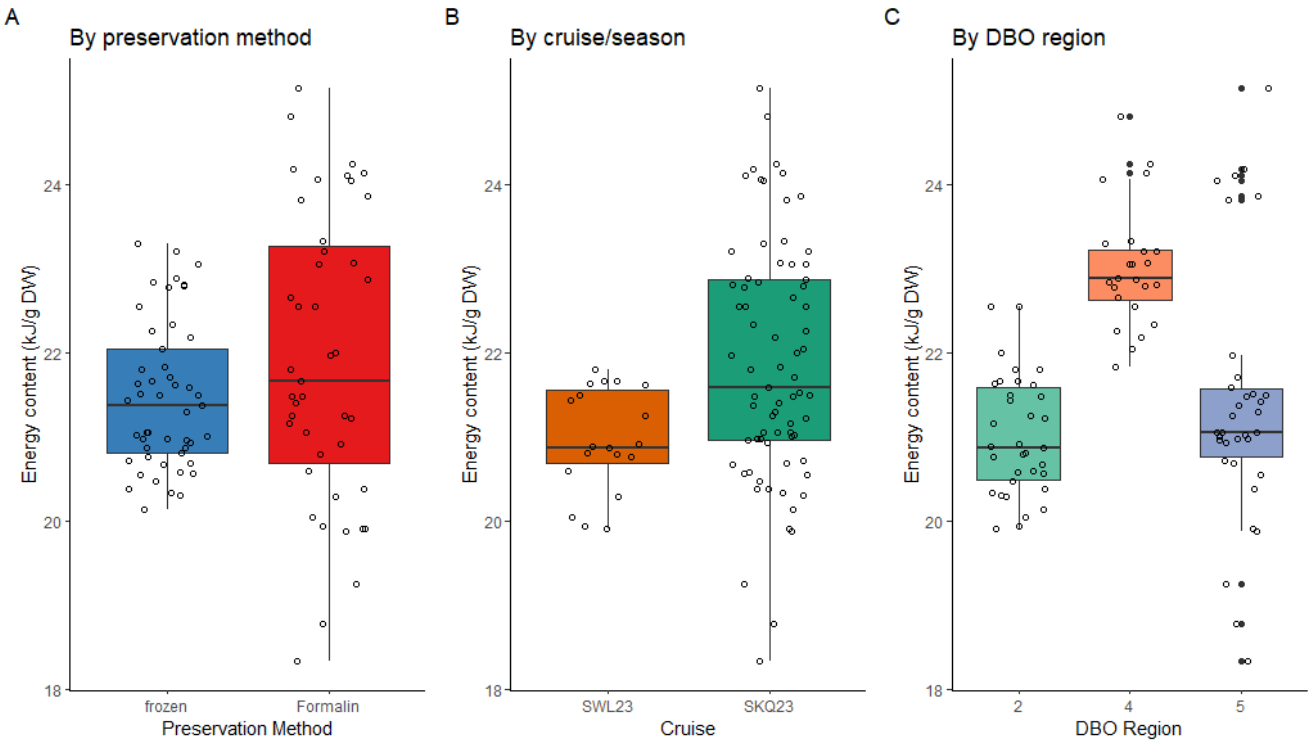

Figure 2.3: Energy content measurements in kJ g^{-1} DW (Dry Weight) for amphipods in the genus *Ampelisca*, comparing A) preservation methods (frozen, n = 49; formalin, n = 43), B) cruises (SWL23/July, n = 19; SKQ23/Sept-Oct, n = 73), and C) DBO regions (DBO2, n = 34; DBO4, n = 24; DBO5, n = 34).

among DBO2, DBO4, and DBO5, since no *Ampelisca* amphipods were collected in DBO3. Results indicate that caloric measurements from DBO4 are significantly different from caloric measurements from DBO2 (p-value < 0.001) and DBO5 (p-value < 0.001) (Table 2.5); values from DBO4 are slightly higher than those in the other two regions (Figure 2.3C). There was no significant difference between DBO2 and DBO5. The mean energy values measured for amphipods in the genus *Ampelisca* in each region are as follows: 21.01±0.70 kJ g^{-1} DW in DBO2, 23.01±0.72 kJ g^{-1} DW in DBO4, and 21.40±1.54 kJ g^{-1} DW in DBO5 (Table 2.3).

Table 2.5: Results of pairwise comparisons using the Wilcoxon rank sum test comparing the energy content of *Ampelisca* samples from the three regions which they were sampled from (DBO2/Chirikov Basin; DBO4/Wainwright; DBO5/Barrow Canyon)

Pairwise comparisons among DBO regions

	p-values	
	DBO2	DBO4
DBO4	1.70E-13	-
DBO5	0.29	6.20E-06

Discussion

The results presented in this study were compared to previously published values for amphipods in this region from three different studies: Hondolero et al. (2012), Stoker (1978), and Wilt et al. (2014) (Figure 2.4, Table 2.6). This was done not only to compare historic caloric measurements from previous years, but also to compare published methodologies with the methodologies used in this study. The published values from previous studies were compared only to the relevant values from this study, with some aggregation applied when needed. For example, the caloric values for formalin-preserved *Ampelisca birulai* and *A. macrocephala* in Stoker (1978) were averaged together and compared to the caloric values for formalin-preserved

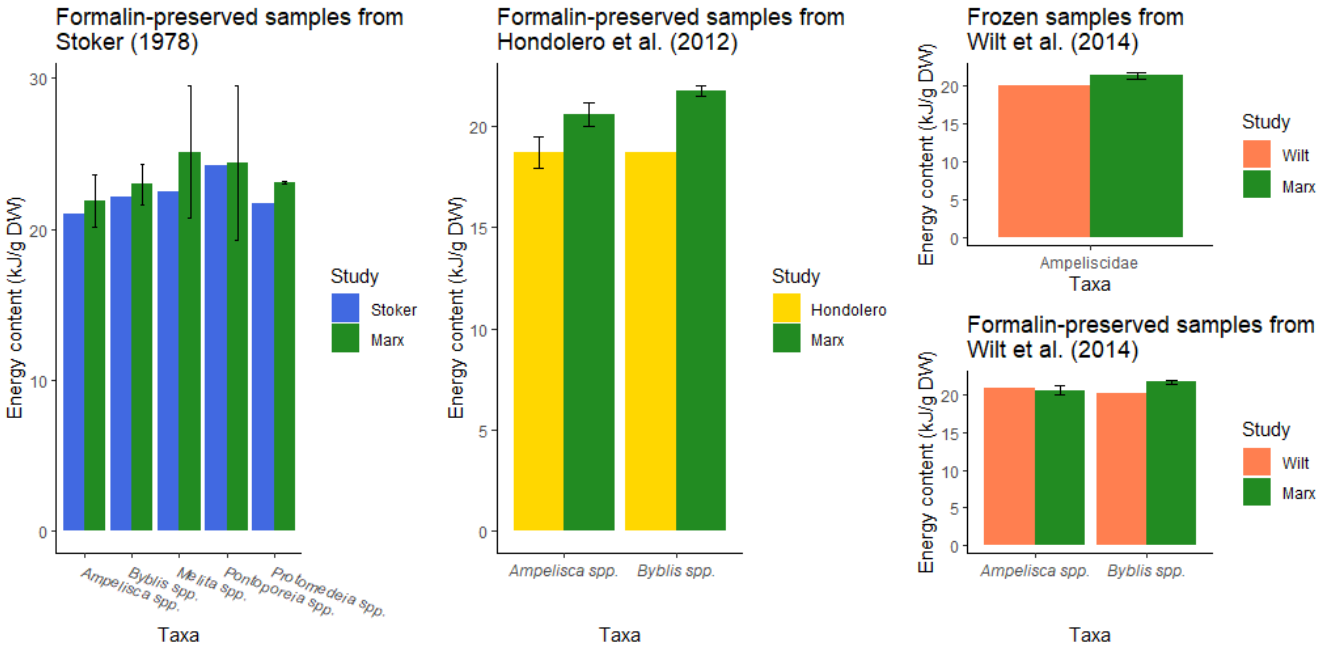

Figure 2.4: Comparison of energy content measurements made in this study with corresponding measurements made in three previous studies conducted in the Pacific Arctic Region: Stoker (1978), Hondolero et al. (2012), and Wilt et al. (2014).

Table 2.6: Previously published values of the energy contents of benthic amphipods in the Pacific Arctic Region, from three different studies: Stoker (1978), Hondolero et al. (2012), and Wilt et al. (2014).

Taxa	Preservation Method	Energy content (kJ g^{-1} DW) ± one std. deviation, where applicable	
		Comparison with Stoker (1978)	
		Stoker (1978)	This study
Ampelisca	formalin	20.97	21.92±1.73
Byblis	formalin	22.14	22.98±1.32
Melita	formalin	22.51	25.12±4.36
Pontoporeia	formalin	24.24	24.40±5.08
Protomedeia	formalin	21.68	23.10±0.08
		Comparison with Hondolero et al. (2012)	
		Hondolero et al. (2012)	This study
Ampelisca	formalin	18.72±0.76	20.60±0.61
Byblis	formalin	18.74	21.74±0.26
		Comparison with Wilt et al. (2014)	
		Wilt et al. (2014)	This study
Ampeliscidae	frozen	19.99	21.36±0.45
Ampelisca	formalin	20.84	20.60±0.61
Byblis	formalin	20.21	21.74±0.26

Ampelisca spp. in this study. Previous studies also had much smaller sample sizes, so error bars were added when available from the published values.

In regard to methodologies, samples from all four studies were collected using a 0.1 m^2 van Veen grab and rinsed with seawater over a 1 mm screen sieve; this study and Hondolero et al. (2011) also collected some samples that were incidentally caught in an epifaunal beam trawl. Formalin-preserved samples in this study, Stoker (1978), Hondolero et al. (2012), and Wilt et al. (2014) were all preserved in a 10% buffered formalin and seawater mixture. Stoker (1978) collected samples in both summer and winter from 1970-1974; Hondolero et al. (2012) collected

samples in summer from 2002-2008; and Wilt et al. (2014) collected samples during summer from 2010-2011. To account for any potential seasonal differences, values compared with Hondolero et al. (2012) and Wilt et al. (2014) only consisted of measurements from SWL23, the July cruise; since Stoker (1978) collected samples during winter and summer, those measurements were compared to samples from both cruises in this study.

Energy content values from formalin-preserved *Ampelisca, Byblis, Melita, Pontoporeia,* and *Protomedeia* were compared with the corresponding published values from Stoker (1978). The measurements from both studies are fairly similar, and published values from Stoker (1978) all fall within one standard deviation of the values in this study, with the exception of *Protomedeia*, which is less than the values in this study (Figure 2.4, Table 2.6). Energy content from formalin-preserved *Ampelisca* and *Byblis* were compared to the corresponding values from both Hondolero et al. (2012) and Wilt et al. (2014). The values from Hondolero et al. (2012) are lower and do not overlap within one standard deviation of the values in this study (Figure 2.4, Table 2.6). The value for *Byblis* in Wilt et al. (2014) is also lower and does not overlap with the range of values of this study, but the value for *Ampelisca* matches quite closely and falls within one standard deviation (Figure 2.4, Table 2.6). Wilt et al. (2014) also published a value for frozen samples of the family Ampeliscidae; this value is lower than the mean value for all Ampeliscidae measured in this study and does not fall within one standard deviation of the data reported here (Figure 2.4, Table 2.6). There are some slight differences in the methods used in each study, though this study closely follows the methods in Wilt et al. (2014) and was carried out with the same isoperibol bomb calorimeter located at Chesapeake Biological Laboratory in Solomons, Maryland, United States.

The caloric values measured in this study are comparable to similar studies previously conducted in the same region (Figure 2.4, Table 2.6). Comparisons with those made by Stoker (1978) are remarkably similar, indicating little change in energy content over 45 years. The similarity between this current study and data reported in Wilt et al. (2014) are also consistent, and this study used the same instrumentation and methodologies, approximately a decade apart. The disparities between this study and Hondolero et al. (2012) could be due to a difference in methodology or conditions at the time of sampling, but it is unknown at this time what caused these differences. Maresh et al. (2022) conducted a study along the coast of Sakhalin Island to evaluate the energy density of prey of Western North Pacific gray whales and found an average value for frozen Amphipoda to be 20.02±3.67 kJ g^{-1} DW; this aligns well with the mean value of frozen samples in this current study, 21.08±1.18 kJ g^{-1} DW.

Energy measurements of amphipods from other regions outside of the PAR are generally lower, indicating the high quality of benthic prey in the PAR. This is also consistent with the assumption that the PAR is highly productive due to the nutrient-rich Pacific Ocean water that is upwelled onto the Bering Shelf and carried northward by currents through Bering Strait, and it is well-documented that numerous benthic-feeding predators, such as walrus, diving sea ducks, and gray whales, thrive in this region. In the Canadian Arctic, Wacasey & Atkinson (1987) measured energy values for various species of freshly collected amphipods ranging from 12.87 to 16.57 kJ g^{-1} DW, and along the coast of Svalbard, Szaniawska & Wolowicz (1986) reported energy values for freshly collected, commonly found amphipod species ranging from 10.93 to 16.96 kJ g^{-1} DW. Both of these studies highlight the substantially higher energy content of amphipods collected from the highly productive northern Bering and Chukchi Seas compared to less productive regions around the Arctic, such as the Canadian Arctic and Atlantic Arctic.

Compared to other prey that gray whales, and cetaceans in general, may feed on, the amphipods in this study can be considered a medium- to high-quality source of food. In the northern Atlantic Ocean, Spitz et al. (2012) measured the energy content of stomach contents of various cetaceans in order to classify high- versus low-quality diets: they determined that an energy content greater than 5.5 kJ g^{-1} WW (Wet Weight) is considered a high-quality diet, and an energy content lower than 4.0 kJ g^{-1} WW is considered a low-quality diet. The wet weight energy content of frozen ampeliscid amphipods collected for this study was 4.97±1.16 kJ g^{-1} WW, making them medium- to high-quality as a lone food source. To compare the energy content of amphipods to some of the varieties of zooplankton that gray whales may feed on, particularly the Pacific Coast Feeding Group along the coasts of the Pacific Northwest, Hildebrand et al. (2021) measured the energy content of frozen samples and compared them to the energy content for *Ampelisca macrocephala*, Liljeborg, 1853, published in Hondolero et al. (2012), 4.473 kcal g^{-1} DW. The zooplankton with the highest energy content was Dungeness crab megalopae, with 4.21 kJ g^{-1} WW, and the remaining zooplankton ranging from 0.83 to 2.42 kJ g^{-1} WW. The converted energy content of *A. macrocephala*, 2.021 kJ g^{-1} WW, is much lower than the Dungeness crab megalopae; however, the value determined in this study for the family Ampeliscidae, 4.97±1.16 kJ g^{-1} WW, identifies ampeliscid amphipods as being of comparable, if not greater, quality and well above the energy contents of the other zooplankton measured.

A formal comparison among the energy contents of the genera sampled in this study is not included due to sample size limitations, but this analysis is included with Appendix 2. A pairwise comparison using the Wilcoxon rank sum test did not detect any significant differences among the genera (Table A2.2), which is not entirely surprising: other caloric studies of marine benthic invertebrates have noted that similar taxa in the same general region are fairly similar in

energy content. Of the various marine benthic invertebrates that Wacasey & Atkinson (1987) measured in the Canadian Arctic, none were found to be significantly different from each other. Hondolero et al. (2012) also postulates that closely related taxa, such as two species of amphipod in the same genus, are going to have similar caloric contents.

Formaldehyde contains carbon atoms that can contribute carbon available for oxidation when combusted, so initial expectations would be that samples preserved in formalin would have a higher energy content than comparable samples that were frozen or analyzed fresh. However, a significant difference was not detected between these two preservation methods for amphipods in the genus *Ampelisca*. Hondolero et al. (2012) report a significant difference between frozen and formalin-preserved samples for three of the taxa measured, but the majority of arthropods in that study did not have a significant caloric difference between the preservation methods. Formalin preservation also appears to introduce a greater amount of variation to caloric measurements, compared to freezing (Figures 2.3 & A2.1). This suggests that there may be other factors at play, such as body size or physiology, or that the carbons added by formaldehyde are not significant relative to the mass of the organism, that may be impacting this trend and are not fully understood yet. Furthermore, the comparison of frozen and formalin-preserved samples includes samples from both cruises and all of the DBO regions, so any correlations with these variables are not accounted for.

A significant difference between the two research cruises, one occurring in July and the other in September-October, is intriguing considering that seasonal differences in energy content have been documented in amphipods and other organisms. Highsmith & Coyle (1990, 1992) noted that the caloric content of various ampeliscids in the PAR peaked in mid- to late summer, most likely due to the accumulation of energy storage compounds to use during winter and

during egg production. One of the amphipods studied by Maresh et al. (2022) off the coast of Sakhalin Island, *Monoporeia affinis,* Lindström, 1855, was shown to accumulate lipid reserves in anticipation of food scarcity. However, seasonal variations in energy content are not universally found. Amongst the amphipod species that Szaniawska & Wolowicz (1986) studied in Svalbard, some did exhibit a seasonal variation, but others did not. Seasonal fluctuations in energy content may be due to one or more of several environmental or physiological factors, although it is not clear what the reasons are for the amphipods studied here. Furthermore, these results should be interpreted with caution, due to uneven spatial sampling between both cruises; some regions were sampled on one cruise, but not the other, due to differences in cruise plans and availability of amphipods at certain stations (Figure 2.1). The comparison between the two cruises also does not account for any correlations with preservation method or DBO region.

It was beyond the scope of this study to fully understand why *Ampelisca* amphipods from the DBO4 region near Wainwright, Alaska are significantly higher in energy content than *Ampelisca* amphipods from the other DBO regions. However, DBO4 and DBO5 in the northeast Chukchi Sea are both at much higher latitudes than DBO2 in the northern Bering Sea and have sea ice cover for a greater portion of the year. The base of sea ice ecosystems that thrive during ice breakup consists of ice algae and ice-associated phytoplankton blooms, which can provide large pulses of organic matter to the benthos when a bloom subsides (North et al., 2014). Fluxes of fresh algal production can be particularly high when associated with sea ice cover, in part due to weak grazing pressure from zooplankton (Lalande et al., 2007). Ice algae can be quite enriched in certain essential fatty acids per total body mass, making them a high-quality food source for benthic deposit- and suspension-feeders (McMahon et al., 2006). It was shown by Koch et al. (2020) that the surface sediments in the northeast Chukchi Sea carry a strong sea ice

algal signal, suggesting that export, advection, and resuspension of ice algal production provides a year-round source of food for the benthos. Therefore, it is reasonable to assume that a diet rich in ice algae may have contributed to the higher energy density of amphipods from DBO4. While *Ampelisca* amphipods from the nearby DBO5 area did not share this same pattern, this area is subject to higher advective current flow (Pickart et al. 2021), so sea ice production may not be as important as advective flow of water associated with production during the open water season. As with the comparison between cruises/seasons, these results should be viewed with caution due to uneven sampling of the regions between the two cruises and the inclusion of samples from both preservation methods.

The comparison of *Ampelisca* caloric contents among the DBO regions where samples were collected also reveals a potentially interesting trend in DBO5; there appears to be two or three distinct groups within the DBO5 samples (Figure 2.3C). To explore this further, the measurements for *Ampelisca* in DBO5 were separated by the stations they were collected at (Figure 2.5). Samples from DBO5.1 and DBO5.2 were consolidated so that there would be enough material to run on the calorimeter, so those are considered as one station for the purposes of this discussion. The stations sampled in DBO5 include DBO5.1/DBO5.2, DBO5.6, and DBO5.7, and measurements from DBO5.6 are significantly higher than measurements from the other stations (Figure 2.5). DBO5 spans Barrow Canyon, with stations traversing the canyon from one side to the other; DBO5.1 is furthest inshore and DBO5.10 is furthest offshore. DBO5.6 and DBO5.7 are both in the center of the canyon yet are distinctly different in the energetic content of their samples. This could be due to the difference in depth, as DBO5.7 is slightly shallower than DBO5.6, which is in the deepest portion of the canyon. The *Ampelisca* at these two stations may also be of different species, which could have caused the variability.

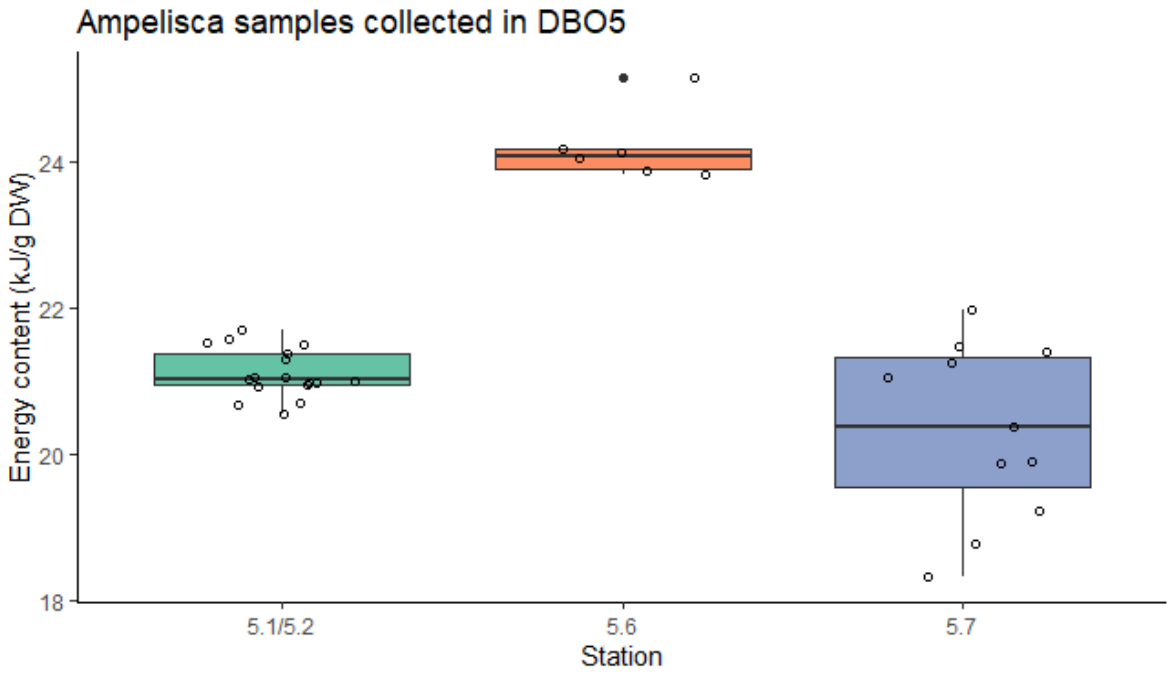

Figure 2.5: Comparison of the energetic contents of samples of *Ampelisca* collected in the DBO5 region, in kJ g^{-1} DW (Dry Weight). Measurements are separated by the station they were collected at: 5.1 and 5.2 combined (n=17), 5.6 (n=6), and 5.7 (n=11).

Additionally, the *Ampelisca* collected at DBO5.6 were quite small and numbered in the hundreds, potentially representing an abundance of earlier life stages, so this may also be the reason for the energetic difference. These results highlight the fact that there are potentially more spatial or taxonomic trends in amphipod energy density that could be explored further with more rigorous and even sampling.

The caloric measurements in this study used whole amphipods, crushed into a fine powder before being pressed into pellets. Other caloric studies have physically removed hard parts, such as shells or tubes from organisms such as bivalves or polychaete worms (Wacasey & Atkinson, 1987; Wilt et al., 2014), or they have soaked organisms in a weak acid in order to remove any undigestible calcium carbonate from crustaceans and echinoderms (Hondolero et al., 2012). Neither of these methods were used in this study, assuming that the whole amphipod should be measured since gray whales consume amphipods whole while feeding. However, there

is the possibility that there is some amount of chitin or calcium carbonate within the amphipod carapace that is not fully digested by gray whales.

In summary, the energy contents measured in this study agree quite well with prior studies conducted in the Pacific sector of the Arctic, including those reported by Stoker (1978), indicating that there has likely been little change in energetic content over the intervening decades. There exist spatial and temporal variabilities among the DBO regions and seasonally, but the overall energetic quality of amphipods in the PAR has not declined. There are also some potential spatial and temporal patterns for benthic amphipods in general that could be investigated further; samples sizes were small for most of the genera considered, limiting the power of the statistical analysis. Benthic amphipods in the PAR continue to be a high-quality food source, but as will be discussed in Chapter 3, the quantity of amphipod biomass available has dropped drastically.

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Chapter 3: Amphipod population time series and caloric conversions

Introduction

Declining amphipod populations

Benthic amphipod populations in the Pacific Arctic Region (PAR) have been monitored since at least the 1970s through abundance and biomass measurements carried out by various organizations and institutions from several countries (Appendix Table A1). Some populations of ampeliscid amphipods (Family Ampeliscidae) are highly productive, and a few are even considered among the most productive benthic amphipod populations in the world (Coyle et al., 2007). This productivity is considered remarkably high for such a northern latitude; however, it is offset by a low productivity to biomass ratio (Highsmith & Coyle, 1990). This low ratio indicates that high ampeliscid amphipod production estimates are the result of a high standing crop, rather than high growth or reproduction rates (Highsmith & Coyle, 1990); the lifespan of ampeliscid amphipods in the PAR is estimated to be 5-6 years, with approximately 75% of the annual production generated by individuals greater than 12 mm in length (Highsmith & Coyle, 1991). At the observed maximum of these populations during the 1980s, ampeliscid amphipods in the Chirikov Basin in the northern Bering Sea attained 30-40 g m^{-2} in dry weight, with maximum energetic production of 170-230 kcal m^{-2} yr^{-1} (Coyle et al., 2007). However, significant declines in ampeliscid amphipod biomass have been observed since the late 1980s and 1990s (Bluhm et al., 2007; Grebmeier, 2012; Moore et al., 2022).

The most dramatic declines in ampeliscid amphipod biomass have been in the Chirikov Basin, just south of the Bering Strait and northeast of St. Lawrence Island (Coyle et al., 2007;

Kędra & Grebmeier, 2021; Moore et al., 2003) (Figure 1.1). Covering approximately 40,000 km^2 (Coyle et al., 2007), the Chirikov Basin is one of the highly productive hotspots that is monitored as part of the Distributed Biological Observatory (DBO). This region, along with the southern Chukchi Sea and the Barrow Canyon region, are considered highly productive advective regimes, fueled by nutrient-rich waters flowing northward from the Pacific Ocean via the Bering Slope near Cape Navarin (Feng et al., 2021). The waters of the Chirikov Basin are particularly high in nutrients, such as nitrate (Giesbrecht et al., 2019), carried into the region by the Anadyr Current flowing along the western and northern edges (Cooper et al., 2012) (Figure 1.1). These nutrients fuel primary production in the water column once sea ice retreats; the combination of nutrient-rich water and a longer ice-free period in the Chirikov Basin relative to more northern regions in the PAR provide for some of the highest levels of primary production throughout the DBO (Frey et al., 2023). Measurements of chlorophyll-a in the Chirikov Basin have remained high in recent years as ampeliscid amphipod biomass has decreased (Cooper & Grebmeier, 2022), suggesting that a lack of primary production is not responsible for the long-term loss of biomass. The exact reasons behind this loss and the subsequent community restructuring are not fully understood yet, but it is known that ampeliscid amphipods, and other benthic invertebrates, are sensitive to sediment structure (Grebmeier et al., 2015). The sediments in the Chirikov Basin are predominantly sandy in nature, due to the strong currents flowing northward through the region (Grebmeier et al., 2006a). Ampeliscid amphipods rely on sandy sediments with a lower fraction of silt and clay to build the structure for their tubes; they are unable to build tubes in sediments that are predominantly silt or mud (Grebmeier et al., 2006a; Highsmith & Coyle, 1992). A shift in the sediment structure of the Chirikov Basin in recent decades is likely a contributing factor to the loss of ampeliscid amphipod biomass (Moore et al., 2003).

A biological factor that is contributing to the loss of biomass is a shift in size frequency towards smaller individuals (Highsmith & Coyle, 1992; Stewart et al., 2023). Benthic amphipods generally exhibit temperature-dependent growth and maturation rates; in warmer locations, individuals tend to reach maturity at an earlier age and smaller size (Highsmith & Coyle, 1991). This is a trend that has been noted around the globe in a wide variety of aquatic organisms, such as bacteria, phytoplankton, zooplankton, and fish (Daufresne et al., 2009). Stewart et al. (2023) showed a decreasing trend in the average body size of benthic crustaceans in the PAR over time, and as global temperatures continue to climb upwards, this trend is likely to continue.

Gray whale energy requirements

The long-term loss of so much ampeliscid amphipod biomass has implications for gray whale foraging behavior; these amphipods have historically been considered the primary prey source for gray whales that migrate to the Pacific Arctic to forage (Bluhm & Gradinger, 2008; Moore et al., 2003). Observers and acoustic detections have noted that gray whales are mostly passing through the Chirikov Basin more recently, instead traveling further north into the Chukchi and Beaufort Seas to forage (Moore et al., 2022). It is not fully understood what gray whales are feeding on in these more northern regions, but it is suspected to be a mixture of benthic and pelagic prey (Brower et al., 2017). Benthic foraging leaves behind characteristic mud plumes that are easily spotted by shipboard and aerial observers, but pelagic foraging is much harder to detect (Brower et al., 2017). Until further dietary studies can be accomplished, it is unclear how much gray whale foraging is pelagic in nature in recent years. An increase in pelagic foraging is likely to put gray whales in competition for food with other marine mammals, both Arctic natives and subarctic visitors (Bluhm & Gradinger, 2008). Bowhead whales, an Arctic endemic species, are known to forage heavily on copepods and euphausiids in the

Chukchi and Beaufort Seas (Citta et al., 2015). Subarctic species, such as humpback, fin, and minke whales, are now being observed in greater numbers in the eastern Chukchi Sea, often in close proximity to gray whales; surveys from 1982-1991 did not observe these subarctic species at all in the eastern Chukchi Sea (Brower et al., 2018). Benthic amphipods are also prey for a variety of other organisms, including benthic-feeding fish, predatory amphipods, shrimps, and crabs (Highsmith & Coyle, 1992); some species of fish have been documented expanding their ranges northward with warming temperatures, in both the Pacific Arctic (Mueter et al., 2021) and the Atlantic Arctic (Fossheim et al., 2015), introducing potentially more competition for a declining food source.

The loss of a significant portion of their prey base has strong implications for the energy budgets of gray whales. Gray whales are capital breeders, relying on hotspots of high-density prey in their summer foraging grounds in the north to build up blubber reserves; for example, Hildebrand et al. (2021) estimates that gray whales must regain 11-29% of their body mass while at their northern foraging grounds. These reserves must be able to sustain their metabolism and reproductive cycle throughout their migration and time spent at winter calving grounds in the lagoons of Baja California (Bluhm & Gradinger, 2008). Given their immense energy requirements needed to reproduce and complete their lengthy migration, one of the longest mammalian migrations on the planet, gray whales have relatively high metabolic costs, making them particularly sensitive to changes in prey availability (Spitz et al., 2012). Adult females and their calves are especially vulnerable to changes in energy availability, and if adult female survival rates drop, other demographic categories in the population are likely to suffer as well (Villegas-Amtmann et al., 2015). Malnutrition and a loss of blubber due to insufficient caloric consumption can have a variety of detrimental effects on adult gray whales, including higher risk

of live stranding, a reduced ability to refloat, and possible death due to asphyxiation or a compartmental-type syndrome; pregnant mothers and females can suffer from infertility, early embryonic loss and fetal resorption, abortion, premature birth, or the death of a dependent calf (Raverty et al., 2024). At the population level, malnutrition can cause reduced fecundity, a prolonged inter-calving period, decreased longevity, and low recruitment (Raverty et al., 2024). Such consequences have serious implications for long-term population trends, hence the concern around food quality and quantity following the observations of starving and emaciated gray whales during the two recent Unusual Mortality Events (1999-2000 and 2019-2023). The goal of this chapter is to use historic formalin-preserved amphipod biomass data to quantify the energy density of amphipod populations in the PAR, using a conversion factor determined using caloric measurements of both formalin-preserved and frozen amphipod specimens (Chapter 2). This conversion method should allow for a more accurate approximation of how the energy density per square meter has changed in gray whale foraging grounds, such as the Chirikov Basin.

Methods

Time series

Using almost five decades worth of data (1970-2019) from numerous cruises and projects in the Pacific Arctic Region (PAR), a time series of abundance and biomass was synthesized for four of the most common amphipod families in the PAR: Ampeliscidae, Isaeidae, Melitidae, and Pontoporeiidae (data archived at the NSF Arctic Data Center; https://arcticdata.io/about/). These four families comprise more than three quarters of the total infaunal benthic crustacean wet weight biomass collected in the Distributed Biological Observatory (DBO) from 2010-2019 (data archived at https://arcticdata.io/catalog/portals/DBO/Data/), and Ampeliscidae makes up

just over half (Figure 3.1). The synthesized data comes from samples collected across the region in the northern Bering, Chukchi, and Beaufort Seas. All samples were collected using a 0.1 m^2 weighted van Veen grab, rinsed with seawater over a 1 mm mesh screen, and preserved in a 10% buffered formalin and seawater solution. To look at data on a smaller regional scale, bounding boxes were used to identify and label samples collected in four separate regions monitored as part of the DBO. These regions are identified as hotspots of benthic production, therefore having high benthic invertebrate biomass. The regions identified are the Chirikov Basin in the northern Bering Sea, the southern Chukchi Sea, the northeastern Chukchi Sea off the coast of Wainwright, Alaska, and the waters around Point Barrow (Figure 3.2).

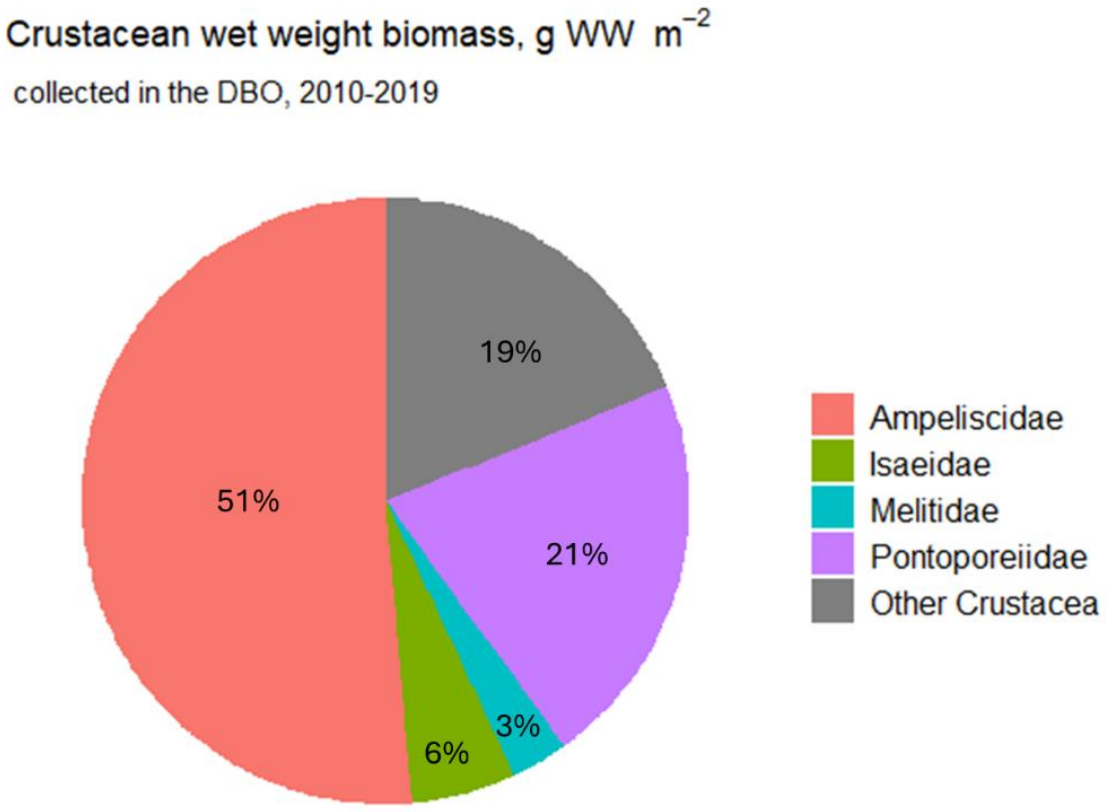

Figure 3.1: Proportions of benthic crustacean wet weight biomass (g WW/m^2) collected at DBO stations, 2010-2019. The four amphipod families highlighted in this study are shown along with their relative proportions of the total wet weight biomass.

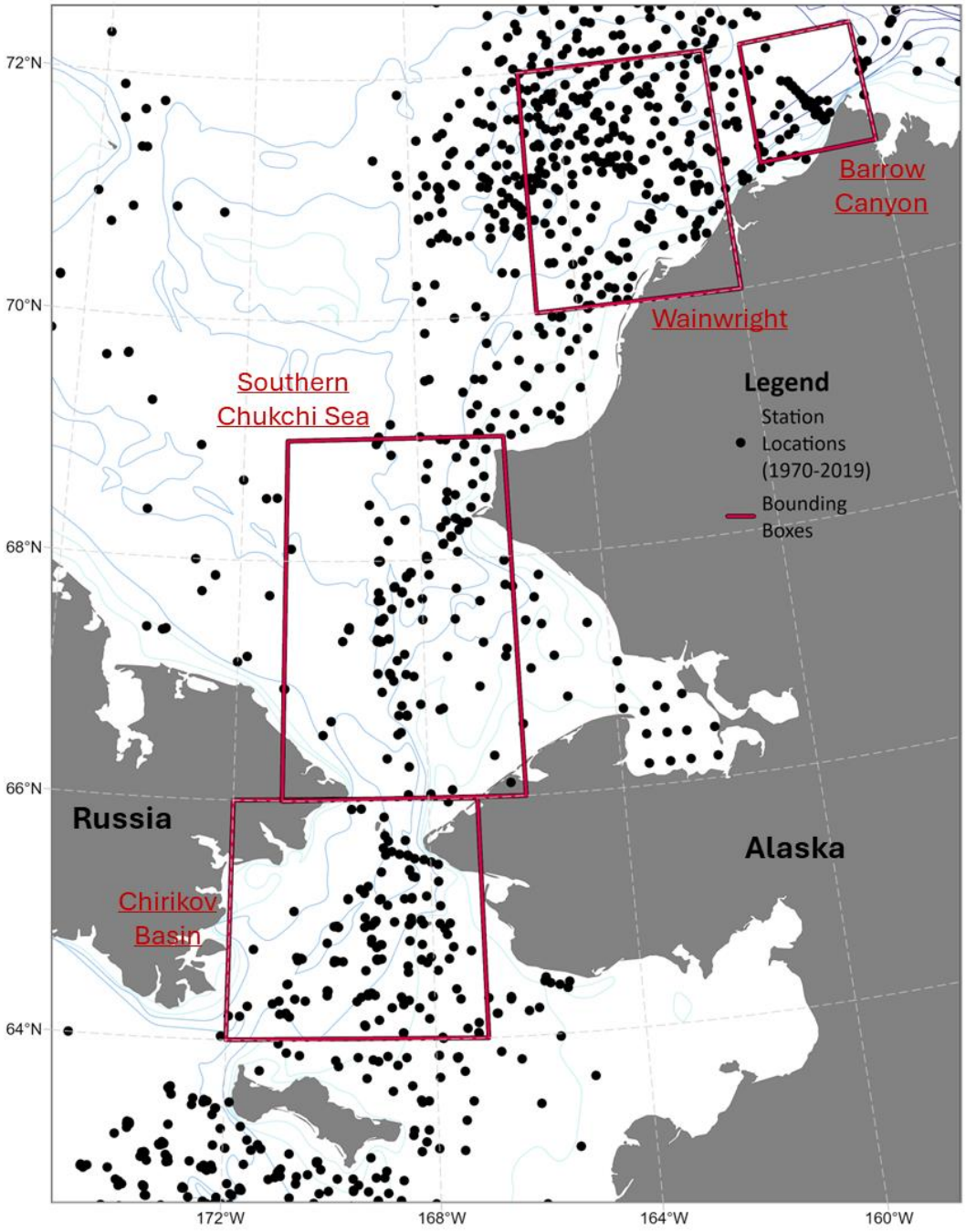

Figure 3.2: Map of the Pacific Arctic Region showing every station sampled in the time series, from 1970-2019. Bounding boxes are drawn around the four biological hotspot regions focused on in this study. From north to south: Barrow Canyon, Wainwright, Southern Chukchi Sea, and Chirikov Basin

The Chirikov Basin, situated between St. Lawrence Island and the Bering Strait, includes the DBO2 region and is bounded north-south by 66°N and 64°N and bounded west-east by

172°W and 167°W. The southern Chukchi Sea, situated just north of the Bering Strait and encompassing DBO3, is bounded north-south by 69°N and 66°N and bounded west-east by 171°W and 166°W. The northeastern Chukchi Sea region encompasses the waters off of the coast of Wainwright, Alaska, and includes the DBO4 region; it is bounded north-south by 72°N and 70°N and bounded west-east by 165°W and 160°W. Finally, the Point Barrow region encompasses the waters offshore of the community of Utqiaġvik, as well as Barrow Canyon, which is transected by DBO5; this region is bounded north-south by 72°N and 71°N and bounded west-east by 159°W and 156°W.

Relative abundance of individual amphipods is scaled to the square meter from measurements made with a 0.1 m^2 van Veen grab. Biomass is reported as relative grams of wet weight per square meter. Relative abundance and biomass estimates from each cruise are reported at various taxonomic levels, ranging from family, genera, and species. All measurements are identified to a minimum of family level, but it was not practical to identify all organisms to the genus or species level in past data; therefore, analyses presented here focus on trends at the family level. Furthermore, all time series biomass estimates are for samples that were preserved in formalin at sea prior to weight determinations at a land-based laboratory.

Biomass:Abundance ratio in samples collected in the PAR

To approximate the average size of amphipods collected in each sample, the ratio of biomass to abundance for samples collected in the PAR was calculated following the method used in Stewart et al. (2023). In that study, the biomass:abundance (referred to as per capita biomass) was calculated for all benthic crustaceans sampled in the PAR using the carbon biomass; for this study, the metric will only focus on the family Ampeliscidae, using wet weight biomass. For each individual sample, the wet weight biomass per square meter is divided by the

abundance per square meter, giving the average amount of wet weight biomass per individual in that sample. These values are grouped and colored by year, with regression lines for each year, to show temporal trends (Figure 3.3).

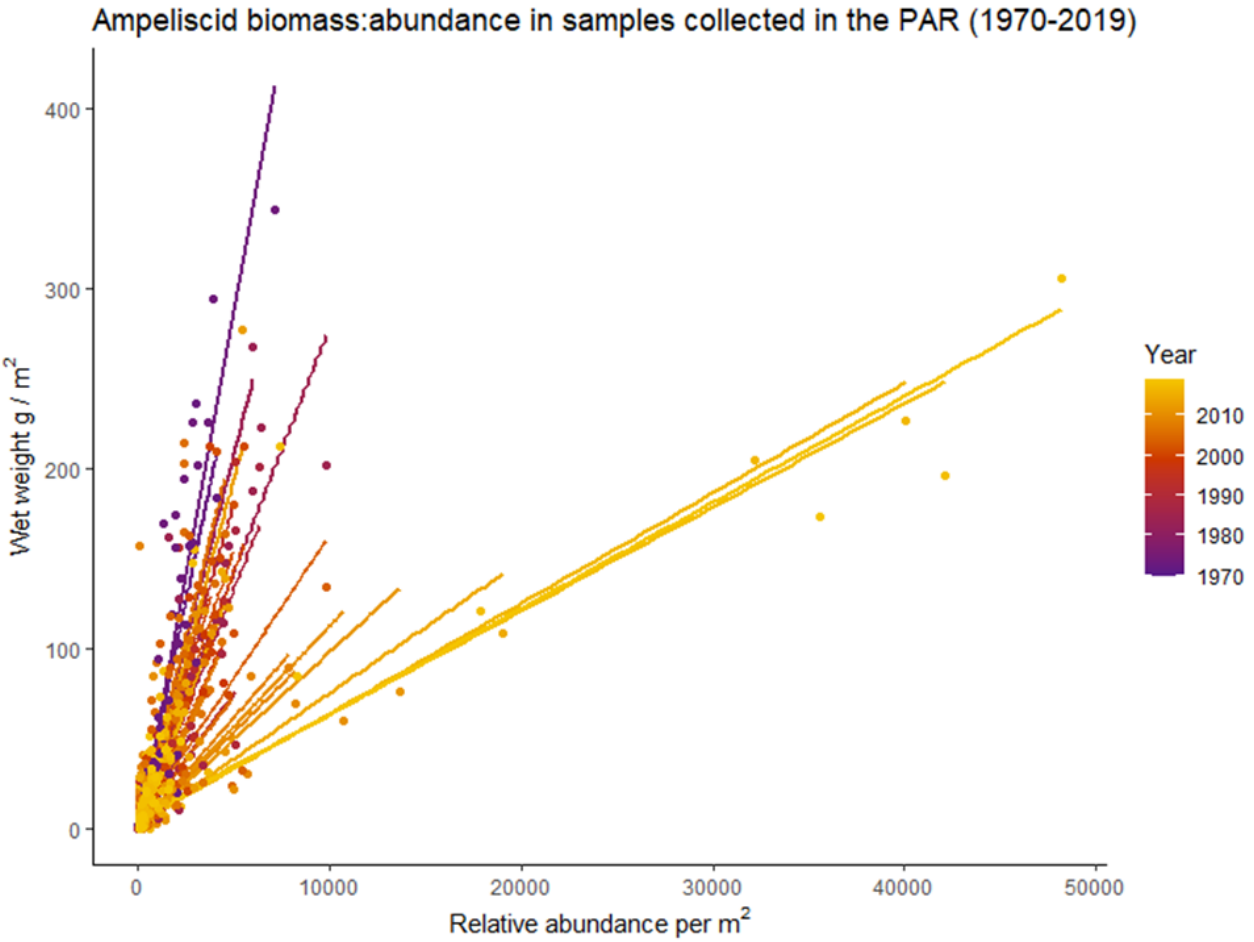

Figure 3.3: The biomass:abundance of ampeliscid amphipods in the Pacific Arctic Region over the course of the time series (1970-2019). Regression lines are drawn for each year and colored based on a gradient from oldest (purple) to most recent (yellow).

Conversion

Formalin-preserved wet weight per square meter for dominant amphipods was converted to kilojoules per square meter to compare with frozen (approximating "fresh") amphipods and their caloric values. The ratio of Dry Weight:Wet Weight in grams was calculated for all of the samples collected for caloric analysis in Chapter 2. These ratios were averaged together by

grouping samples by Preservation Method, Cruise, DBO Region, and Genus. The mean ratio of grams of Dry Weight to grams of Wet Weight for all formalin-preserved samples collected for this study was then calculated for each amphipod family; individual values were determined for each family due to uneven sample sizes and outliers within the smaller sample sizes. The Dry Weight:Wet Weight ratios for formalin-preserved Ampeliscidae, Isaeidae, Melitidae, and Pontoporeiidae are 0.145, 0.089, 0.413, and 0.103, respectively. This ratio was then multiplied by the mean kilojoules per gram of formalin-preserved dry weight measured for each Family (Ampeliscidae = 22.27 kJ g^{-1} DW; Isaeidae = 23.11 kJ g^{-1} DW; Melitidae = 25.12 kJ g^{-1} DW; and Pontoporeiidae = 24.40 kJ g^{-1} DW) to calculate the mean kilojoules per gram of formalin-preserved wet weight; this value was then multiplied by grams of formalin-preserved wet weight per square meter to determine the kilojoules of formalin-preserved wet weight per square meter for each family. This value was then multiplied by the ratio of kilojoules per gram for frozen samples to kilojoules per gram for formalin-preserved samples for each family (from results of Chapter 2). The ratios of kJ g^{-1} of frozen samples to kJ g^{-1} of formalin-preserved samples for Ampeliscidae, Isaeidae, Melitidae, and Pontoporeiidae are 0.96, 0.83, 0.77, and 0.83, respectively. This resulted in an estimated value for the energetic value (kJ) associated with each square meter of "fresh" (frozen) biomass.

Equation 3.1: Conversion between formalin-preserved wet weight per square meter to kJ per square meter of frozen samples to approximate the energy density of fresh animals.

$$\frac{g\ WW\ (formalin\ preserved)}{m^2} \times \frac{g\ DW\ (formalin\ preserved)}{g\ WW\ (formalin\ preserved)} \times \frac{kJ}{g\ DW\ (formalin\ preserved)} = \frac{kJ\ (formalin\ preserved)}{m^2}$$

$$\frac{kJ\ (formalin\ preserved)}{m^2} \times \frac{kJ\ g^{-1}\ (frozen)}{kJ\ g^{-1}\ (formalin\ preserved)} = \frac{kJ\ (frozen)}{m^2}$$

Results

Time series and caloric conversions

The final time series consists of 8,027 amphipod samples, collected in the years 1970-2019. Samples from the family Ampeliscidae make up approximately 78% of the total energy density in the time series (n = 4,260); the remainder of the total energy density in the time series is approximately 12% Pontoporeiidae (n = 1,399), 7% Melitidae (n = 641), and 3% Isaeidae (n = 1,727) (Table 3.1). The full time series results are available in Supplementary File S2. More than three-quarters of the total energy density in the time series was collected within the bounding boxes placed around the DBO regions, with approximately 48% from the Chirikov Basin/DBO2 (n = 906), 16% from the southern Chukchi Sea/DBO3 (n = 1,147), 10% from Wainwright/DBO4 (n = 2,237), and 10% from Point Barrow/DBO5 (n = 499) (Table 3.2). The remaining 16% of the total energy density (n = 3,238) occurred outside of the bounding boxes but still within the PAR. The converted energy densities of all samples range from 0.00017 to 1,070.87 kJ m^{-2}, with a mean of 13.56 kJ m^{-2} and a median of 0.73 kJ m^{-2}, due to several prominent outliers (Table 3.3). The highest value (1,070.87 kJ m^{-2}) was converted from a measurement by Stoker in 1974; this sample, collected in the Chirikov Basin, consisted of 343.62 grams of *Ampelisca macrocephala*, Liljeborg, 1853 (Supplementary File S2).

The mean amount of energy measured for each family in each of the four study regions from 1970-2019 was calculated using whatever data was available that year (Figure 3.4). The yearly means for the Family Ampeliscidae are listed in Table 3.4; years with no samples collected are labelled as “no data”. In the Point Barrow/DBO5 region, Ampeliscidae made up the

Table 3.1: Total energy densities of each amphipod family in the time series, grouped by region. Sample sizes and proportion of total energy density that each family comprises in the time series are included.

Family	Region	Total energy density (kJ/m^2)	Sample size (n=)	Proportion of total energy density in time series
Ampeliscidae	DBO2	50,107	470	
	DBO3	4,387	357	
	DBO4	9,247	1,547	
	DBO5	10,450	280	
	Other	11,100	1,606	
	Sum:	85,290	4,260	78%
Isaeidae	DBO2	1,228	250	
	DBO3	894	419	
	DBO4	623	287	
	DBO5	175	94	
	Other	807	677	
	Sum:	3,727	1,727	3%
Melitidae	DBO2	660	60	
	DBO3	1,700	128	
	DBO4	760	110	
	DBO5	444	43	
	Other	3,422	300	
	Sum:	6,986	641	7%
Pontoporeiidae	DBO2	113	126	
	DBO3	10,709	243	
	DBO4	266	293	
	DBO5	296	82	
	Other	1,471	655	
	Sum:	12,855	1,399	12%
All	Total:	108,858	8,027	100%

Table 3.2: Total energy densities measured in each of the four DBO regions examined in this study, compared to measurements outside of DBO regions and the total energy density in the time series

Region	Total Energy Density (kJ/m2)	Sample size (n=)	Proportion of total energy density in time series
DBO2/Chirikov Basin	52,108	906	48%
DBO3/S. Chukchi Sea	17,689	1,147	16%
DBO4/Wainwright	10,895	2,237	10%
DBO5/Barrow Canyon	11,365	499	10%
Other/Outside DBO2-5	16,802	3,238	16%
Sum:	103,934	8,027	100%

majority of the mean energy density, though data were quite sparse before 2000 (Figure 3.4A); mean ampeliscid energy density was highest in 2000, at 140.44 kJ m^{-2} (Table 3.4). Amphipod biomass and energy density were both relatively quite low in the Wainwright/DBO4 region, and none of the four families appear to be dominant (Figure 3.4B); mean ampeliscid biomass was highest in 2019, with only 12.06 kJ m^{-2} (Table 3.4). The southern Chukchi Sea/DBO3 region had greater mean biomass and energy density than the two previously mentioned regions; however, this region has been dominated by the family Pontoporeiidae since around 2000 (Figure 3.4C). The greatest mean ampeliscid energy density occurred in 1988, with 62.59 kJ m^{-2} (Table 3.4). The Chirikov Basin/DBO2 region by far had the highest mean amphipod biomass and energy density of these four regions, and it was dominated by Ampeliscidae over the time series study (Figure 3.4D). The mean ampeliscid amphipod energy density was highest in the Chirikov Basin in 1984 at 347.08 kJ m^{-2} before dropping to its lowest mean energy density in 2010 at 31.07 kJ m^{-2} (Table 3.4).

For the family Ampeliscidae (n = 4,260), the converted energy densities range from 0.00031 to 1,070.87 kJ m^{-2}, with a mean of 20.02 kJ m^{-2} and a median of 1.00 kJ m^{-2} (Table 3.3).

Table 3.3: Summary statistics for amphipod energy densities in the time series, grouped by family and region.

Family	Region	Energy density (kJ/m2) Minimum	Mean	Median	Maximum
Ampeliscidae	DBO2	0.0031	106.61	18.94	1,070.87
	DBO3	0.00031	12.29	0.88	356.57
	DBO4	0.00031	5.98	0.93	489.39
	DBO5	0.0062	37.32	1.43	953.24
	Outside DBO2-5	0.00031	6.91	0.67	660.74
	All	0.00031	20.02	1.00	1,070.87
Isaeidae	DBO2	0.0017	4.91	1.24	54.33
	DBO3	0.00017	2.13	0.33	80.44
	DBO4	0.0017	2.17	0.18	203.77
	DBO5	0.00017	1.86	0.24	48.79
	Outside DBO2-5	0.00017	1.19	0.14	57.60
	All	0.00017	2.16	0.25	203.77
Melitidae	DBO2	0.14	11.00	4.46	71.74
	DBO3	0.00079	13.28	3.96	186.23
	DBO4	0.016	6.91	3.12	99.94
	DBO5	0.11	10.33	4.69	70.13
	Outside DBO2-5	0.00079	11.41	3.62	125.78
	All	0.00079	10.90	3.72	186.23
Pontoporeiidae	DBO2	0.0021	0.90	0.35	10.48
	DBO3	0.00021	44.07	7.12	403.50
	DBO4	0.0042	0.91	0.27	19.11
	DBO5	0.00021	3.61	0.93	32.15
	Outside DBO2-5	0.00021	2.25	0.46	59.18
	All	0.00021	9.19	0.48	403.50
All samples:		0.00017	13.56	0.73	1,070.87

Samples collected in the DBO region bounding boxes make up 87% (n = 2,654) of the total ampeliscid amphipod energy content in the time series; of those samples, 59% is from the Chirikov Basin/DBO2 region (n = 470), 12% is from the Point Barrow/DBO5 region (n = 280), 11% is from the Wainwright/DBO4 region (n = 1,547), and 5% is from the southern Chukchi Sea/DBO3 region (n = 357) (Table 3.1). When looking at trends in the mean ampeliscid

Table 3.4: Yearly mean energy densities (kJ m^{-2}) for the Family Ampeliscidae, grouped by the four study regions and any measurements outside of those regions/bounding boxes. Years with no measurements are labelled "no data".

	Mean energy density (kJ/m^2)				
	Region				
Year	Barrow Canyon	Wainwright	South Chukchi	Chirikov Basin	Other/outside bounding boxes
1970	no data	no data	no data	no data	0.31
1971	no data	no data	no data	no data	0.62
1972	no data	no data	no data	no data	19.95
1973	no data	2.29	8.27	132.14	2.47
1974	no data	3.37	2.22	166.54	46.95
1975	no data	no data	no data	no data	no data
1976	no data	no data	no data	no data	no data
1977	no data	no data	no data	no data	no data
1978	no data	no data	no data	no data	no data
1979	no data	no data	no data	no data	no data
1980	no data	no data	no data	no data	no data
1981	no data	no data	no data	no data	no data
1982	no data	no data	no data	no data	no data
1983	no data	no data	no data	no data	no data
1984	no data	no data	no data	347.08	19.05
1985	no data	1.28	51.17	289.88	4.32
1986	0.86	7.49	17.90	no data	1.77
1987	no data	no data	47.40	no data	0.60
1988	no data	no data	62.59	143.85	20.98
1989	no data	no data	no data	no data	no data
1990	no data	no data	no data	no data	46.51
1991	no data	no data	no data	no data	no data
1992	no data	no data	no data	no data	no data
1993	no data	6.79	8.73	343.67	24.33
1994	no data	no data	52.78	no data	9.75
1995	no data	no data	59.76	no data	6.70
1996	no data	no data	no data	no data	no data
1997	no data	no data	no data	no data	no data
1998	no data	no data	12.72	no data	6.57
1999	0.79	no data	5.54	132.69	3.02
2000	140.44	no data	9.77	133.73	15.67
2001	no data	no data	10.94	238.29	3.34

2002	0.83	no data	16.57	316.85	3.24
2003	no data	no data	15.25	198.49	0.14
2004	5.53	no data	27.81	170.90	15.39
2005	7.68	no data	11.91	83.48	0.39
2006	no data	no data	9.25	140.13	13.46
2007	no data	no data	0.95	66.90	6.49
2008	no data	3.23	0.11	34.65	1.61
2009	0.84	10.20	11.61	no data	2.16
2010	0.27	5.70	3.61	31.07	2.71
2011	20.34	5.14	0.73	55.54	2.41
2012	28.37	3.39	0.62	72.24	2.19
2013	75.25	2.69	0.37	32.90	2.30
2014	2.32	3.18	1.11	67.71	0.11
2015	29.71	6.01	0.72	74.10	4.28
2016	no data	3.49	1.29	51.43	5.80
2017	51.77	8.57	1.91	38.74	5.87
2018	82.44	4.78	2.19	59.86	1.56
2019	57.59	12.06	1.43	44.42	1.21

amphipod energy density each year throughout the time series, the Chirikov Basin/DBO2 had the greatest amount of energy density, peaking at 347.08 kJ m^{-2} in 1984 and dropping significantly to a minimum mean of 31.07 kJ m^{-2} in 2010 (Table 3.4). The Chirikov Basin/DBO2, southern Chukchi Sea/DBO3, and samples outside the DBO region bounding boxes all exhibit a decreasing trend in mean energy density (Figure 3.5). The Wainwright/DBO4 region does not exhibit a strong trend but has the overall lowest values (Table. 3.4). Point Barrow/DBO5 actually has an increasing trend in mean energy density, and maximum values have risen to the same magnitude as observed in the Chirikov Basin/DBO2 in the 2010s (Figure 3.5). Mean ampeliscid energy densities are generally higher in the 2010s in the Barrow Canyon/DBO5 region, despite the highest mean value occurring in 2000 (Table 3.4).

The mean energy density was calculated each year to estimate the quantity of ampeliscid amphipod energy density lost in the Chirikov Basin/DBO2 region over the study period. The

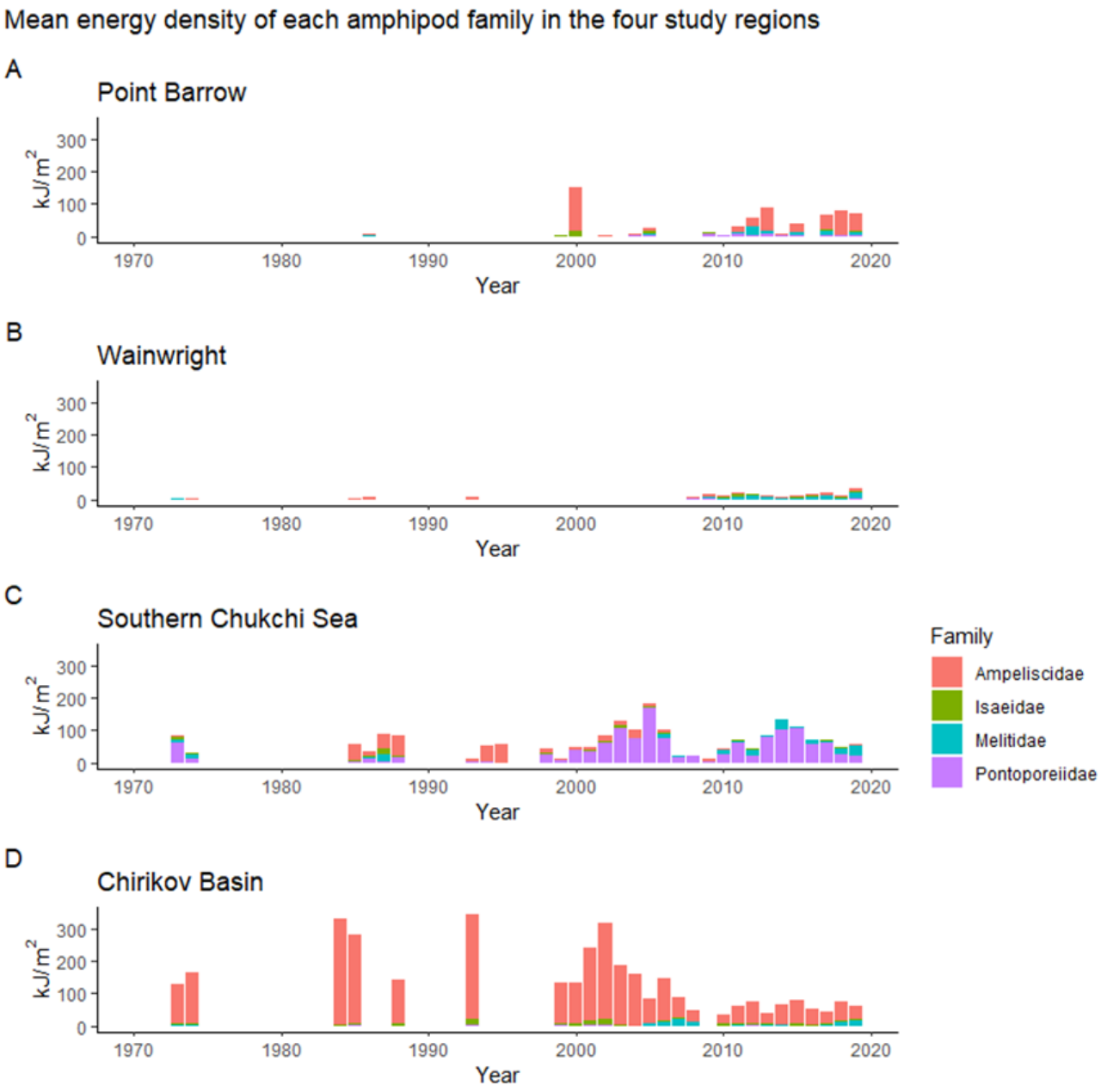

Figure 3.4: Mean energy density measurements of the four dominant amphipod families in the Pacific Arctic Region, grouped by regions where they were collected.

maximum mean energy density for this region occurred in 1984, (347.08 kJ m^{-2}) and the minimum mean energy density occurred in 2010 (31.07 kJ m^{-2}). As a result, over 26 years, the mean amount of energy available from ampeliscid amphipods in the Chirikov Basin declined by approximately 90%.

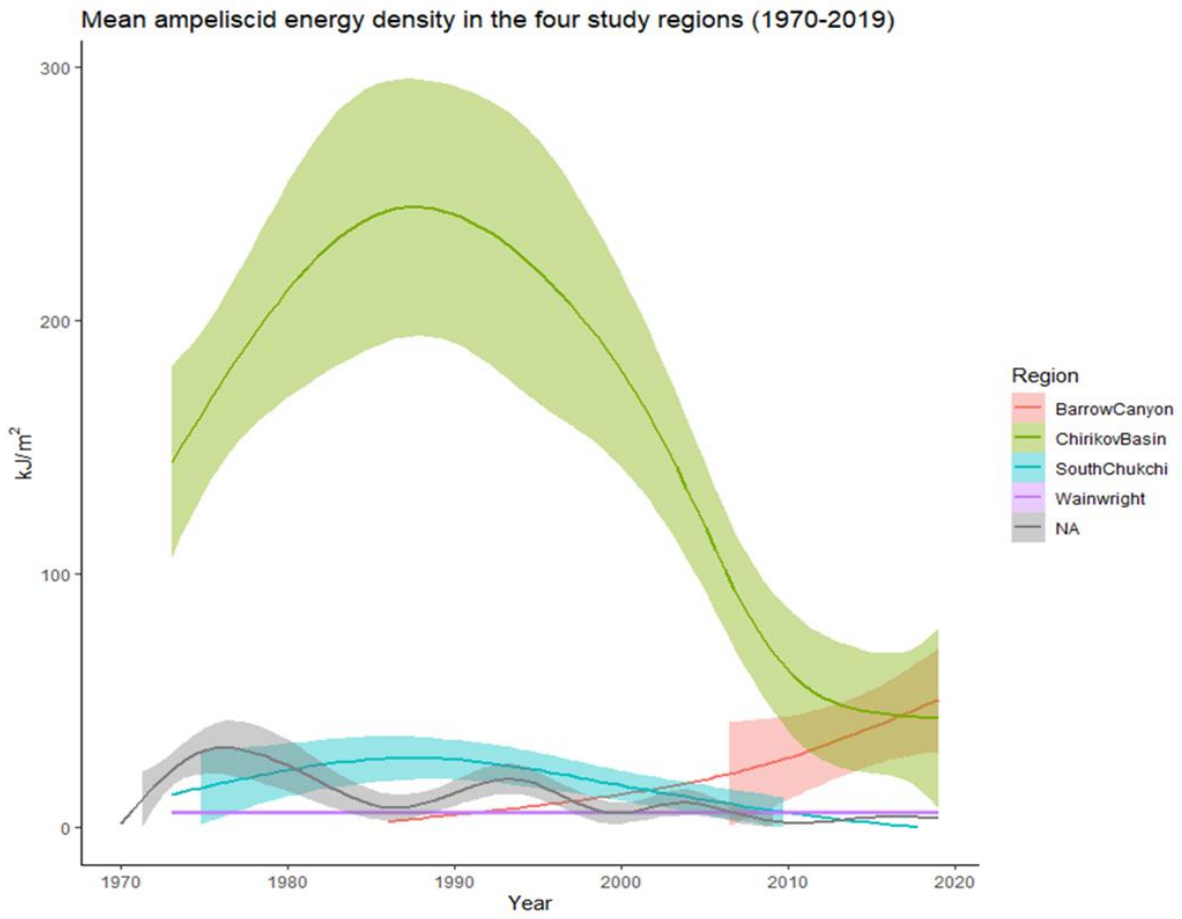

Figure 3.5: Trends in ampeliscid amphipod energy density (1970-2019), grouped into the four regions examined in this study. All measurements outside of the four regions are labelled NA.

Biomass:Abundance

Using the approach of Stewart et al. (2023), the wet weight biomass of ampeliscid amphipod samples was divided by the number of individuals in each sample in a set surface area (m^2) to estimate per capita biomass, or the ratio of biomass to abundance per sample. The mean biomass:abundance for individual ampeliscid amphipods across the whole time series is 49.15±171.57 mg individual^{-1}; the values for the remaining families are 10.02±145.26 mg individual^{-1} for Isaeidae, 93.36±274.83 mg individual^{-1} for Melitidae, and 13.34±22.18 mg individual^{-1} for Pontoporeiidae. The greater amounts of average biomass per individual ampeliscid amphipod in each sample tend to be the earlier samples (~1970s) and are clustered as

darker purple and pink shades (Figure 3.3). The yellows and oranges, corresponding to more recent years, fan outwards to the right of the plot; this translates to decreasing biomass per individual ampeliscid amphipod in each sample (Figure 3.3). Clearly, these patterns can be interpreted as a decline in the ratio of biomass to abundance in each discrete sample, i.e. the average size of ampeliscid amphipods has decreased since 1970. This result is consistent with findings in Stewart et al. (2023) for all benthic crustaceans in the PAR, but our analysis here provides more detail at the family level for Ampeliscidae.

Discussion

It is not surprising that the family Ampeliscidae makes up the majority of the samples in the synthesized time series, since it makes up just more than half of total benthic infaunal crustacean wet weight biomass collected from DBO sites from 2010-2019 (Figure 3.1). It is also not surprising that more than half of the compiled samples in the time series occur within the general region of DBO transects, since these locations were selected because they are known hotspots of benthic production (Grebmeier et al., 2010). Samples from outside of the four DBO regions in this study only made up 16% of the total energy density in the time series, despite having the greatest sample size (Table 3.2). The Chirikov Basin and the southern Chukchi Sea were highest in proportion of total amphipod energy density in the time series (48% and 16%, respectively, Table 3.2), which makes sense since these two regions on either end of the Bering Strait are considered highly productive, both in the benthos and in the water column. Among the samples collected in proximity to DBO transects, the Wainwright/DBO4 region had the highest sample size of amphipod samples collected, but had one of the lowest proportions of amphipod energy density in the time series (10%); while this hotspot is not associated with great numbers of amphipods, it is still considered a productive benthic ecosystem due to overall benthic

biomass observed in the region (Feng et al., 2021). The northeastern Chukchi Sea along the coast of Alaska has also been sampled heavily as part of projects assessing the potential impacts of oil and gas drilling on marine ecosystems (Blanchard et al., 2013). The Point Barrow/DBO5 region had the smallest sample size of amphipod samples in the time series due to a scarcity of data before 2000; in recent years, especially since the inception of the DBO, this region, particularly Barrow Canyon, has been sampled with greater regularity. This region was tied for Wainwright/DBO4 for having the lowest proportion of energy density in the time series (10%, Table 3.2).

The distribution of energy densities is very heavily skewed to the right, as seen in a histogram of raw data frequency (Figure 3.6), mainly due to some highly energy dense samples of Ampeliscidae from the Chirikov Basin. This extreme skewing can also be seen in the mean and median for the whole time series (Table 3.3): the median of the data sits at 0.73 kJ m^{-2}, while

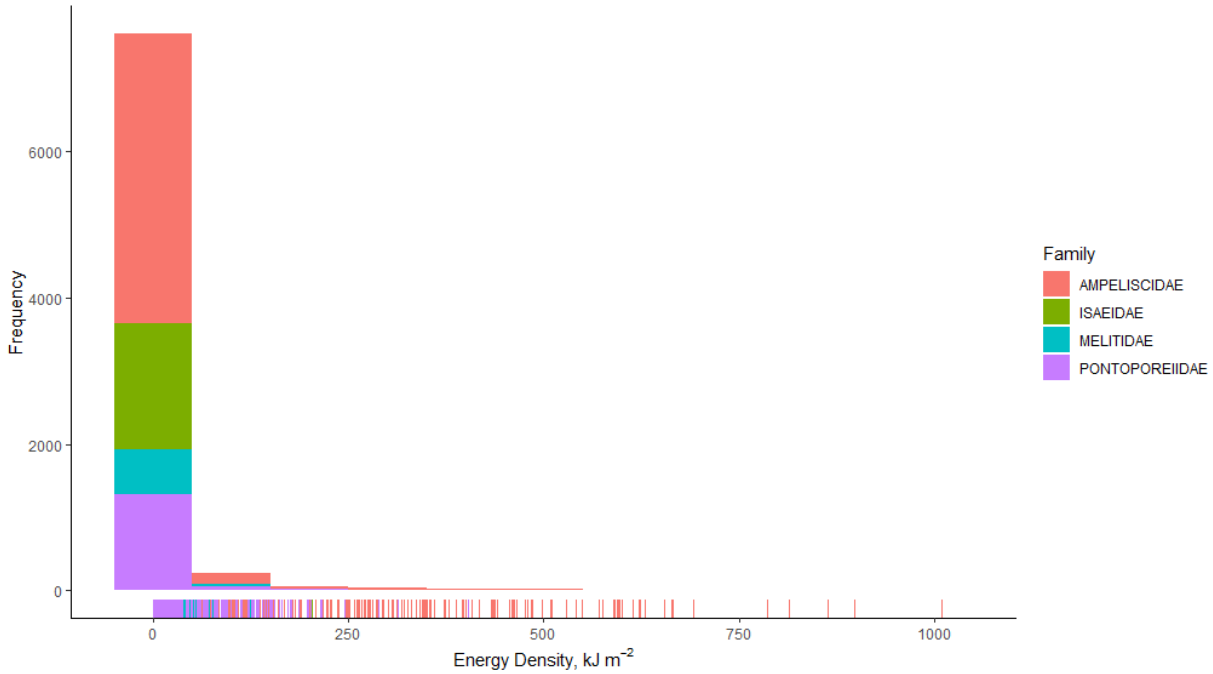

Figure 3.6: A stacked histogram of energy density measurements from the synthesized time series (1970-2019), with families color-coded. Tick marks are included on the x-axis to show outliers that do not appear on the scale of the histogram.

the mean, 13.56 kJ m^{-2}, is pulled upward by the extreme outliers. The top 50 highest energy densities are all from Ampeliscidae, with values ranging from 433.21 to 1,070.87 kJ m^{-2}; 39 of these measurements come from the Chirikov Basin/DBO2, eight from the Point Barrow/DBO5 region, one from the Wainwright/DBO4 area, two from outside of the DBO bounding boxes, and none from the southern Chukchi Sea/DBO3. These results reinforce the finding that ampeliscid amphipods are the dominant benthic amphipod in the PAR, particularly in the Chirikov Basin.

The family Pontoporeiidae is the second most dominant benthic amphipod family by wet weight (Figure 3.1) and energy density (Table 3.1). Pontoporeiid amphipods are particularly dense in the southern Chukchi Sea/DBO3 region, where ampelisicid amphipods are much less common. Moore et al. (2022) reported that there was a shift in the dominant benthic amphipod in the DBO3 region from *Byblis spp.* (Ampeliscidae) to *Pontoporeia femorata*, Krøyer, 1842, (Pontoporeiidae), and the results of this study are consistent with that conclusion. From 1998 onward, the mean energy density of pontoporeiid amphipods is nearly always consistently greater than mean values for ampeliscid amphipods. The exact conditions driving this shift are not fully understood, but, when viewed alongside the dramatic decline in ampeliscid amphipod biomass in the Chirikov Basin/DBO2, it seems reasonable to conclude that conditions south and north of Bering Strait, such as sediment structure or bottom water temperature, have become less suitable for ampeliscid amphipods. Gray whales have been observed feeding in the southern Chukchi Sea in greater numbers in recent years, but it is uncertain what they are feeding on (Bluhm et al., 2007). Other results (Table A2.2) show that the energy contents of ampeliscid and pontoporeiid amphipods may not be significantly different from each other, so *Pontoporeiia femorata* could be a comparable source of food. However, the energy densities (per square meter) of pontoporeiid amphipods in the southern Chukchi Sea/DBO3 are only a fraction of the

energy densities of ampeliscid amphipods observed in the Chirikov Basin/DBO2 during peak densities in the 1980s and 1990s.

The biomass:abundance of ampeliscid amphipods follows the same trend as the per capita biomass metric (biomass per individual amphipod in a sample) for all benthic crustaceans in Stewart et al. (2023) and is consistent with observations made by Highsmith & Coyle (1992) of a size frequency shift in ampeliscid amphipods towards smaller individuals. The comparable results with Stewart et al. (2023) are not unexpected, since ampeliscid amphipods made up slightly more than half of the benthic infaunal crustacean biomass measured in the DBO from 2010-2019 (Figure 3.1). Air and ocean temperatures throughout the Arctic have been rising at an accelerated rate compared to the rest of the globe (Danielson et al., 2020; Screen & Simmonds, 2010), and Highsmith & Coyle (1991) showed that benthic amphipods in the PAR exhibit temperature-dependent growth and maturation rates. In their study, individuals in warmer locations likely matured at an earlier age and smaller size than individuals in colder waters; the continued warming of the Arctic therefore may be partly responsible for the decrease in average body size. This phenomenon has been documented in a variety of other organisms and has the potential to severely disrupt trophic interactions (Daufresne et al., 2009).

Another possible theory for the decrease in biomass:abundance in collected samples is selection by predation. Nerini & Oliver (1983) estimated that gray whales can turn over as much as 9-27% of the northern Bering Sea benthos annually when they excavate their feeding pits on the seafloor, making them a key top-down structuring agent of the benthos. For a long-lived, slow growing benthic amphipod, repeated heavy foraging by a top predator that has been close to carrying capacity in recent years (Moore et al., 2001) could have resulted in selection for smaller body sizes and thus impacting production rates. Grant (1981) observed this pattern in two species

of coastal amphipods that were preyed upon by shorebirds; the removal of larger individuals by bird predation decreased the mean size of the two species and caused them to exhibit negative production values. Highsmith & Coyle (1992) noted that a 26% decrease in ampeliscid amphipod biomass between 1986-1987 was accompanied by reduced densities of larger individuals; they hypothesized that ampeliscid amphipods in the PAR could be sensitive to heavy predation by a growing gray whale population. While it is beyond the scope of this study to fully evaluate these possibilities, further study would help to verify which biological or ecological factors are responsible.

The dramatic decline in ampeliscid amphipod biomass and energy density studied here has serious implications for the energy requirements of gray whales foraging in the PAR. Highsmith & Coyle (1992) published an estimated daily energy requirement for a standardized 19.6 mt individual gray whale, based on their own modeling and the results of three other studies: Rice & Wolman (1971), Sumich (1983), and Thomson & Martin (1986). This energetic requirement averaged 3.8×10^5 kcal day^{-1}, or 1.6×10^6 kJ day^{-1}. If one of these standardized individuals were to feed at maximum efficiency exclusively on ampeliscid amphipods in the Chirikov Basin/DBO2 in a hypothetical scenario, the area of seafloor that they would need to feed on changes dramatically depending on the year of this study. The maximum mean energy density for ampeliscid amphipods in the Chirikov Basin occurred in 1984, with 347.08 kJ m^{-2}, and the minimum mean energy occurred in 2010 with 31.07 kJ m^{-2}. In this scenario, an individual adult in 1984 would need to feed on approximately 4,610 m^2 day^{-1} of seafloor (with maximum feeding efficiency) to achieve this daily caloric requirement, but an individual adult in 2010 would need to feed on approximately 51,497 m^2 day^{-1} of seafloor, more than ten times the area than 26 years earlier. Villegas-Amtmann (2015) estimated the total energy that an adult

female would need for a two-year period to survive and successfully wean a calf to be approximately $118.2x10^4$ MJ; this includes the total cost of pregnancy, $8.7x10^4$ MJ, and the total cost of lactation, $13.3x10^4$ MJ. These massive energy demands emphasize the vulnerability of pregnant and new mothers to a large decline in food availability, particularly for a prey item that they have heavily relied on historically. This scenario is not realistic for how gray whales actually forage for food; they are opportunistic foragers, feeding on benthic or pelagic prey whenever they encounter it in a high enough density (Moore et al., 2003). However, it does highlight the dramatic loss of food energy in what was once a highly productive foraging ground.

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Chapter 4: Conclusions

Benthic amphipod populations in the Pacific Arctic Region (PAR) have been declining in biomass and spatial extent for decades, although the exact causes for this trend are not fully understood (Coyle et al., 2007; Moore et al., 2022). This dramatic loss in biomass has been accompanied by a downturn in available energy per square meter for predators from these populations. However, comparisons to past studies suggest that the energy density per gram of amphipod tissue has not changed. Published caloric contents for some of the most common benthic amphipod taxa in the PAR from Stoker (1978) and Wilt et al. (2014) align quite well with caloric contents measured in this study, despite the many years of separation. Therefore, it seems reasonable to conclude that there are environmental factors that are influencing the shrinking benthic amphipod populations, particularly in the Chirikov Basin, but the average energy density of benthic amphipod tissue has remained relatively constant since the 1970s.

None of the amphipod genera that were measured for caloric content differed significantly from each other when compared with a nonparametric pairwise comparison (Table A2.2). This is not entirely surprising, since other caloric studies that measured a wide variety of taxa in the same region found that numerous closely related taxa did not differ significantly in caloric content (Hondolero et al., 2011; Wacasey & Atkinson, 1987). Therefore, it seems reasonable to conclude that the overall loss of biomass available for predation has had more of an impact on the energy density of these populations than taxonomic differences. The four dominant amphipod families in the PAR are represented in this study, and these are the primary benthic prey for gray whales. However, no direct comparisons can be made within this study to other

benthic invertebrates or other prey items that gray whales may feed on in the PAR, such as cumaceans.

The significant seasonal difference between the two cruises, SWL23 in July and SKQ23 in September-October, merits further investigation, since the samples in this study were only collected in a single year (2023). A seasonal spike in caloric content of amphipod prey could be quite beneficial to gray whales if the phenology of their migration and foraging aligns with the period of higher prey energy content. However, a mismatch in phenology or a weakening of the seasonal signal of water column production and subsequent amphipod energy content due to climate change in the Arctic could reduce the amount of energy that gray whales are able to obtain from these crustacean prey (Kędra et al., 2015; Reeves et al., 2014).

The effects of different forms of preservation on the apparent energy content of amphipod tissues is another complexity that merits further study. While it would be reasonable to assume that formalin-preserved samples would have a higher apparent energy content compared to frozen samples, this difference was not significant at the genus level for *Ampelisca*, the most abundant genus that was sampled. Samples preserved in formalin also had greater variability in apparent energy density, suggesting that using formalin for preservation has variable effects on tissues, which in turn cause variations in energy content that are not present in frozen samples. Hondolero et al. (2012) similarly found that the majority of arthropods measured for caloric content did not vary significantly between preservation methods, but that formalin preserved samples showed a greater degree of apparent variation in energy density. Furthermore, the frozen samples are assumed to replicate freshly caught samples, even though the samples were kept frozen for several months during transport and storage before analysis. Analyzing the caloric

content of fresh samples would ideally be carried out at sea, but this was not possible with the shipboard facilities available.

Geographically, samples from the Wainwright/DBO4 region were significantly higher in energy density than the rest of the samples, an interesting finding that suggests that there were factors that significantly increased the caloric content of benthic amphipods in this region in 2023. Additional work could confirm if this pattern repeats itself in other years, or even if this difference is seasonal and related to conditions at the time of sampling. Lipid-rich ice algae are a more energy dense food source than phytoplankton that are not ice-associated, due to the synthesis of certain essential fatty acids associated with sea ice productivity (McMahon et al., 2006). It seems plausible that there was a significant flux of ice algae to the benthos at the DBO4 sites towards the end of summer in 2023 prior to sample collection, especially since the northeastern Chukchi Sea DBO sites are the furthest north, and therefore are located where sea ice remains the longest. The northeastern Chukchi Sea sediments often have a moderate to elevated concentration of IP25, one of the ice algae-associated lipid biomarkers, so it is reasonable to hypothesize that ice algal production and subsequent export, advection, and resuspension maintain a year-round source of sea ice algal material to the benthos (Koch et al., 2020). However, without further analysis of the biochemical makeup of the amphipods and of sediment biogeochemistry, this hypothesis remains to be tested.

Since the “fresh” energy densities of samples (per square meter) in the time series are converted from biomass measurements, the trends in energy density closely follow the trends in biomass from 1970-2019. There is a noticeable decreasing trend in spatial energy density throughout the PAR, particularly in the Chirikov Basin, between St. Lawrence Island and the Bering Strait. Biomass and energy density were highest in the Chirikov Basin during the 1980s

and 1990s, which is also when gray whales were observed in the highest densities in this region (Bluhm et al., 2007; Moore et al., 2022). Since the 1990s, amphipod biomass and energy density have dropped noticeably, accompanied by a significant downturn in gray whale sightings in the Chirikov Basin (Moore et al., 2022). Increased sightings of gray whales further north in the Chukchi and Beaufort Seas in recent decades reinforces the notion that the Chirikov Basin is no longer a prime foraging ground; instead, it seems that gray whales are migrating further north in search of food in greater numbers (Bluhm et al., 2007; Grebmeier et al., 2006b; Moore et al., 2022).

Evidence from the two recent Unusual Mortality Events (UMEs) involving gray whales, the first from 1999-2000 and the second from 2019-2023, suggest that a significant amount of energy has been lost from gray whale foraging grounds in the Arctic. During both UMEs, emaciated and malnourished whales were observed at a higher rate than normal, and body conditions were noticeably decreased in many observed whales (Moore et al., 2003; Raverty et al., 2024). During the most recent UME from 2019-2023, post-mortem examinations of beached whales revealed many to be malnourished and severely underweight; furthermore, stomach contents of some whales even contained large amounts of plant material and woody debris, indicating that the whales were feeding in benthic habitat that was not suitable (Raverty et al., 2024). Being opportunistic foragers, gray whales should be able to prey switch when an adequate food source is available, both on the seafloor or in the water column (Brower et al., 2017). Gray whales were observed in abundance in the Chirikov Basin in the 1980s and 1990s because there was a high density of benthic prey that was available year after year; however, in light of the contraction of amphipod biomass and energy density from the Chirikov Basin and the two recent

UMEs, it seems reasonable to conclude that gray whales may not have yet found alternate sources of food to fully support a growing population.

As the gray whale population recovers from the most recent UME (2019-2023), it will be helpful to determine exactly what they are feeding on and what proportion of their diet is still benthic. The disruption of benthic-pelagic coupling in the Pacific Arctic and associated loss of benthic biomass has negative implications for all benthic-feeding predators, including gray whales (Grebmeier et al., 2006b). Gray whales are able to opportunistically feed on zooplankton crustaceans in the water column, but it is unclear if this is an energy-efficient method of foraging, compared to their apparent preference for benthic foraging (Hildebrand et al., 2021). Furthermore, feeding in the water column on copepods and euphausiids can potentially put gray whales in competition with other baleen whales in the Pacific Arctic, such as bowheads, humpbacks, fins, and minkes (Brower et al., 2018; Reeves et al., 2014). The Pacific Coast Feeding Group (PCFG) of gray whales is able to survive by foraging on benthic and pelagic prey along the coasts of Vancouver Island and the Pacific Northwest, but this population is, at most, a couple hundred whales (Calambokidis et al., 2017). The whole of the Eastern North Pacific gray whale population is usually two orders of magnitude larger than the PCFG (as high as 26,960 gray whales in 2015/2016; Eguchi et al., 2024), and most of this population is still returning to the Arctic annually to forage. Therefore, it seems the foraging grounds used by the PCFG are not able to support the much larger proportion of the ENP population that returns to the Arctic to forage.

A next step for this project would be to determine the biogeochemical features of benthic amphipods in the PAR that make them such a high-quality, sought after source of food. A relatively simple variable that could be incorporated into a future caloric study is determining the

lipid composition of amphipods and other prey items. The percentage of lipids per weight could be compared to the caloric content to determine if there is a significant relationship. An inverse relationship between the caloric contents of lipids and proteins would mean that organisms with higher proportions of lipids in their tissues should be more calorically dense (Percy, 1979). Furthermore, lipid biomarkers that are associated with ice algae could be analyzed in the amphipod tissues to determine how much of their diet is composed of ice algae. If ice algae are a high-quality source of food for benthic deposit and filter feeders, then a high proportion of ice algae in an amphipod diet may increase their quality as food themselves. If this should prove true, then the decline of sea ice extent and overall ice algal production could further reduce the energy contents of benthic invertebrates on a spatial basis.

While not the main focus of this study, the reduction in biomass per individual for ampeliscid amphipods since the 1970s is an interesting trend that could be part of the larger trend towards a reduction in body size in organisms globally in response to a warming climate (Daufresne et al., 2009). To explore this further, a size class comparative study could be carried out for ampeliscid amphipods in the Chirikov Basin and compared to results published previously in the 1990s (Highsmith & Coyle, 1990 & 1991). In addition to documenting size classifications, those prior studies determined productivity values for ampeliscid amphipod populations in the Chirikov Basin, determining that the apparent high production is due to a high standing biomass of larger individuals (Highsmith & Coyle, 1990). The Highsmith & Coyle (1991) study determined that benthic amphipods exhibit temperature-dependent growth and maturation rates, which is something that could be revisited in the context of bottom water temperatures in the Chirikov Basin that have warmed since the time of that prior study (Moore et al., 2022). Comparing modern-day values to those measured by Highsmith & Coyle could shed

some light on how these amphipod populations are responding physiologically to a warming climate and ocean.

Continued monitoring of benthic amphipod populations through abundance and biomass measurements should occur in tandem with continued monitoring of gray whale populations. If benthic amphipods continue to be important elements of the gray whale diet, then it is imperative to understand and monitor the decline in biomass throughout the PAR; if another UME occurs in the next few decades due to declining food quality and malnourishment, then there could be long-term impacts for gray whale populations and recruitment. Notwithstanding these uncertainties, if benthic amphipods are no longer available in adequate quantities, then responses to future UMEs could also emphasize other dangers that gray whales are facing in a changing ocean, including vessel strikes, entanglement in fishing gear, parasites, disease, pollutants, and toxins from harmful algal blooms (Raverty et al., 2024; Reeves et al., 2014). On the other hand, if UMEs do not re-occur in the next few decades and benthic amphipod biomass remains low, then it is possible that gray whales will have found an adequate replacement for benthic amphipods in their diet. In any case, it is imperative that until we more clearly understand the mechanisms behind the loss of benthic amphipod biomass and the linkages to recent UMEs for gray whales, continued monitoring is needed.

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Appendices

Appendix 1

Appendix Table A1: A list of all of the cruises from which benthic macrofaunal invertebrate biomass and abundance measurements were taken for synthesis in the time series analysis done in Chapter 3. The year and Principal Investigator are included. For additional information or access to this data, contact Alynne Bayard (bayard@umces.edu) with the Grebmeier-Cooper Lab, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Sciences.

Cruise	Year(s)	Principal Investigator
AK47	1988	Grebmeier, J.
AMB15	2015	Iken, K.
AMB17	2017	Iken, K.
B2008	2008	Blanchard, A.
COM09	2009	Grebmeier, J.
COM10	2010	Grebmeier, J.
HL172	2017	Pickart, R.
HL181	2018	Pickart, R.
HL191	2019	Pickart, R.
HL201	2002	Grebmeier, J.
HL203	2002	Cooper, L.
HL402	2004	Grebmeier, J.
HL403	2004	Cooper, L.
HL601	2006	Grebmeier, J.
HL702	2007	Grebmeier, J.
HL801	2008	Cooper, L.
HL802	2008	Cooper, L.
HL901	2009	Cooper, L.
HLY12	2012	Grebmeier, J.
HX059	1984	Grebmeier, J.
HX073	1985	Grebmeier, J.
HX074	1985	Grebmeier, J.
HX085	1986	Grebmeier, J.
HX139	1990	Grebmeier, J.
HX171	1993	Grebmeier, J.
HX177	1994	Grebmeier, J.
HX189	1995	Grebmeier, J.
HX214	1998	Grebmeier, J.
HX224	1999	Grebmeier, J.
J2010	2010	Jewett, S.
J2011	2011	Jewett, S.

J2012	2012	Jewett, S.
LAU00	2000	Grebmeier, J.
LAU01	2001	Grebmeier, J.
LAU02	2002	Grebmeier, J.
LAU03	2003	Grebmeier, J.
LAU04	2004	Grebmeier, J.
LAU05	2005	Grebmeier, J.
LAU06	2006	Grebmeier, J.
LAU07	2007	Grebmeier, J.
LAU08	2008	Grebmeier, J.
LAU10	2010	Grebmeier, J.
LAU11	2011	Grebmeier, J.
LAU12	2012	Grebmeier, J.
LAU13	2013	Grebmeier, J.
LAU14	2014	Grebmeier, J.
LAU15	2015	Grebmeier, J.
LAU16	2016	Grebmeier, J.
LAU17	2017	Grebmeier, J.
LAU18	2018	Grebmeier, J.
LAU19	2019	Grebmeier, J.
LAU98	1998	Grebmeier, J.
LAU99	1999	Grebmeier, J.
NO871	1987	Feder, H.
OC862	1986	Feder, H.
OC863	1986	Feder, H.
OK93	1993	Grebmeier, J.
PS01	2001	Grebmeier, J.
PS010	2010	Grebmeier, J.
RUS04	2004	Grebmeier, J.
RUS09	2009	Grebmeier, J.
RUS12	2012	Grebmeier, J.
SHL08	2008	Grebmeier, J.
SHL09	2009	Grebmeier, J.
SHL10	2010	Grebmeier, J.
SL99	1999	Grebmeier, J.
STOKE	1970-1974	Stoker, S.
SU872	1987	Feder, H.
W2009	2009	Blanchard, A.
W2010	2010	Blanchard, A.
W2011	2011	Blanchard, A.
W2012	2012	Blanchard, A.
XUE08	2008	Cui, S.

Appendix 2

The results of statistical comparisons between preservation methods and cruises using Kruskal-Wallis rank sum tests and comparisons among amphipod genera and DBO regions where they were collected using pairwise comparisons using Wilcoxon rank sum tests. These results were not included in the main body of the thesis due to sample size concerns but are included in the Appendix for reference.

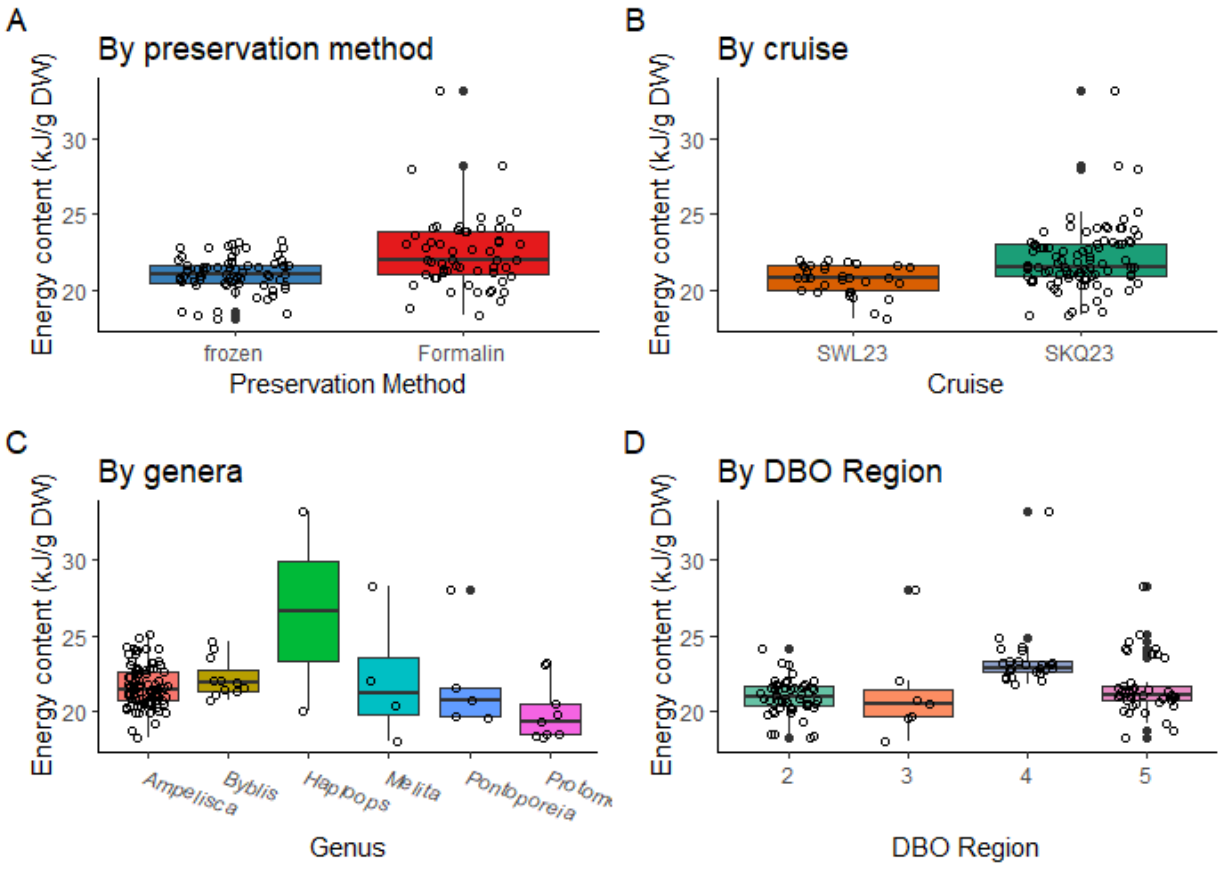

Figure A2.1: Energy content measurements in kJ/g DW (Dry Weight) using all amphipod samples to compare **A)** preservation method (frozen, n = 67; formalin-preserved, n = 56), **B)** cruise/season (SWL23/July, n = 31; SKQ23/Sept-Oct, n = 92), **C)** genera (*Ampelisca,* n = 92; *Byblis*, n = 11; *Haploops*, n = 2; *Melita*, n = 4; *Pontoporeia*, n = 5; *Protomedeia*, n = 9), and **D)** DBO region (DBO2, n = 50; DBO3, n = 7; DBO4, n = 25; DBO5, n = 41).

Table A2.1: Results of the Kruskal-Wallis rank sum tests performed on all caloric content measurements made in Chapter 2 of this study to test for significant differences between preservation methods, cruises/season, genera, and DBO regions sampled from.

	Variable	chi-squared	p-value
All samples	Preservation Method (frozen vs. formalin)	13.632	0.00022
	Cruise/Season (SWL23/July vs. SKQ23/Sept-Oct)	12.834	0.00034
	Genus (*Ampelisca, Byblis, Haploops, Melita, Pontoporeia, Protomedeia)*	10.621	0.059
	DBO Region (DBO2 vs. DBO3 vs. DBO4 vs. DBO5)	37.059	4.47E-08

Table A2.2: Results of pairwise comparisons using the Wilcoxon rank sum tests looking for significant differences in caloric content among samples of different genera and among DBO regions sampled from.

Pairwise comparisons among genera

	Ampelisca	*Byblis*	*Haploops*	*Melita*	*Pontoporeia*
Byblis	1.000	-	-	-	-
Haploops	1.000	1.000	-	-	-
Melita	1.000	1.000	1.000	-	-
Pontoporeia	1.000	1.000	1.000	1.000	-
Protomedeia	0.075	0.136	1.000	1.000	1.000

Pairwise comparisons among DBO regions

	DBO2	DBO3	DBO4
DBO3	0.579	-	-
DBO4	2.40E-09	0.012	-
DBO5	0.579	0.579	6.10E-05

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