Yay Copepods

A Thesis
Presented to
The Established Interdisciplinary Committee for Environmental Studies
Reed College

In Partial Fulfillment
of the Requirements for the Degree
Bachelor of Arts

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May 2025

List of Abbreviations

You can always change the way your abbreviations are formatted. Play around with it yourself, use tables, or come to CUS if you'd like to change the way it looks. You can also completely remove this chapter if you have no need for a list of abbreviations. Here is an example of what this could look like:

ENSO	El Niño Southern Oscillation
OCNMS	Olympic Coast National Marine Sanctuary
OMZ	Oxygen Minimum Zone
IPC	Intergovernmental Policy Council
NOAA	National Oceanic and Atmospheric Administration
PMEL	Pacific Marine Environmental Laboratory
OME	Ocean Molecular Ecology
PPS	Phytoplankton and Particle Sampler
TH042	Teawhit Head, 42 meter deep mooring
DVM	Daily Vertical Migration

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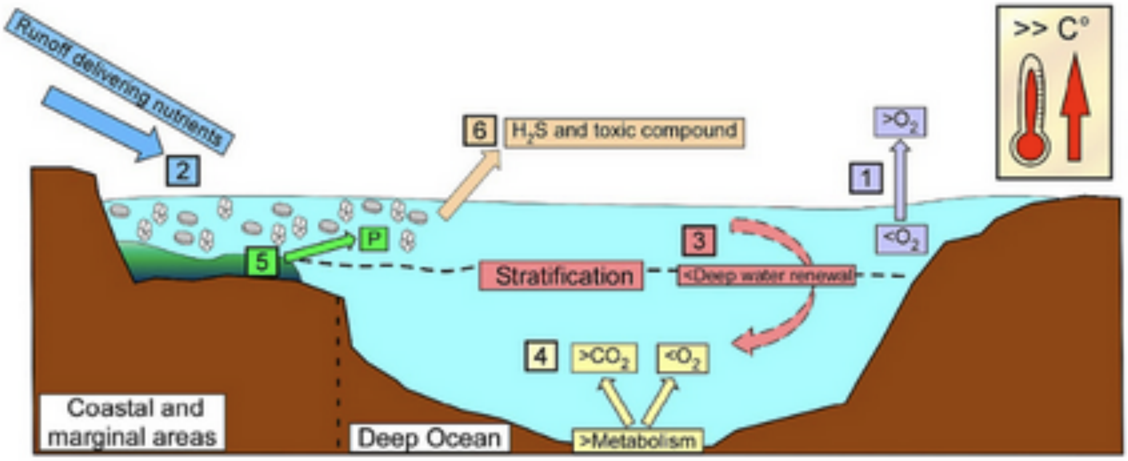
Introduction

Figures are currently uncaptioned and some are placeholders. They are placed near the paragraphs that will reference them, but I haven't properly referenced most of them yet. I've been using CO1 for the primer, if it is actually spelled COI I can change it.

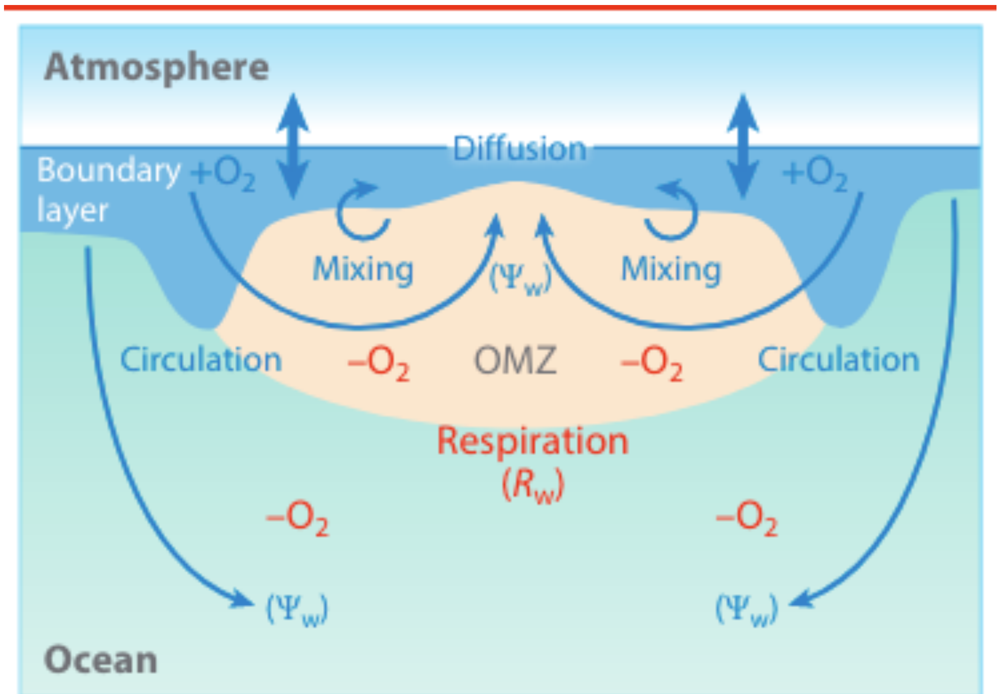
0.1 Climate Change, Hypoxia, and OCNMS

Due to human greenhouse gas emissions, the Earth's oceans are warming and losing oxygen. Over 90% of the excess heat trapped by greenhouse gases has been absorbed by the ocean, causing a significant increase in temperature in most regions in the ocean (Bindoff et al. 2013). According to the United Nations Intergovernmental Panel on Climate Change, the global sea surface temperature has risen 0.65 ºC above pre-industrial levels as of 2022 (Pörtner et al. 2019). This warming has reduced the solubility of dissolved oxygen in water, which accounts for 15-50% of the climate change driven oxygen decrease in the global ocean (Helm, Bindoff, and Church 2011; Ito et al. 2017; Schmidtko, Stramma, and Visbeck 2017). The loss of 0.5-3.3% of the open ocean's oxygen down to 1000 m depth is very likely, and it is very likely that oxygen minimum zones are expanding (Bindoff et al. 2013). This decline has been particularly pronounced in the North Pacific, where this study is located (Bindoff et al. 2013; Ito et al. 2017). The rest of the decrease is caused by decreased sea-air and surface ocean-deep ocean oxygen flux due to increasing stratification (Barth et al. 2024; Mancini 2024; Pörtner et al. 2019). Ocean stratification refers to the way that layers of ocean water with different densities form, restricting heat, carbon, and oxygen exchange between layers of different depths. This density difference is primarily caused by differences in temperature and salinity between water masses. As the ocean's surface water warms, it becomes less dense, increasing the magnitude of the density difference between surface and deep waters and increasing stratification by 5.3% globally between 1960 and 2018 (G. Li et al. 2020). This increased stratification decreases the flow of nutrients and oxygen to the deeper layers of the ocean.



4. Sketch showing the main biogeochemical and oceanographic changes related to deoxygenation in response to warming.

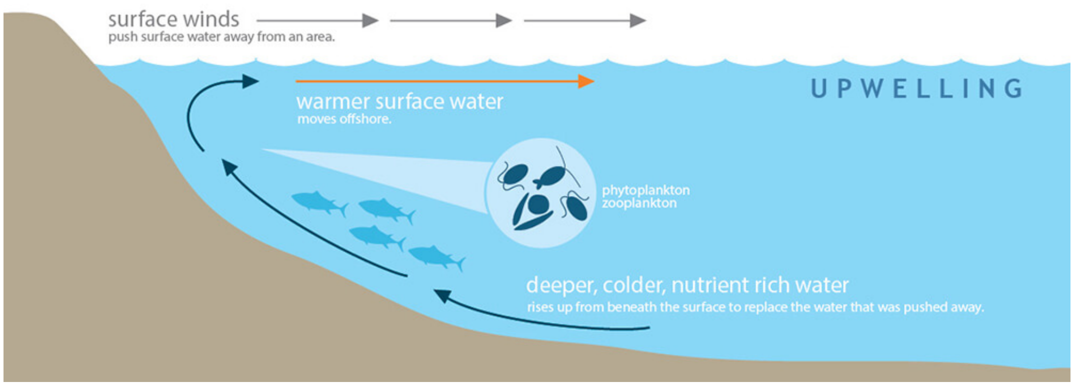
The surface ocean has a relatively high dissolved oxygen concentration, because the atmosphere and the surface ocean rapidly exchange oxygen in order to equilibrate the partial pressure of oxygen in both systems (Ito and Deutsch 2010). According to a 1948 study, 40% of air-sea exchange at a study site in the Gulf of Maine was due to organisms producing and consuming oxygen, while the remaining 60% of the exchange was due to the solubility of oxygen in water (Redfield 1948). Because the upper ocean receives sunlight, phytoplankton live there and photosynthesize, producing oxygen that primarily remains in the ocean (C. Li et al. 2020). However, the rate at which oxygen leaves the ocean is increasing as the ocean's temperature increases (C. Li et al. 2020). Ocean circulation moves this oxygen to the deep ocean over the course of centuries, where the oxygen is consumed via respiration but cannot be replenished by photosynthesis or atmospheric exchange (Karstensen, Stramma, and Visbeck 2008; Deutsch, Penn, and Lucey 2024; Ito and Deutsch 2010). As a result, deeper ocean waters are lower in oxygen, and the middle of the water column is the most oxygen-poor due to its relative stillness, with the Oxygen Minimum Zone (OMZ) in the middle of the Pacific Ocean water column ranging from less than [1 µmol/kg] to [45 µmol/kg] compared to the [61-120 µmol/kg] of shallower waters along the Oregon and Washington coasts in the summertime (Karstensen, Stramma, and Visbeck 2008; Deutsch, Penn, and Lucey 2024; Barth et al. 2024; Pierce et al. 2012; Wyrtki 1962) (see Figure [OMZ]).



As a result of these interactions, as well as increased nutrient inputs from agriculture causing eutrophication, hypoxic events in which the oxygen concentration in water becomes low enough to harm or kill marine organisms are increasing in frequency, duration, and severity throughout the world's oceans. Most marine organisms require oxygen to survive, and these hypoxic events can cause severe fish die-offs or force migrations which change the distribution of species (Pihl, Baden, and Diaz 1991; Miller, Poucher, and Coiro 2002). Because different species have different tolerances to hypoxia and different levels of mobility, not all species distributions will be affected in the same way by hypoxia, which may result in predator and prey populations becoming offset from each other.

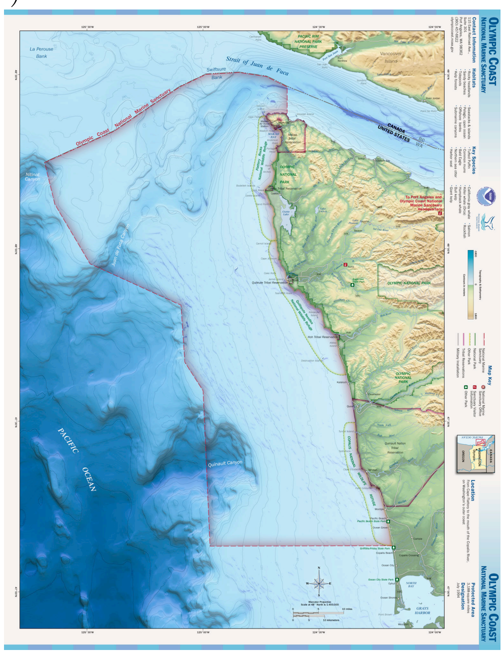
Understanding the effects of this global decrease in ocean oxygen levels is crucial to predicting the overall effects of climate change on the oceans and to developing climate-aware management strategies for marine resources. Studies of the effects of hypoxia on marine organisms use a variety of lab and fieldwork methods. Laboratory experiments on hypoxia's effects typically involve subjecting organisms to different levels of dissolved oxygen over a certain period of time, then measuring factors such as survival, growth rate, metabolism, and reproductive rate in order to determine whether the hypoxia has a negative effect (Steckbauer, Klein, and Duarte 2020). Field studies typically entail measuring dissolved oxygen levels and organismal abundance, using methods such as satellite tagging and trawl surveys that vary by scale and organism type (for example, (Keister, Winans, and Herrmann 2020)). Field experiments have more ecological relevance, but present difficulties in untangling the effects of other environmental factors (Borges et al. 2022; Boyd et al. 2018).

This study will focus on hypoxia in Olympic Coast National Marine Sanctuary (OCNMS), off the coast of Washington state, U.S.A.. The Olympic Coast is an upwelling zone, meaning that when summer winds push the surface water offshore, nutrient-rich and oxygen-poor water flows upwards from the deep Pacific Ocean towards the coast ("Oceanography — Olympic Coast National Marine Sanctuary," n.d.; Hickey and Banas 2003). After this oxygen-poor water reaches the shallower waters of the continental shelf, respiration and decaying organic matter on the continental shelf reduce the water's oxygen content even further (Pierce et al. 2012). Hypoxic events in OCNMS often occur in the summer, are driven by upwelling, not nutrient runoff, and are increasing in severity (Barth et al. 2024). Hypoxic zones have occurred annually in the US Pacific Northwest since 2002, and their increasing size and severity has been linked to climate change. These nutrients sustain a rich ecosystem with high primary productivity, but as oceans warm and the deep water gets progressively more hypoxic, the seasonal hypoxic events in OCNMS are increasing in their severity and duration, which will eventually harm organisms more than the nutrients help them. Additionally, as climate change warms the land and ocean at different rates, the summer winds that cause upwelling are getting stronger, resulting in upwelling events that push more deep water up towards the coast (Barth et al. 2024).



OCNMS is located off the Olympic Peninsula of Washington state, and extends 25 to 45 miles into the ocean. It regularly experiences rough seas, wave heights up to 49 feet, and intense winter storms. The sanctuary contains a wide variety of habitats, including rocky shores, kelp forests, sandy seafloor, and deep ocean canyons. The sanctuary is home to many marine mammals, fish, invertebrates, and seaweeds, and is a major feeding area for migrating seabirds. The sanctuary covers habitat for rockfish, salmon, halibut, Dungeness crab and other ecologically, commercially, and culturally important species of the Olympic Coast ("Fish — Olympic Coast National Marine Sanctuary," n.d.). Within the sanctuary, prohibited activities include oil, gas, and mineral development; discharging certain types of waste from boats; moving or injuring historical resources; seabed drilling; taking or possessing any marine mammal, bird, or turtle; disturbing marine mammals or birds with low-flying aircraft; Department of Defense bombing activities ("15 CFR Part 922 – National Marine Sanctuary Program Regulations," n.d.). The Olympic Coast National Marine Sanctuary Advisory Council provides advice on the sanctuary's management. The council is comprised of representatives of Native American tribes, state and local governments, other federal agencies, maritime industry, fishing, education, tourism, conservation organizations, and the community. The sanctuary lies within the Usual and Accustomed treaty fishing, hunting, and gathering areas of the

Hoh Tribe, Makah Tribe, Quileute Tribe, and the Quinault Indian Nation, or the Coastal Treaty Tribes. Fisheries and other marine resources off the Olympic Coast are co-managed by the state of Washington, the United States (specifically the National Oceanographic and Atmospheric Administration's Office of National Marine Sanctuaries), and the Coastal Treaty Tribes, who formed the Olympic Coast Intergovernmental Policy Council (IPC) in 2007 to provide a forum for resource managers ("Intergovernmental Policy Council — Olympic Coast National Marine Sanctuary," n.d.).

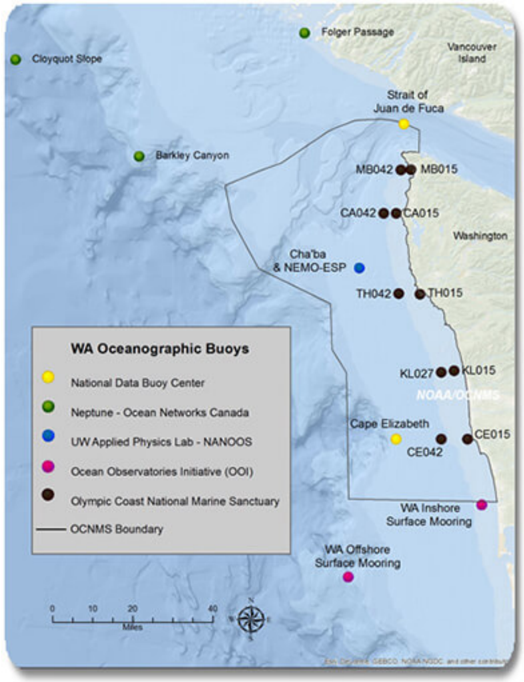


0.2 Environmental DNA

Environmental DNA (eDNA) is the genetic material present in the environment, including extracellular DNA, fragments of cells and tissues, and entire small organisms (Power et al. 2023). In marine environments, eDNA can be filtered out of the water and sequenced to detect many species at the place and time where the water sample was collected. eDNA is a powerful tool for detecting multiple species at once with relatively little sampling effort, but it cannot detect more specific data such as size, sex, and age. The general process of eDNA sampling begins by physically filtering seawater with 0.4 micron filters, then extracting and amplifying the resulting DNA and chromosome fragments using polymerase chain reaction (PCR) (Power et al. 2023). PCR for eDNA studies is conducted using general primers, small pieces of DNA that attach to and duplicate regions of DNA common across species. After this amplification, the resulting fragments of DNA are sequenced using high-throughput sequencing and then identified using a process called metabarcoding. The sequence fragments are compared to a reference database of genes sequenced from known species, allowing the species present in the water column at the time of sampling to be identified through only a small region of their genome known as a barcoding region (Miya 2022). eDNA can detect species with relatively high spatial resolution, from as little as 60 meters in a kelp forest (Port et al. 2016)— to 800 meters in deep-water habitats in Maizuru Bay, Japan (Yamamoto et al. 2017), because eDNA levels drop below the detection limit soon after being released via diffusion and decay. However, our understanding of how far eDNA can migrate in the environment is still relatively limited, and eDNA dispersal and decay can be affected by a number of environmental factors (Cristescu and Hebert 2018). Because of the high sensitivity of eDNA methods, contamination must be diligently avoided. Because metabarcoding requires reference sequences, any species whose barcoding region in question has not been sequenced cannot be detected by a study (Miya 2022). This is not an issue with heavily-studied species like salmon, but can present an issue in other areas. eDNA metabarcoding results provide read abundances, or numbers of DNA fragments, but these are affected by PCR replication efficiency, so they are difficult to compare between different species and methods (Miya 2022). While it is difficult to get quantitative results from eDNA, it is possible to calculate a metric of relative abundance within species known as eDNA index. Kelly et al. used simulations and found that this index accurately captures trends in the biomass of detected organisms. eDNA index is calculated in two steps. First, the read counts of each species within a sample are converted to a proportion of reads within the sample. Then, within each species, those proportions are normalized to range from zero to 1. After this, each species has one sample where it has an eDNA index of one, and that is the sample where that species was most abundant. This method cannot be used to compare different species, only to determine trends within each species, and it will be used in this study (Kelly, Shelton, and Gallego 2019).

Since 2021, the National Oceanic and Atmospheric Administration's Pacific Marine Environmental Laboratory (NOAA PMEL) Ocean Molecular Ecology (OME) lab has been collecting eDNA samples in OCNMS using a modified McLane phytoplankton and particulate sampler (PPS). The PPS was deployed for four, month-long intervals between May 2021 and August 2023, at the Teawhit Head 42 meter depth mooring (see Figure [OCNMSbuoymap]). This sampler collected, filtered, and preserved 1 L water samples every 36 hours. Samples were taken using 0.4 micron filters taken off the sampler, preserved in 95% ethanol, frozen, and taken to the lab. Additionally, some samples were taken using Niskin bottles during PPS deployment and recovery. These samples were filtered using Sterivex filters and vacuum filtration? . In total, 84 samples were collected in 2021, 122 in 2022, and 60 in 2023. 24 of these samples had three PCR technical replicates each. eDNA was extracted from the samples according to the DNeasy Blood and Tissue Kit protocols with adaptations from Spens et al. 2017 (Spens et al. 2017). The full protocol is available on the Ocean Molecular Ecology Zenodo (Weinrich and Gold 2025). This study focuses on copepods, and only uses data from the CO1 (mitochondrially encoded cytochrome c oxidase I, a common barcoding gene for studies on eukaryotes) primer. Amplified regions were sequenced using the Leray F / mICOlinF forward primer and Folmer R / HCO2198 reverse primer, according to OME protocols (Gold, Weinrich, and Brown 2024; Spens et al. 2017). The CO1 sequences were then matched to available reference genomes, resulting in species detection data that includes the number of reads (DNA strands) of each species detected. After bioinformatics and quality filtering, the total number of reads with the CO1 primer was 2,454,571, with 611,924 from copepods. The highest number of reads in one sample was 62,940, and the highest number of copepod reads in a sample was 19,335.

My summer 2024 research included combining the results of these eDNA detections with oceanographic measurements collected by the Teahwhit Head oceanographic mooring in 42 meter deep water (TH042), where the PPS sampler was deployed. I first matched the species detections to their associated metadata, including the sample date and time, using their unique sample IDs. I then matched each of those detections to the oceanographic mooring measurements that were closest to their sample date and time. The Teawhit Head mooring collects data on temperature, pH, salinity, dissolved oxygen, and other physical conditions every 10 minutes, so the environmental data was extremely close to the eDNA samples in both space and time. The resulting dataset contains detections and non-detections of 674 species, with their associated dates, times, oceanographic conditions, and number of DNA reads. I then conducted preliminary data analysis focusing on a list of 64 priority species identified by OCNMS and the Makah, Quileute, Hoh, and Quinault coastal treaty tribes bordering the sanctuary. The species were identified as priorities because of their cultural, economic, and biological significance, and the 2021 and 2022 eDNA sampling data detected 24 of those species. After calculating binomial regressions comparing oxygen saturation to species presence and absence, I found that a northern copepod, Pseudocalanus mimus, became less common during hypoxic events, and a southern copepod, Paracalanus sp. C AC-2013, became more common during hypoxic events. Because copepods are so important to the OCNMS food web, and because of the potentially interesting pattern of northern and southern copepods having different levels of hypoxia tolerance, further research into how these species respond to changes in dissolved oxygen and temperature is warranted (Fisheries 2024). The combined eDNA and oceanographic data contains detections of 20 species of copepods, with 17 of those detected in 2021-2022, which is the time period for which the TH042 mooring was taking dissolved oxygen measurements.



0.3 Copepods

Copepods are crustacean zooplankton of the class Copepoda, formerly combined with the class Thecostraca under the class Hexanauplia (Oakley et al. 2013; Lozano-Fernandez et al. 2019). Copepods are abundant in nearly every body of water on Earth, including oceans, freshwater, groundwater, and New York City's tap water (Vakati et al. 2023; Berger 2004). Copepods are an important component of marine and freshwater food chains, as they eat phytoplankton and are eaten by a wide variety of fish. Some copepods are fish parasites (Vakati et al. 2023). This study will focus on free-living marine copepods found in OCNMS. In the northeast Pacific Ocean, copepods are important food sources for many pelagic fishes, including juvenile salmon (Brodeur and Pearcy 1990). The copepod species most commonly found in OCNMS are classified as Northern (cold-water) and Southern (warm-water) based on their seasonal pattern of occurrence (See Table 1,(Fisheries 2024; Peterson and Keister 2003; Peterson and Miller' 1977)). Northern copepods, especially Calanus marshalls and Pseudocalanus mimus, are known to be more lipid-rich and serve as important food sources for salmon populations (Fisheries 2024). In the North Pacific, where this study is located, *Calanus pacificus* is the dominant *Calanus* copepod (Star and Mullin 1981), and in Arctic ecosystems *Calanus* copepods play an important role in food webs by consuming diatoms and being a large component of fish and bird diets (Falk-Petersen et al. 2007). In studies of the Oregon coast, *Pseudocalanus*, *Acartia*, *Oithona* and *Calanus* were the dominant genera in the summer, while *Paracalanus* and *Ctenocalanus* dominated in the winter (Peterson and Miller' 1977; Peterson and Keister 2003). Copepods are eaten by herring and juvenile salmon, especially chum and sockeye salmon, off the west coast of North America. (Brodeur and Pearcy 1990;

Friedenberg, Bollens, and Rollwagen-Bollens 2012). Because of their importance to the food chain, it is important to understand how copepod populations are affected by hypoxic events, and how they might be affected by worsening hypoxia in the future as climate change intensifies.

Literature on copepod hypoxia tolerance is limited, but the existing literature indicates that dissolved oxygen levels below 0.9-1.5 mg/L can kill many copepods within days, and levels below 0.66-0.9 mg/L kill nearly all copepods (He et al. 2021; Marcus et al. 2004; Stalder and Marcus 1997; Grodzins, Ruz, and Keister 2016). However, hypoxia exposure does not appear to impact copepod eggs (Invidia, Sei, and Gorbi 2004). Oxygen levels above 1.7 mg/L are generally safe for copepods (Grodzins, Ruz, and Keister 2016). In situ zooplankton abundance is generally lower at sites with dissolved oxygen levels of 2 mg/L or lower, and copepod abundance is extremely low below 1 mg/L (Keister, Winans, and Herrmann 2020; Roman et al. 1993). Additionally, copepods behaviorally avoid dissolved oxygen levels between 1.0 and 2.0 mg/L in lab and field observations (Keister, Winans, and Herrmann 2020; Roman et al. 1993; He et al. 2021; Elliott, Pierson, and Roman 2012; Keister and Tuttle 2013), although Marcus & Stalder 1997 did not find this pattern (Marcus & Stalder 1997). These patterns vary by age and sex, but the environmental DNA methods used in this study are unable to distinguish these characteristics (He et al. 2021). These patterns also differ between species and populations, which this study does hope to address (Grodzins et al. 2016).

In the Pacific Northwest specifically, Keister & Tuttle 2013 found that copepods in Puget Sound, WA behaviorally avoided hypoxia. They found that *Paracalanus parvus* was found almost entirely above the oxycline, or the boundary where oxygen decreases sharply to deepwater levels, and *Oithonas similis* did not appear to change its habitat use based on dissolved oxygen. Additionally, they found that copepods in the genus *Acartia* altered their daily vertical migration (DVM) patterns to stay above the oxycline when the deeper water had a dissolved oxygen level below 2 mg/L.

Even at nonlethal levels from 2.0-3.0 mg/L of dissolved oxygen, moderate hypoxia lowers copepod egg production, egg survival, and prey consumption. Egg production was delayed and reduced in studies that exposed copepods to 2.0 mg/L, 1.0 mg/L and 0.7 mL/L (Marcus et al. 2004; Richmond et al. 2006; Roman et al. 1993). This may be because energy reserves must be spent coping with the physiological effects of low oxygen instead of on egg production or digestion, and egg production is very energy0intensive (Marcus et al. 2004; Elliott, Pierson, and Roman 2013; Lutz, Marcus, and Chanton 1992; Stalder and Marcus 1997; Roff 1992). Different studies have reached different conclusions regarding whether decreased oxygen results in increased or decreased prey consumption (He et al. 2021; Elliott, Pierson, and Roman 2013).

The physiological problems that copepods face in hypoxic conditions are exacerbated by warmer temperatures, as crustaceans in general consume oxygen more rapidly at higher temperatures (Vaquer-Sunyer and Duarte 2011). Higher temperatures on their own are also a source of stress for copepods, although copepod thermal tolerances are understudied (M. Sasaki and Hans G Dam 2021). Copepods are capable of rapid thermal acclimation, but they can still be harmed or killed by high enough temperatures, and copepods acclimated to lower temperatures have lower thermal tolerances (M. Sasaki and Hans G Dam 2021; Hahn and Brennan 2024). Additionally, copepod body size decreases with increasing temperature (Hahn and Brennan 2024). In many copepod species acclimated to 15-20 ºC, about 50% of the population will die at 25 ºC, but the present study is at a site where water temperatures typically range from 8-12 ºC (M. C. Sasaki and Hans G. Dam 2019; Sunar and Kır 2021; Jiang 2009). Based on the lower average temperatures in OCNMS, I expect these copepods to have a thermal tolerance of lower than 25 ºC, but literature on the topic is limited. One study on Baltic Sea *Acartia hudsonica* copepods found that copepods collected in the winter from 7 ºC water had a critical thermal maximum of 25-27 ºC, and the same copepods acclimated to 11 ºC had a critical thermal maximum around 28 ºC, so it is (Hahn and Brennan 2024). The critical thermal maximum is defined at the temperature at which an individual is no longer capable of moving away from harmful conditions, eventually resulting in death. Therefore, it is likely that these copepods experience sublethal impacts at temperatures lower than 25 ºC, and that temperatures above that threshold are harmful to them.

Table 1: Classification of copepods as cold-water (primarily occurring in the summer upwelling season) and warm-water (primarily occurring in the winter) (Fisheries 2024; Peterson and Keister 2003; Peterson and Miller' 1977)

Species	Group
Acartia clausii	Cold-water
Acartia longiremis	Cold-water
Calanus marshallae	Cold-water
Centropages abdominales	Cold-water
Microcalanus pusillus	Cold-water
Pseudocalanus mimus	Cold-water
Pseudocalanus spp.	Cold-water
Oithona similis	Cold-water/year-round
Acartia tonsa	Warm-water
Calanus pacificus	Warm-water
Calocalanus spp.	Warm-water
Calocalanus styliremis	Warm-water
Clausocalanus spp.	Warm-water
Corycaeus anglicus	Warm-water
Ctenocalanus vanus	Warm-water
Mesocalanus tenuicornis	Warm-water
Metridia pacifica	Warm-water
Paracalanus parvus	Warm-water
Paracalanus spp.	Warm-water

0.4 Study Plan

Many lab and field studies have established that oxygen levels below 2 mL/L have negative effects on copepods and reduce their abundance, but few of these studies compare the hypoxia tolerance of different copepod species, and many copepod species considered OCNMS species of interest have not been directly studied for hypoxia tolerance. In this study, I will assess the effects of hypoxia on copepod abundance and community composition, as well as potential trophic effects of lower copepod abundance if it occurs. I will compare copepod eDNA index, a measure of relative abundance using eDNA detections, to dissolved oxygen data in order to assess whether hypoxia decreases copepod abundance in OCNMS. I will also generate preferred ranges of environmental conditions for each copepod species, and compare northern and southern copepod biodiversity and abundance across normoxic and hypoxic conditions. I predict that copepod and fish abundance will decrease with hypoxia, and that the northern copepods will be detected in colder conditions than the southern copepods. Based on preliminary data analysis from the previous research, I expect southern copepods to persist at lower oxygen levels than northern copepods. I also predict that lower copepod populations will correlate with lower populations of fish known to consume copepods, such as herring and salmon (Surma, Pakhomov, and Pitcher 2022; Friedenberg, Bollens, and Rollwagen-Bollens 2012; Brodeur and Pearcy 1990). Understanding these patterns will inform predictions of climate change effects on OCNMS food chains and culturally and economically important species such as salmon.

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I am going to look through the citations and correct issues later, some of these are missing authors or dates.

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