

Zooplankton composition and copepod lipid content over Fall 2014 in the Salish Sea

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Abstract

Zooplankton are secondary producers that play a major role in carbon sequestration, the microbial loop, and energy transfer across trophic levels. Zooplankton are abundant in the Salish Sea, a productive inland sea with a complex estuarine circulation that is subject to seasonal physical processes. We studied the zooplankton composition in the Salish Sea and measured the relation of biotic factors to water properties. We estimated zooplankton abundance and diversity in the San Juan Channel and compared to broader Salish Sea and five physical factors (temperature, salinity, dissolved oxygen, fluorescence, and dissolved inorganic carbon). The most abundant zooplankton in the Salish Sea was calanoid copepod. However, copepod nauplii were more abundant at North station during the beginning of the sampling period. The fall transition marked a steady zooplankton density decrease. Salinity and dissolved oxygen had a strong correlation with total zooplankton abundance, copepod abundance, and % of copepods with lipid content. Zooplankton abundance and composition in late October reflected how downwelling conditions and river flow, among other oceanographic variables, greatly affect spatial zooplankton distribution. The spatial variation of zooplankton, influenced by tides and the fall transition, was pronounced in the estuary and may be due to different water properties at the sampled stations.

Introduction

Zooplankton play many roles in the ecosystem. They are predators on members of the microbial loop; they mainly prey on phytoplankton, although smaller zooplankton and earlier life stages feed on bacterioplankton and heterotrophic protists (Turner 2004). Zooplankton are also important for carbon sequestration in the benthos. Due to their larger size and higher density, zooplankton's fecal pellets sink at a faster rate than phytoplankton detritus and are more efficient at sequestering carbon on the bottom sediment (Turner 2002). As secondary producers, zooplankton are an essential link between algae and higher trophic level groups, such as commercially and ecologically important larval fish and crustaceans (Zamon 2002).

However, in assessing any one role, the diversity of zooplankton must be considered. Zooplankton, including juvenile stages of many vertebrates and invertebrates, cover a wide range of marine organisms. They can be divided into two groups, the meroplankton and the holoplankton, depending on their life cycles. Meroplankton are organisms that are only planktonic for a part of their life cycle, while holoplankton are organisms that are planktonic for their entire life cycle. Therefore, the predation, carbon export and trophic linkage will vary. Due to the high diversity of the group, these secondary producers, which dominate a

large part of the total oceanic biomass, are useful biological indicators. They respond differently to environmental changes and can serve as indicator species to climate change and other environmental phenomena (Strickland 1983; Beaugrand 2004).

Zooplankton are ideal candidates for studying ecosystem responses to atmospheric-oceanic variability because they drift at sea. They respond quickly to abiotic (e.g. salinity, temperature, freshwater flow) and biotic factors (e.g. food availability, predation) in order to secure their survival (David et al. 2005). Studying the abundance and diversity of zooplankton has been found to be as compelling as using physical and chemical methods to observe long-term changes in marine ecosystems (Hsieh et al. 2004).

The zooplankton community can be very diverse, but in coastal ecosystems and inshore estuaries in the northern hemisphere, it is typically dominated by copepods (Turner 1981; Strickland 1983). Copepods are a group of small crustacean zooplankton that are the most abundant metazoans on Earth (Turner 2004). The three major orders of copepods are Calanoida, Cyclopoida, and Harpacticoida; calanoid copepods are more abundant and diverse in physically unstable estuaries (Turner 1981).

Copepods are crucial for understanding trophic energy transfers because they sequester lipid oil and fatty acids derived from their main food source, phytoplankton, which is then transferred up the food web (Parrish et al. 2012). Phytoplankton are the primary producers of lipids and fatty acids, which are then ingested, synthesized and incorporated by copepods and other zooplankton. Lipid oil is essential for the growth and survival of many zooplankton. The amount of lipid oil also determines when copepods can mate, produce eggs, molt into an adult, and enter diapause (Peterson 2001). The latter is experienced only by some life stages and species. Copepod generation time is usually less than a year, so not all generations undergo diapause (Landry 1983), which begins in fall for northern hemisphere temperate systems.

The Salish Sea is a productive, complex estuarine system on the west coast of North America. This analysis focuses on the zooplankton composition and copepod lipid content to better understand the roles zooplankton are playing in the Salish Sea and gain insight on copepod dynamics. The Salish Sea is situated east of Vancouver Island and west of British Columbia, Canada, and Washington State, USA. The sea consists of three major bodies of water, the Strait of Georgia, the Strait of Juan de Fuca, and Puget Sound. The influx of oceanic water from the Strait of Juan de Fuca and the discharge of a myriad of rivers, including the Fraser River which dominates total freshwater input, make this a complex, semi-enclosed estuary. The estuarine exchange with oceanic shelf waters forces a strong seasonal modulation cycle determined by freshwater discharge, coastal wind stress, basin morphology, and tides (Masson & Cummins 2004). The estuarine circulation brings nutrients to the euphotic layer and transports zooplankton between Straits (Li et al. 2000).

Zooplankton biomass and distribution in the Salish Sea are dependent on the estuarine circulation. Along with semidiurnal tidal currents, bathymetry plays a major role in determining the local zooplankton abundance and distribution (Zamon 2002). Two sills, one in the Strait of Juan de Fuca and a second at the entrance of the San Juan Channel, obstruct tidal flows, cause vigorous mixing, and reflux outflowing water back into the system (Masson 2002). In certain areas of the estuary, such as the San Juan Archipelago and Puget Sound, zooplankton can have a long residence time and retain biomass. In addition, nutrient availability and long summer photoperiods contribute to favorable growing conditions. These factors collectively explain why the Salish Sea is very productive.

The Salish Sea and the zooplankton populations within it are substantially affected by upwelling and downwelling periods characteristic of marine environments along the outer Washington coast. Upwelling is driven by northwesterly winds from the North Pacific High atmospheric pressure during the summer. Upwelling introduces cold, saline, nutrient-rich

waters with low pH and dissolved oxygen concentrations (Harris et al. 2013). Downwelling is driven by southeasterly winds from the Aleutian low atmospheric pressure during winter and brings the opposite water characteristics since surface waters accumulate at the coast.

Downwelling also increases zooplankton biodiversity by introducing warm-water species from the poleward-flowing Davidson current system (Hooff & Peterson 2006). All of these physical drivers make the Salish Sea a unique and complicated place to study. What is less known is how zooplankton respond seasonally to these drivers. Study of spatial and temporal variability in zooplankton composition and diversity is crucial for understanding how physical processes, such as upwelling and downwelling, affect biological processes.

Despite the importance of zooplankton, their abundance and diversity is not well monitored in the Salish Sea (Keister & Tuttle 2013). Moreover, the relationship between these biotic factors and water properties is even less understood. Because different species will dominate depending on temperature, salinity, dissolved oxygen, and chlorophyll levels, biotic factors can indicate water sources. This study aims to assess the abundance and diversity of zooplankton and estimate the temporal variability in lipid content in calanoid copepods in the San Juan Channel over fall 2014. The study further compares the zooplankton population in the San Juan Channel to broader Salish Sea and measures the relation of biotic factors to water properties.

Methods

Sample sites

I. San Juan Channel

The study was conducted as part of the Pelagic Ecosystem Function apprenticeship, which completed a total of seven sampling cruises (September 30, October 7, 14, 21, 29, and November 5 and 10) aboard the University of Washington's *R/V Centennial* during fall 2014. Zooplankton were sampled from two stations along a North-South transect in the San Juan

Channel (Fig. 1). The southern part of the San Juan Channel connects to the east of the Strait of Juan de Fuca, while the northern part connects to the Strait of Georgia. The San Juan Channel connects and constricts water flow between the two Straits.

North Station (48° 35.00' N, 123° 02.50' W) is closest to the Strait of Georgia and Fraser River, and lies between San Juan Island and Orcas Island. The station is >100m deep and is relatively well-mixed with periodic surface Fraser River plumes. South Station (48° 25.20' N, 122° 56.60' W) is located after a sill near Cattle Pass and is bordered by San Juan Island and Lopez Island. The station is >80m deep and has a two-layer profile with an estuarine surface and an oceanic deep layer.

II. Puget Sound

An additional part of the study was conducted as part of a Puget Sound Regional Synthesis Model (PRISM) cruise. On this cruise, we collected zooplankton samples and water-column profiles aboard the University of Washington's *R/V Thomas G. Thompson*. Zooplankton were sampled at six stations: P22, P8, P12, P4, P28, and P38 (Fig. 2). Stations P4, P28 and P38 were sampled on October 29, 2014; stations P12 and P8 on October 30, 2014; and station P22 on October 31, 2014. These stations were chosen because of their differing characteristics and location.

P22 (48° 16.311' N, 123° 01.015' W) is in the eastern bank of the Strait of Juan de Fuca and has a depth of 95m. P8 (47° 53.840' N, 122° 36.386' W) is at the entrance of Hood Canal, near Admiralty Inlet, and is 135m deep. P12 (47° 25.533' N, 123° 06.483' W) lies in the South Hood Canal and is 130m deep, while P4 (48° 14.482' N, 122° 33.288' W) is located in Skagit Bay and is 83m deep. P28 (47° 42.203' N, 122° 27.279' W) is in the Main Basin and is 196m deep. Along with P22 and P8, this station receives oceanic input before the rest of the stations. P38 (47° 16.599' N, 122° 42.025' W) is located near Carr Inlet in South Sound and is 103m deep.

Sample collection

For *R/V Centennial* cruises, zooplankton samples were collected by vertical tows using a ring net with a 70cm diameter and 153 μ m mesh and weighted at the cod end. For the *R/V Thomas G. Thompson* cruises, the net had a diameter of 50cm and a mesh size of 200 μ m. Both nets were lowered to 10m above the bottom and sampled a cylindrical mass of water. The following equation was used to calculate the volume of the water sampled,

$$V = \pi r^2 \times l$$

where V stands for the total tow volume of water in m^3 , r for the radius of the net's mouth in meters, and l for the depth in meters of the plankton tow, derived from the length of the water surface to the net's mouth.

Once at the surface, the nets were rinsed with seawater to retrieve all organisms that may have remained on the nets. All zooplankton samples were preserved in jars with 30mL of 10% buffered formaldehyde solution. Samples were left untouched to settle for 24h and then analyzed.

Sample analysis

Samples for each station and cruise date were filtered through a 102 μ m sieve while being rinsed with freshwater to remove buffered formalin. Zooplankton samples were put back into a jar with freshwater and then split to 1/4 dilution. The split sample was diluted to a range of 250mL to 700mL depending on estimated density and subsampled to one aliquot of 5mL using a Hensen-Stempel pipette. Zooplankton were counted from each subsample using a Petri dish with wells and a Nikon SMZ-2T dissecting microscope. Zooplankton were identified to the lowest taxonomic level possible, life history stage (e.g. nauplii vs. copepodite) and type (holoplankton vs. meroplankton). A list of zooplankton, types, and taxonomic level addressed in this study is provided as Appendix 1.

For the most common zooplankton group, Calanoid copepods, we measured lipid content to estimate energy stores. Lipid content was divided into five classes. Class one had no lipid; class two had less than half of body size full of lipids; class three was half full of lipids, class four was more than half full of lipids; and class five was full of lipids (Fig. 3).

The total density per taxonomic group was derived using the following equation,

$$D = \frac{N \times S}{V(d \times a)}$$

where D is the total density of each taxon; N is the count of all organisms in subsample; S is the split volume in mL; d is the split dilution as a fraction of one; a is the aliquot volume in mL; and V is the total tow volume of water in m^3 .

After all samples were processed, species diversity was estimated using the Shannon-Wiener Diversity Index's equation,

$$H^l = -\sum_{si=1} (p_i * \ln p_i)$$

where S is species richness and \sum is the sum of all of them. P_i is the relative proportion of individuals in a given taxonomic group to the total of organisms in the subsample. The values for this index range from 0.0-4.0, where higher values indicate higher species diversity.

Zooplankton were categorized to Class in order to normalize measurements. Eggs were excluded in this analysis.

Water property & spatial species comparison

Zooplankton samples from late October at each station were compared to water properties collected with a Seabird SEACAT SBE-19 conductivity-temperature-depth (CTD) instrument for *R/V Centennial* and with a SBE911 model for *R/V Thomas G. Thompson*. The water properties considered in this study were temperature, salinity, dissolved oxygen, chlorophyll *a* or fluorescence, and dissolved inorganic carbon (DIC). Water samples were taken from the CTD and analyzed for chl*a* and dissolved oxygen concentrations. Water sampled for chl*a* was filtered through a GF/F filter and extracted in 90% acetone. We

calculated chl a for all samples by using a Turner 10 Analog fluorometer and methodology as outlined by Lorenzen 1966.

Dissolved oxygen concentrations were estimated using Winkler titrations following Carpenter 1965's methodology, using a Beckman® Dosimat microburet. Dissolved inorganic carbon was calculated using an algorithm generated by Simone Alin from NOAA for the outer coast of Washington State. The algorithm is,

$$\text{DIC} = 1006.197 + (-0.7584 * \text{O}_2) + (49.959 * \sigma_T)$$

where O_2 is a measure of oxygen in $\mu\text{mol/kg}$ and density is quantified with sigma-t (σ_T).

The mean for each water property was taken for each station. This mean was then compared to a total mean from all stations for a given water property. For example, the mean for temperature in one station was compared to the mean from all stations for temperature. Means for the stations were plotted to evaluate water anomalies across space.

Statistical analysis

Stations were spatially plotted by creating a multidimensional scaling (MDS) plot. The MDS plot was constructed using a Bray-Curtis dissimilarity matrix. Sites closest to each other are more similar in species composition. For abiotic and biotic comparisons, linear regressions were run to assess correlation between the two variables. Abiotic variables that resulted in high R^2 values were analyzed with all biotic factors using a two-way ANOVA. All analyses were performed using the statistical program R Version 3.1.0.

Results

Chlorophyll a levels in the San Juan Channel

At North and South stations, chlorophyll a levels decreased over time. Average levels dropped from 1.77 $\mu\text{g/L}$ on September 30 to 1.61 $\mu\text{g/L}$ on November 10 at North station (Fig. 4). Values dropped from 1.51 $\mu\text{g/L}$ on September 30 to 1.42 $\mu\text{g/L}$ on November 10 in South station (Fig. 5). At North station, chlorophyll a levels reached the highest values at near

surface (1.95 $\mu\text{g/L}$) and 5m (1.92 $\mu\text{g/L}$) on September 30. No other cruise date had values higher than the above mentioned. Chlorophyll *a* levels showed no trend from one cruise to the next. However, levels steadily decreased after the fall transition on October 17.

Total zooplankton abundance in the San Juan Channel

Total zooplankton abundance followed a similar pattern to chlorophyll *a* levels at North and South stations. Overall, total abundance decreased over time at both stations. At North station, total zooplankton abundance on September 30 was over 13,000/m³, the highest density during sampling time. Within a week, total abundance lowered to 4,729/m³ on October 7 (Fig. 6). On October 14, total zooplankton abundance slightly increased to 5,014/m³ and began to decrease after the fall transition. Densities steadily decreased from 4,246/m³ on October 21 to 2,854/m³ on November 10, the last sampling date (Fig. 6). The last measured total density had 619/m³ more than the previous sampled date, November 5.

At South station, there was no clear pattern before the fall transition. Before the transition, total zooplankton abundance was 6,548/m³ on September 30, 3,883/m³ on October 7, and 6,962/m³ on October 14 (Fig. 6). The highest density sampled was 7,770/m³ and occurred on October 21 after the fall transition. Zooplankton abundance decreased from 5,264/m³ on October 29 to 3,282/m³ on November 10 (Fig. 6). Despite the overall decrease in abundance, the last cruise date had 31/m³ more than the previous sampled date, November 5.

Species composition & diversity in the San Juan Channel

The most abundant zooplankton taxa at North and South stations was calanoid copepod, with a seasonal average of 1,921/m³ at North station and 2,976/m³ at South station (Table 1). At North station, copepod nauplii were the most abundant taxon on September 30, with a total of 5,268/m³ and comprising 41% of the total zooplankton (Fig. 7). The seasonal average of copepod nauplii was 1,442/m³. Nauplii abundance decreased after the first sampled date, while calanoid copepods increased throughout the fall season. Calanoid

copepods consisted of 22% of total zooplankton on September 30 and 63% by the end of our sampling time.

On all cruise dates, calanoid copepods were more than 40% of total zooplankton at South station (Table 2). They were most abundant on October 14 with a density of 4,695/m³ and comprised 68% of the total zooplankton (Fig. 8). Although abundance was lower, calanoid copepods were 71% of total zooplankton on November 10. Copepod nauplii were the second most abundant taxon at South station, with a total abundance of 828/m³ on the first sampling date and 97/m³ on the last sampling date. On October 21, copepod nauplii reached its highest density, 2076/m³, where it consisted 28% of total zooplankton (Table 2). Copepod nauplii did not exceed more than 30% of total zooplankton on any of the cruise dates and had a seasonal average of 857/m³.

For North and South stations, the following three most abundant taxa were copepod metanauplius, cyclopoid copepod and larvacean. Copepod metanauplius was the third most common zooplankton at North station and the fifth most common at South station. At North station, its seasonal average was 274/m³ and its highest abundance was 1,208/m³ on September 30. Copepod metanauplius had a lower seasonal average of 80/m³ at South station, where it was most abundant on September 30 (291/m³).

Cyclopoid copepod was the fourth most abundant in North station and third most abundant in South station. Its seasonal average was 325/m³ at North station and 493/m³ at South station. Cyclopoid copepods were most abundant on September 30 at North station (611/m³) and on November 5 at South station (772/m³). Larvaceans were the fifth most abundant zooplankton at North station and fourth most abundant at South station. The seasonal average was 273/m³ at the North station and 220/m³ at the South station. The highest abundance of larvaceans at North station was on September 30 with a total of 566/m³. Although their density decreased with time, larvaceans had an increased percentage of the

total zooplankton (Fig. 7). At South station, they were most abundant on November 5 ($359/\text{m}^3$).

A Shannon-Wiener diversity index gave results below 1 for all cruise dates at both stations. No specific trend can be extrapolated from the values (Fig. 9). Biodiversity was highest at North station on September 30, with a value of 0.8. At South station, biodiversity remained relatively low until November 5 when it reached 0.9. When compared to tidal types and phases, biodiversity at North and South stations mimicked an oscillation pattern from the tides. North station was most diverse when sampled on spring flood tides. South station was opposite and exhibited more diversity or equal diversity to North station when sampled on neap ebb tides (Fig. 9).

Total calanoid copepod abundance in the San Juan Channel

Calanoid copepods were the most abundant zooplankton and had an average of about 50% of total zooplankton at North and South stations. Therefore, they merit their own examination. Total calanoid abundance was higher at South station for all sampled dates (Fig. 10). The seasonal average was $2,096/\text{m}^3$ at North station and $3,065/\text{m}^3$ at South station. We found that calanoid copepod abundance decreased over fall 2014 at both stations. Calanoid abundance lacked a trend before the fall transition. Once downwelling period began, there was a clearer downward trend in calanoid abundance (Fig. 10). At North station, calanoid density began at $2,852/\text{m}^3$ on September 30 and continued to decrease until October 14 and 21, where values were over $2,000/\text{m}^3$. For the rest of the cruises, calanoid abundance continued to fall and reached $1,686/\text{m}^3$ on the last sampling date.

South station began with a calanoid density of $3,829/\text{m}^3$ on September 30. It followed a similar pattern to North station, where values increased again on October 14 and 21. The station reached its highest calanoid density on October 14 ($5,575/\text{m}^3$). Calanoid abundance

decreased again for the remaining cruises. It totaled 2,160/m³ on the last sampling date, still over 400/m³ more calanoid copepods than North station.

Lipid content of calanoid copepod in the San Juan Channel

The five classes of lipid content exhibited different trends over fall 2014. At both stations, lipid content 1 remained consistently higher than other classes until the fall transition. Calanoid copepods with lipid content 1 at North station were most abundant on the first sampling date (1,863/m³), whereas calanoid copepods from the other classes were 989/m³ all together (Fig. 11a). Before the fall transition, lipid content 1 constituted an average of 64% of calanoid copepods and classes containing lipid added to an average of 36% (Fig. 11b). Lipid content 2 surpassed lipid content 1 on two occasions after the fall transition. Lipid content 2 on October 29 was 813/m³, whereas lipid content 1 was 794/m³. On November 5, the difference was more noticeable. Lipid content 2 reached 547/m³ and lipid content 1 lowered to 402/m³. After the fall transition, classes containing lipid added to an average of 55%, while lipid content 1 decreased to an average of 45% (Fig. 11b).

At South station, lipid content 1 attained highest abundance (4,948/m³) right before fall transition on October 14 (Fig. 12a). Classes containing lipid amounted to a total of 628/m³ on that same date. Lipid content 1 constituted a high average of 90% before the fall transition, while the remaining classes containing lipid added to a low average of 10% (Fig. 12b). Calanoid copepods containing lipid (lipid content 2 to 5) became more abundant after the fall transition. On October 29, lipid content 2 arrived at 1,643/m³ and lipid content 1 dropped to 736/m³. Calanoid copepods with no lipid content represented an average of 40% of the sampled community and calanoid copepods containing lipid represented an average of 60% (Fig. 12b).

Zooplankton composition in late October in Salish Sea

Total zooplankton abundance varied among stations, although stations in close proximity were more similar to each other (Fig. 13). Total abundance in October was highest at South Station with a total of 5,264/m³ and lowest at P38, South Sound, with 1,395/m³ (Fig. 14). P22, P8, and North stations had similar zooplankton abundances, all with a density higher than 2,800/m³. Stations farthest from the Strait of Juan de Fuca had lower abundances than the rest of the Salish Sea. Stations P12, P28, P38, and P4 had abundances lower than 2,300/m³ in late October (Fig. 14).

All stations in Puget Sound had a substantially higher density of calanoid and cyclopoid copepods than meroplankton and other holoplankton. Copepods were 64% or more of the total zooplankton in all Salish Sea stations (Fig. 14). South Station had the highest abundance of copepods with a total of 3,372/m³, but P22 had the highest percentage of copepods relative to its total zooplankton abundance (74%). P38 had the lowest density of copepods, while South station and P12 contained the lowest percentage of copepods relative to their total abundance (64%).

In late October, at least 40% of copepods contained lipid in their bodies. Stations closer to the Strait of Juan de Fuca had a higher percentage of copepods with lipid oils (Fig. 14). P22 had 80% of its copepods with some amount of lipid in their bodies. The lowest percentage of copepods was at P4, station closest to the Skagit River (44%). The other stations ranged from over 50% to about 70% of copepods containing lipid (Fig. 14).

Meroplankton abundance was below 8% of the sampled community in any station. The meroplankton community ranged from a low 64/m³ at P28, Main Basin, to 183/m³ at P12, South Hood Canal. Meroplankton were most abundant at P12 and least abundant at P28. Overall, Puget Sound had low densities of meroplankton relative to the total zooplankton abundance in late October.

Comparison of zooplankton abundance and water conditions in Salish Sea

Temperature average for all Salish Sea in late October was 11.54 °C. P38 had the highest average temperature, 13 °C, and P12 had the lowest average temperature, 10 °C (Fig. 15). No significant correlation was found between temperature and any of the biotic factors (i.e. total abundance, copepod abundance, meroplankton abundance, and % of copepods with lipid) (Table 3). However, we did find a correlation between salinity and all biotic factors, with the exception of meroplankton abundance. Salinity average was 31 PSU, being highest at P22 (31 PSU) and lowest at P4 (29 PSU). The strongest correlation between salinity and biotic factors was with % of copepods with lipid ($R^2 = 0.77$, p-value= 0.01), followed by copepod abundance ($R^2 = 0.60$, p-value= 0.01) and total abundance ($R^2 = 0.49$, p-value= 0.02).

The average concentration of dissolved oxygen was 4 mg/L and reached a low concentration of 2 mg/L at P12 and a high of 6 mg/L at North and South stations (Fig. 15). Dissolved oxygen also exhibited strong relationships with copepod abundance ($R^2 = 0.58$), total abundance ($R^2 = 0.55$), and % of copepods with lipid content ($R^2 = 0.55$). None of the correlations between dissolved oxygen and biotic factors were significantly strong (Table 4).

Fluorescence levels were consistent across Salish Sea, with a range from 0.9 to 2 mg/m³ (Fig. 15). Meroplankton abundance was the only biotic factor which indicated some degree of correlation with fluorescence ($R^2 = 0.30$). The rest of the biotic factors did not exhibit a correlation with fluorescence (Table 3). The last measured water property, dissolved inorganic carbon, had an average of 2,070 µmol/kg and was highest at P12 (2,115 µmol/kg) and lowest at P38 (2,045 µmol/kg). Only meroplankton abundance had some degree of correlation with dissolved inorganic carbon ($R^2 = 0.40$), while the other biotic factors lacked a correlation (Table 3).

Discussion

Total zooplankton abundance in the San Juan Channel

As may be expected in northern hemisphere fall season with decreased sunlight and temperature, total zooplankton abundance decreased over the fall period in the San Juan Channel and followed a similar pattern to chlorophyll *a* levels. Abundance was higher at North station for the first two cruises but remained lower than South station for the rest of the sampling time. We speculate this higher abundance in early fall was partly due to a fall phytoplankton bloom, as indicated by the high concentration of chlorophyll observed in late September. The first sampling at North station occurred during a spring flood tide, which may have brought more zooplankton advected from the Strait of Juan de Fuca, where zooplankton are often more abundant (Li et al. 2000). The pairing of a bloom and spring flood tide could be contributing factors to the high abundance observed at North station on September 30; 7,000/m³ more zooplankton were found at the North station than at South station. The observed high zooplankton abundance and high chlorophyll concentration, assuming zooplankton grazing at North station on September 30, suggest a quick response to phytoplankton blooms (David et al. 2005). These data corroborate biological-physical models that have predicted quick responses from zooplankton to phytoplankton blooms in the Salish Sea, especially during advection (Li et al. 2000).

Despite this early peak in the season, zooplankton abundance at North station remained lower than at South station throughout the fall. North station is situated closer to a freshwater source, which is typically characterized by lower zooplankton abundance (Moderán et al. 2010). Advection of oceanic zooplankton into the channel through the Strait of Juan de Fuca reaches South station first and could explain the moderately higher zooplankton abundance seen at that station (Li et al. 2000). The sill located south of South station may further increase zooplankton abundance by refluxing outflowing water back into

the system and prolonging residence time (Masson 2002; Zamon 2002). Therefore, the combination of a sill and tidal currents would contribute to the higher zooplankton abundance, as was found at South station.

South station, and to a lesser extent North station, experienced a peak in zooplankton density on the sampling date ~one week before the fall transition, which was followed by a steady zooplankton density decrease (Fig. 6). Previous PEF years (2007-2011) have found this same pattern in zooplankton density. Blackstone (2011) hypothesized that an optimal window occurs before fall transition where conditions are conducive to higher zooplankton abundance. The fall transition could temporarily increase abundance by decreasing the flushing of surface waters caused by upwelling and introducing more relaxed downwelling conditions (Mackas et al. 2001). However, after the fall transition, food became less available and zooplankton abundance decreased in the San Juan Channel.

Species composition & diversity in the San Juan Channel

During our sampling period, calanoid copepods were the most abundant zooplankton at both stations. This agrees well with other studies that found calanoid copepods to be consistently the most abundant zooplankton throughout the Salish Sea (Strickland 1983; Keister & Tuttle 2013). Copepods are generally more diverse and abundant in physically unstable estuaries, such as Salish Sea, than in other environments (Turner 1981). While copepods dominated both stations, they had greater abundance at South station, most likely due to oceanic sources from the Strait of Juan de Fuca reaching the station first.

The balance between copepod nauplii and Calanoid copepods was variable. Copepod nauplii were more abundant at North station in early fall but were outnumbered by calanoid copepods as the season progressed. Copepod nauplii of the order Calanoida have six life stages, of which the majority has both high growth and mortality rates (Peterson 2001). Therefore, we would expect that copepod nauplii found toward the beginning of our sampling

period at North station would mature into calanoid copepodites. We indeed found more calanoid copepods toward the end, which could indicate development of nauplii to copepodite or high mortality rates. Though not considered in this study, higher nutrient concentrations from the Fraser River discharge may have contributed to a high population of nauplii, which requires more nutrients to develop (Peterson 2001). Less bottom stress from tidal currents could also explain the higher densities of nauplii found at North station, as eggs hatch more successfully under these conditions (Engel & Hirche 2004). A steady egg population could be sustaining nauplii population at North station rather than at South station.

Larvaceans were also one of the five most abundant zooplankton groups in the San Juan Channel. North station had a higher number of larvaceans that increased over fall season. The late increase of larvaceans relative to other zooplankton could be attributed to the unseasonably high discharge from the Fraser River (Cougan 2014). North station may be an ideal location for these filter feeders due to higher concentrations of silt and suspended particulate organic matter coming from the Fraser River (Meybeck 1982). However, later in the fall period, cyclopoid copepod concurrently became a prominent zooplankton at both stations. These copepods have been found to become more abundant closer to wintertime in Puget Sound (Keister & Tuttle 2013). Most cyclopoids inhabit subtropical zones with more temperature stability, and their presence could be indicative of warm-water species brought by the Davidson current system (Turner 1981).

Zooplankton diversity followed an oscillation pattern that mimicked tidal phases sampled at North and South stations. During fall season, North station had higher diversity on spring flood tides and South station on neap ebb tides. Our findings fit with previous studies in the San Juan Channel that have found higher diversity and abundance during flood tides at North Station (Blackstone 2011; Sigley 2012). The external forcing of a tide and its direction may have influenced the level of diversity in the San Juan Channel. However, diversity index

values were below one, which indicates low diversity as defined by the Shannon-Wiener diversity index.

The Shannon-Wiener diversity index can be used to estimate biodiversity in all ecosystems and may underestimate diversity in a marine ecosystem by comparing its values to terrestrial ecosystems. From previous research conducted in California and the Oregon coastal upwelling zone, it appears that values below one are common in marine ecosystems (Hooff & Peterson 2006; Peterson 2009). Both studies describe an increase in biodiversity during El Niño years and Pacific Decadal Oscillation, which bring warm waters to the coast and increase species richness. Our diversity values are comparable to values estimated by Hooff & Peterson 2006 in the Oregon coastal upwelling zone. We infer that diversity would be higher if zooplankton were classified to species.

Total calanoid copepod abundance and lipid content in the San Juan Channel

Despite a moderate diversity in zooplankton, calanoid copepod abundance had a high seasonal average in the San Juan Channel, with 2,096/m³ at North station and 3,065/m³ at South station. We further investigated changes in lipid content as calanoid copepods approached winter dormancy period. Autumn months in the northern hemisphere are known to have resting copepod populations (Miller et al. 1998). Before the fall transition, calanoid copepods with no lipid content formed 64% of total copepods at North station and 90% at South station. Calanoid copepod classes containing lipid at both stations surpassed those without lipid after the fall transition.

The fall transition coincided with a shift in the amount of lipid content during fall 2014. It also influenced chlorophyll concentrations, which had a marked decrease after the fall transition. Higher chlorophyll concentrations toward the beginning of sampling time may indicate more food available for calanoid copepods to use or reserve for diapause later in the season. The precise combination of cues to initialize and terminate diapause remains

unknown, but temperature, photoperiod, food availability, and predators are the most common (Dahms 1996; Williams-Howze 1996). In this study, lack of food availability later in the season may have been one predictable cue for copepods to initiate diapause.

Diapause prevails in higher and temperate latitudes, where the advent of adverse winter conditions prompts copepods to remain dormant for three to four months (Marcus 1980; Williams & Bieosit 2004). We hypothesize copepods in the San Juan Channel began diapause during autumn months due to cues found in other similar marine environments in temperate regions (Williams-Howze 1996). The majority of calanoid copepods sampled were in their copepodite stage V, which is the last juvenile stage and is the one entering diapause during winter. Calanoid copepodites in stage V store enough lipids over fall season to arrest feeding and development. They then migrate to deeper depths because bottom waters are colder and require less metabolism (Williams & Biesoit 2004). In this study, calanoid copepod abundance decreased with time at North and South stations and could suggest migration to deeper depths where we may not have sampled.

Zooplankton composition in late October in Salish Sea

When comparing results from the San Juan Channel to Puget Sound, we noticed spatial patterns in zooplankton composition in late October. Stations in the San Juan Channel were more similar to each other than the rest of Puget Sound. They were, however, also similar to P22, which is the station closest to the Strait of Juan de Fuca. One common trend found in all stations sampled in late October was high copepod abundance relative to other zooplankton. Copepods were the most abundant zooplankton in Salish Sea, which is expected in temperate regions where copepod species form a large part of the zooplankton community (Strickland 1983). However, copepods spatially varied in the amount of lipid content stored in their bodies. Stations closer to the Strait of Juan de Fuca had calanoid copepods with

higher levels of lipid content. This implies that a substantial number of copepods enter the estuarine system during fall season already containing lipid oil.

Meroplankton abundance was spatially more homogeneous than copepod abundance. The meroplankton community was low throughout the Salish Sea in late October and should be further examined to see whether oceanic waters are the main source of meroplankton in the estuary. Another explanation for low meroplankton abundance could be the typically lower nutrient availability during late fall season. Larval stages have faster growth rates than their adult stages and may be limited by low nutrient availability during autumn months (Peterson 2001; Irigoien et al. 2004). Further research should investigate the seasonal shifts in holoplankton and meroplankton abundances in productive estuaries.

Comparison of zooplankton abundance and water conditions in Salish Sea

Zooplankton drift at sea and are dependent on water conditions to survive and reproduce. It is therefore relevant to study how water properties can determine the zooplankton population. Our results illustrated that zooplankton composition and abundance varied in relation to certain water properties characteristic of late fall in the Salish Sea. We first describe the characteristics of oceanic waters entering the Salish Sea in late October. Oceanic waters, which introduce zooplankton to the estuary, first reach station P22 situated in the Strait of Juan de Fuca. These waters were moderate in temperature and dissolved oxygen concentrations but high in salinity. Salinity levels decreased as waters entered and dispersed throughout the Salish Sea. Levels were especially low in stations close to Skagit Bay and South Sound.

Dissolved oxygen concentrations declined the farther stations were from the main oceanic source, which could point to uptake from primary and secondary productivity. However, concentrations increased in stations in the San Juan Channel mainly due to vigorous mixing of the water column. Tidally-mixed near shore environments tend to support

more zooplankton communities, which explains the higher zooplankton abundance seen at North and South stations (Lopes et al. 1999). Temperature had a different spatial pattern than that observed for dissolved oxygen. Temperature depended more on basin depth and water residence time. For instance, temperature was below average in South Hood Canal, where waters from previous winters can remain for a couple of years. Shallow basins, on the contrary, had warmer than average temperatures. Salinity, temperature, and dissolved oxygen varied spatially in the Salish Sea. Fluorescence was the only measured water property that remained slightly constant across the estuary. Fluorescence levels were less variable than other water properties, and may be characteristic of low primary productivity expected in late October. Overall, water conditions in the Salish Sea were spatially distinct and showed to have an effect on zooplankton distribution.

Total zooplankton abundance, copepod abundance, and % of copepods with lipid content changed significantly depending on salinity levels. We found that species organization could largely be attributed to salinity levels. In stations close to rivers, lower salinity correlated with decreased zooplankton biomass. Zooplankton composition and abundance have been previously linked to salinity and temperature, but salinity was the only abiotic factor that significantly affected zooplankton communities in our study (Moderán et al. 2010). Results could differ for other seasons that have more temperature variability than the fall season.

Abiotic influences on zooplankton abundance were predominant in basins with long residence time and low flushing waters, such as South Hood Canal, where low dissolved oxygen concentrations affected abundance. South Hood Canal had less zooplankton abundance than other stations in Salish Sea, mainly because low dissolved oxygen concentrations are known to affect performance, survival, and reproduction of zooplankton (Keister & Tuttle 2013). We saw an increase in zooplankton abundance in the San Juan

Channel, which was correlated with higher dissolved oxygen. Stations with lower dissolved oxygen concentrations in the Salish Sea could potentially experience a shift in zooplankton composition toward more gelatinous zooplankton (Keister & Tuttle 2013). By studying shifts in community composition, zooplankton could be important indicators of hypoxic conditions.

Salinity and dissolved oxygen were the only two water properties that highly correlated with three biotic factors. However, these results only pertain to a particular season. Further research should consider seasonal and interannual variability to better explain how other water properties affect zooplankton assemblage. For example, temperature and fluorescence had no significant effect on biotic factors in our study, but this may be because these water properties are temporally controlled. Temperature and fluorescence could seasonally affect species organization during specific times of the year or across years.

Seasonal and interannual changes could explain how zooplankton composition responds to hydrometeorological events. On a large scale, warm-water copepod species in the North Atlantic have been moving toward the North Pole as a consequence of an increase in the Northern Hemisphere temperature (NHT) anomalies (Beaugrand et al. 2002). In Taiwan, copepod species have been indicative of Kuroshio Branch Current entering the Taiwan Strait (Hsieh et al. 2004). In our study, we found that zooplankton can be indicative of seasonally distinct water sources entering the Salish Sea. Focusing on a smaller spatial scale, zooplankton abundance varied depending on the water properties measured at each station. Zooplankton abundance and composition in late October reflected how downwelling conditions and river flow, among other oceanographic variables, greatly affect spatial zooplankton distribution.

Estuaries are transition zones and highly productive areas of ecological and economic importance (Moderán et al. 2010). To understand how water conditions affect the overall productivity of an estuary, it is important to first understand how zooplankton, which link

primary productivity to higher trophic levels, change spatially and temporally (Li et al. 2000). We evaluated zooplankton productivity and its distribution in a complex estuarine circulation. Salish Sea demonstrated to be heterogeneous in zooplankton assemblage in late October. The spatial variation of zooplankton, influenced by tides and the fall transition, was pronounced in the estuary and may be due to different water properties at the sampled stations. The importance of zooplankton as secondary producers and a major food source for juvenile fishes argues for more monitoring and understanding of their distribution and diversity. Further research should expand on the study of zooplankton spatial assemblages over longer periods of time in order to better understand how current and predicted environmental conditions could potentially affect zooplankton communities and marine food web dynamics.

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Appendix 1. List of zooplankton counted and analyzed, including type and taxonomic level. *Holo* stands for holoplankton and *Mero* for meroplankton.

Zooplankton	Type	Taxonomic level
<i>Cirripedia nauplii</i>	Mero	Infraclass
<i>Cirripedia cyprid</i>	Mero	Infraclass
<i>Bivalvia</i>	Mero	Class
<i>Bracyura</i>	Mero	Infraorder
<i>Chaetognatha</i>	Holo	Phylum
<i>Cladocera</i>	Holo	Order
<i>Calanoida</i>	Holo	Order
<i>Copepod metanauplii</i>	Holo	Order
<i>Copepod nauplii</i>	Holo	Order
<i>Ctenophora</i>	Holo	Phylum
<i>Cyclopoda</i>	Holo	Order
<i>Echinopluteus</i>	Mero	Class
<i>Eggs</i>	Other	Other
<i>Euphausiid</i>	Holo	Order
<i>Gammaridea</i>	Holo	Suborder
<i>Gastropoda</i>	Mero	Class
<i>Hydrozoa</i>	Holo/Mero	Class
<i>Hyperiidea</i>	Holo	Suborder
<i>Larvacea</i>	Holo	Class
<i>Medusae</i>	Holo/Mero	Subphylum
<i>Nematoda</i>	Holo	Phylum
<i>Ostracoda</i>	Holo	Class
<i>Polychaeta</i>	Mero	Class
<i>Pteropoda</i>	Holo	Clade
<i>Shrimp Zoea</i>	Mero	Order
<i>Siphonophorae</i>	Holo	Order

Table 1. Percentage and density of two most abundant zooplankton at North station in the San Juan Channel. Density is number of zooplankton per m³.

Zooplankton	Date	Percentage (%)	Density
Copepod Nauplii	09/30	41	5268
	10/07	32	1470
	10/14	26	1194
	10/21	33	1367
	10/29	11	321
	11/5	11	227
	11/10	9	248
Calanoid copepod	09/30	22	2852
	10/07	39	1812
	10/14	43	2068
	10/21	48	2032
	10/29	63	1904
	11/5	55	1094
	11/10	63	1686

Table 2. Percentage and density of two most abundant zooplankton at South station in the San Juan Channel. Density is number of zooplankton per m³.

Zooplankton	Date	Percentage (%)	Density
Copepod Nauplii	09/30	41	828
	10/07	32	819
	10/14	26	980
	10/21	33	2076
	10/29	11	950
	11/5	11	250
	11/10	9	97
Calanoid copepod	09/30	22	3829
	10/07	39	1937
	10/14	43	4695
	10/21	48	4133
	10/29	63	2868
	11/5	55	1209
	11/10	63	2160

Table 3. Linear regressions between water properties (temperature, salinity, dissolved oxygen, fluorescence, dissolved inorganic carbon) and biotic factors (total abundance, copepod abundance, meroplankton abundance, % of copepods with lipid content) for eight stations in Salish Sea in late October. R^2 values are presented in decimal form. Positive correlation is indicated by (+) and negative correlation by (-).

Abundance	Ranges				
	10-13 °C Temperature	29-32 PSU Salinity	2-6 mg L ⁻¹ Dissolved Oxygen	0.5-2 mg m ⁻³ Fluorescence	2040-2115 µmol kg ⁻¹ Dissolved Inorganic Carbon
Total	- 0.29	+ 0.49	+ 0.55	+ 0.04	- 0.05
Copepod	- 0.21	+ 0.60	+ 0.58	+ 0.01	- 0.04
Meroplankton	- 0.37	+ 0.03	- 0.05	+ 0.30	+ 0.40
% of copepods with lipid content	- 0.01	+ 0.77	+ 0.55	- 0.11	+ 0.05

Table 4. Results of a two-way ANOVA for four biotic factors (total abundance, copepod abundance, meroplankton abundance, % of copepods with lipid content) compared to salinity and dissolved oxygen.

Abundance	Salinity	Dissolved Oxygen	Salinity:Dissolved Oxygen
Total	0.02 *	0.13	0.06
Copepod	0.01 *	0.09	0.07
Meroplankton	0.62	0.21	0.20
% of copepods with lipid content	0.01 *	0.17	0.36

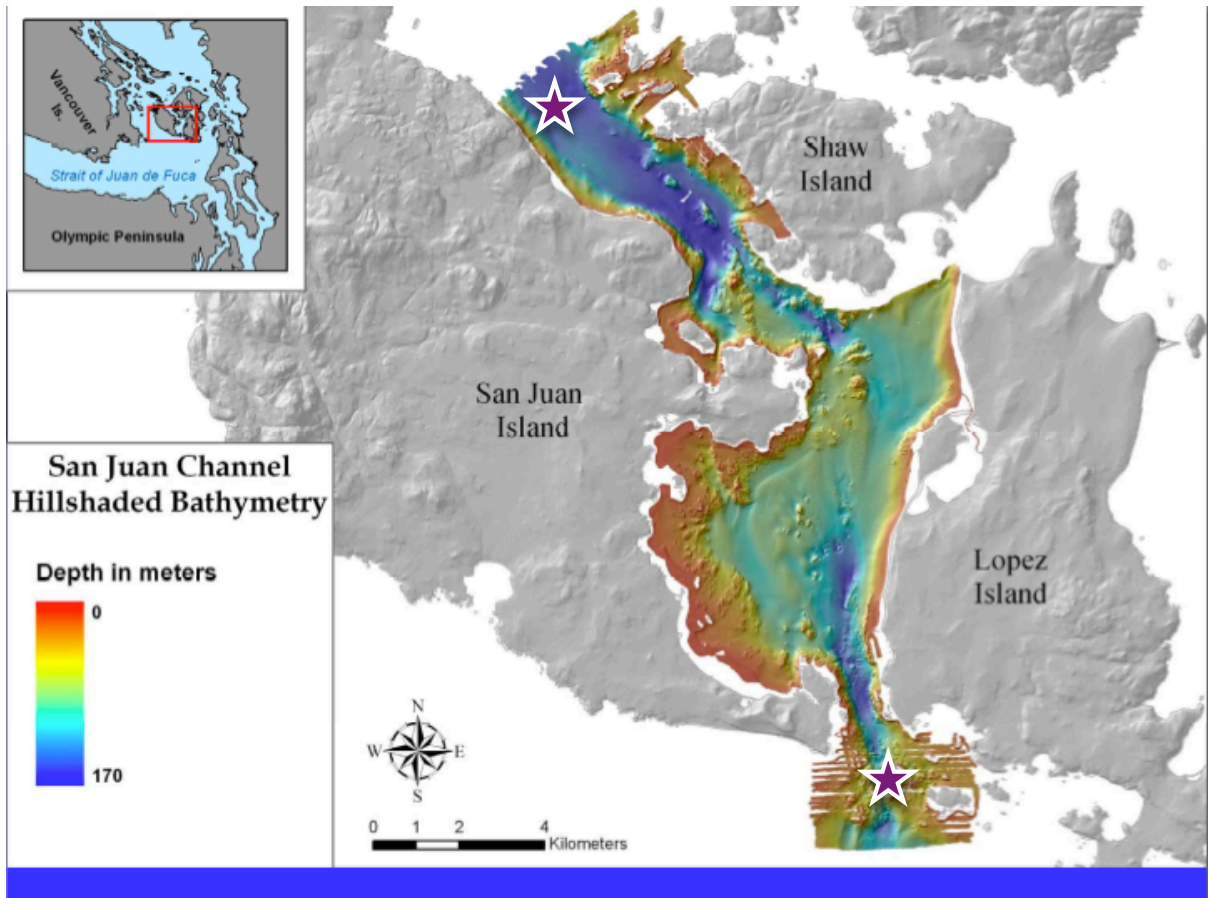


Figure 1. Map depicting the topography and bathymetry of the San Juan Channel in the San Juan Archipelago. North and South stations are represented as stars. The depth range is from 0 (red) to 170m (dark blue). (Credit: Garry Greene)

TGT Cruise -- 15-19, June 1998 Station Map

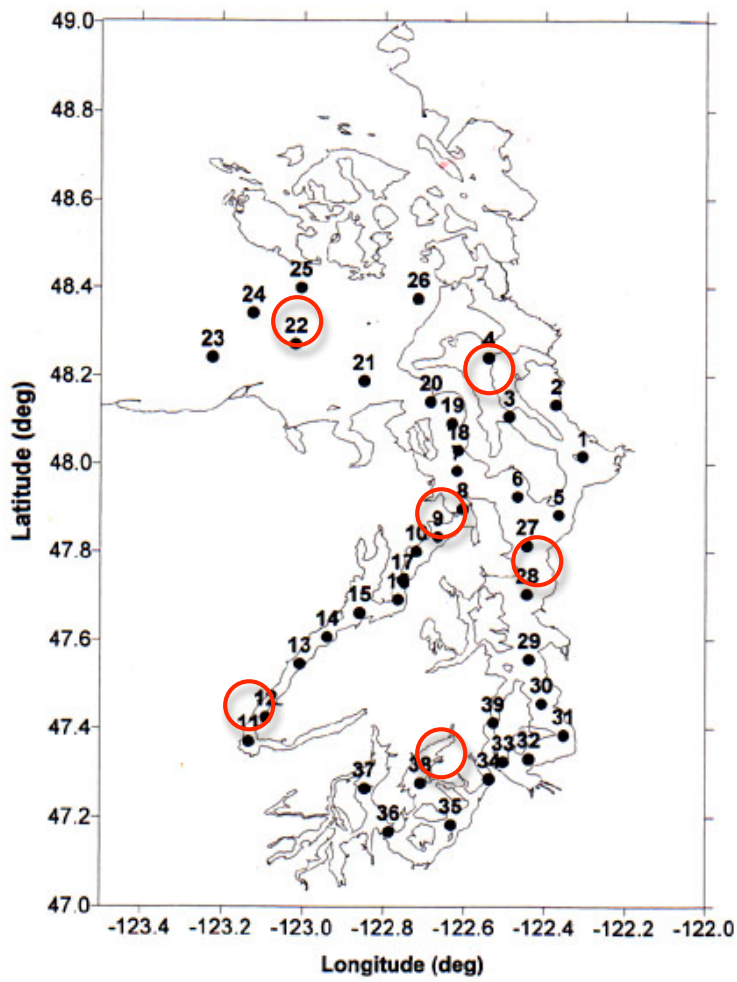


Figure 2. Map of all PRISM cruise stations in Puget Sound. Stations sampled in late October are circled in red.

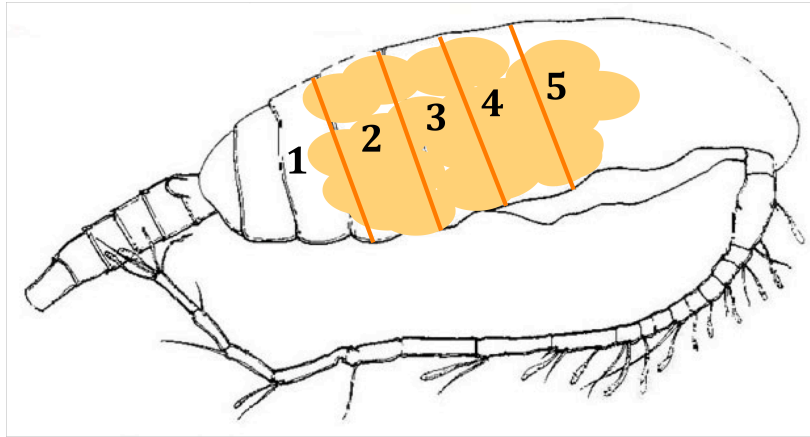


Figure 3. Five classes of lipid content in copepods. Class 1 has no lipid; Class 2 has less than half of the body filled with lipids; Class 3 has half; Class 4 has more than half; and Class 5 has body full of lipids.

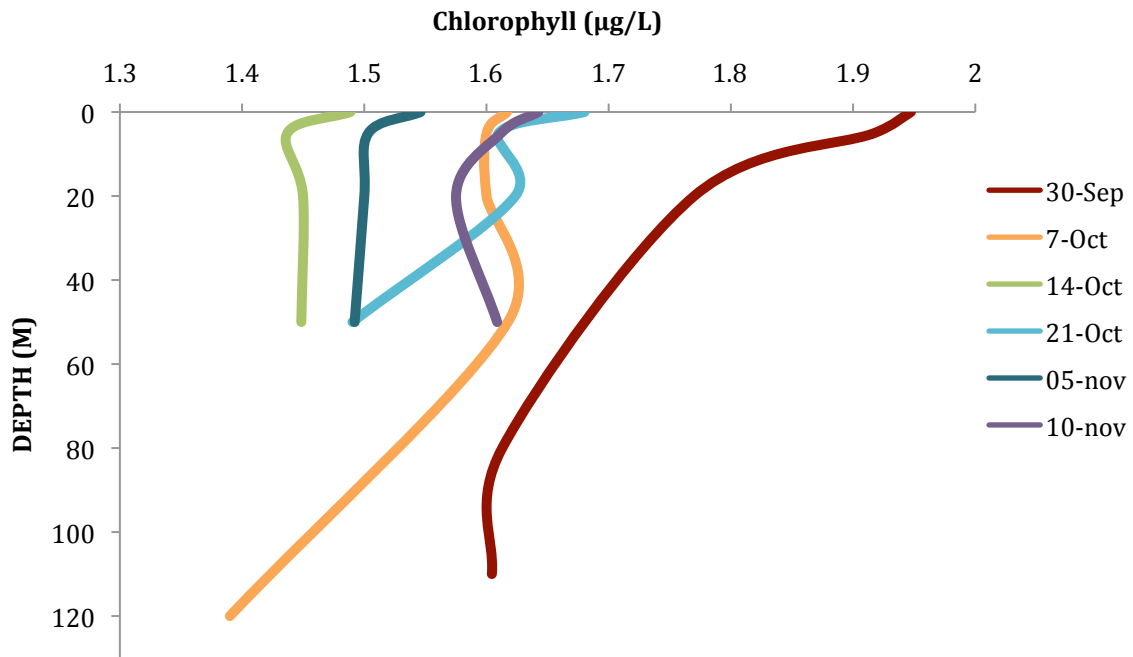


Figure 4. Chlorophyll *a* during fall season levels at North station in the San Juan Channel. Each sampling date is assigned with a different color.

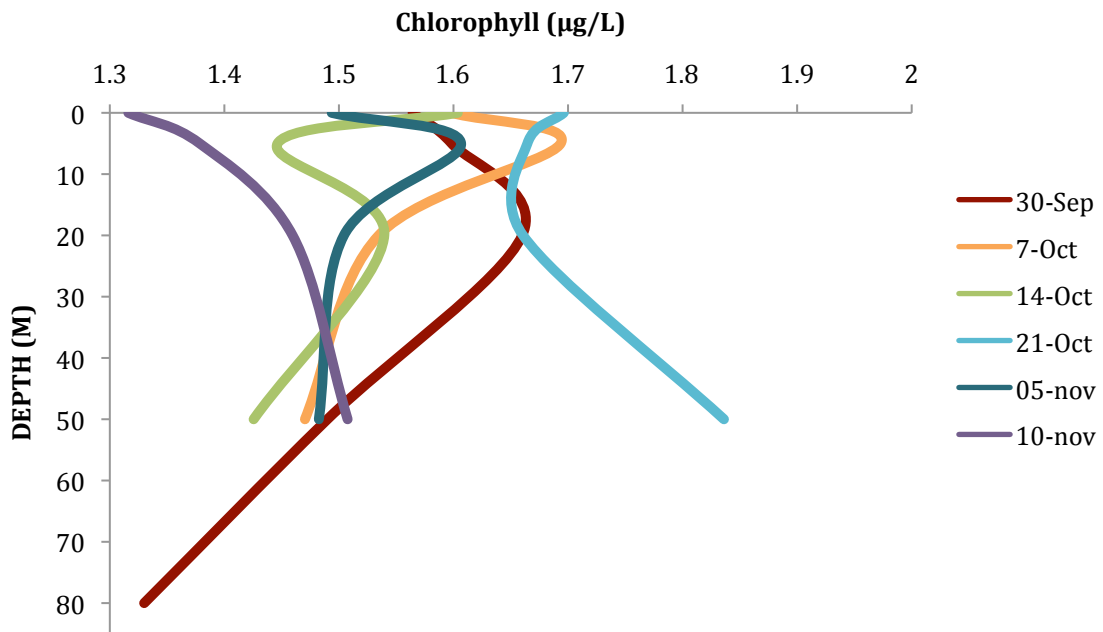


Figure 5. Chlorophyll *a* levels during fall season at South station in the San Juan Channel. Each sampling date is assigned with a different color.

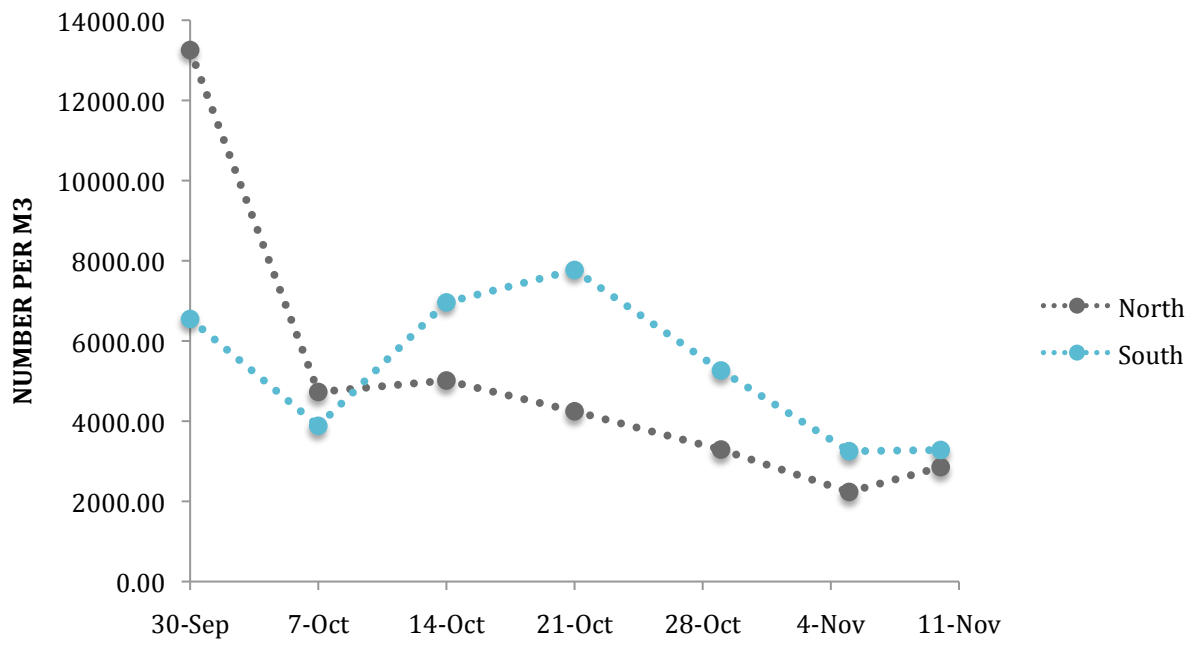


Figure 6. Total zooplankton abundance during fall season at North and South stations.

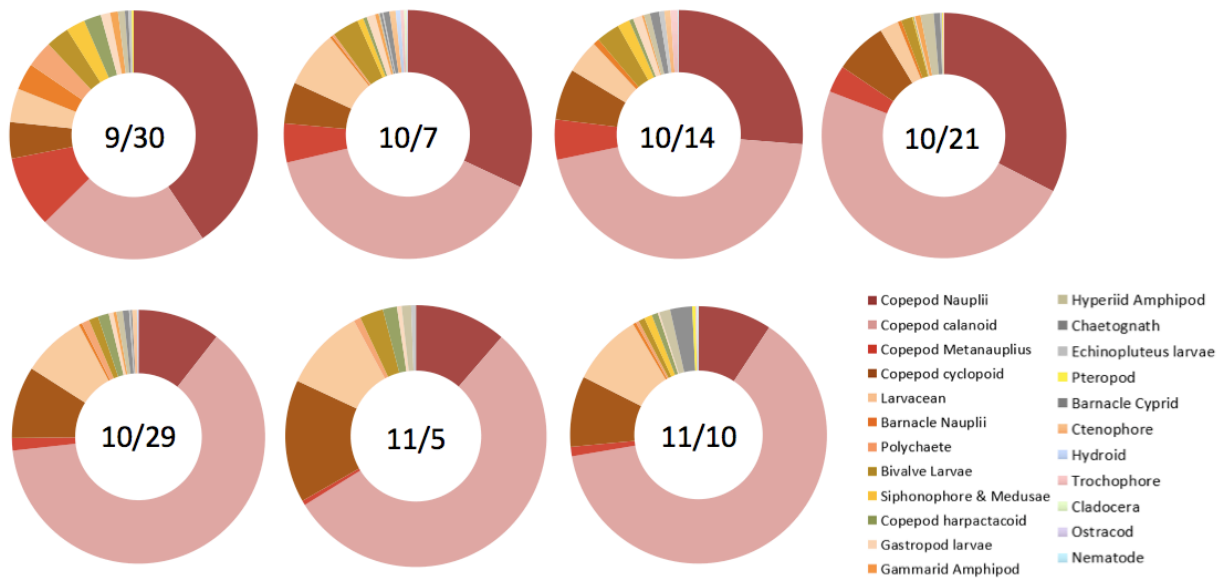


Figure 7. Species composition at North station over fall 2014. Sampling dates are indicated at the center of the charts.

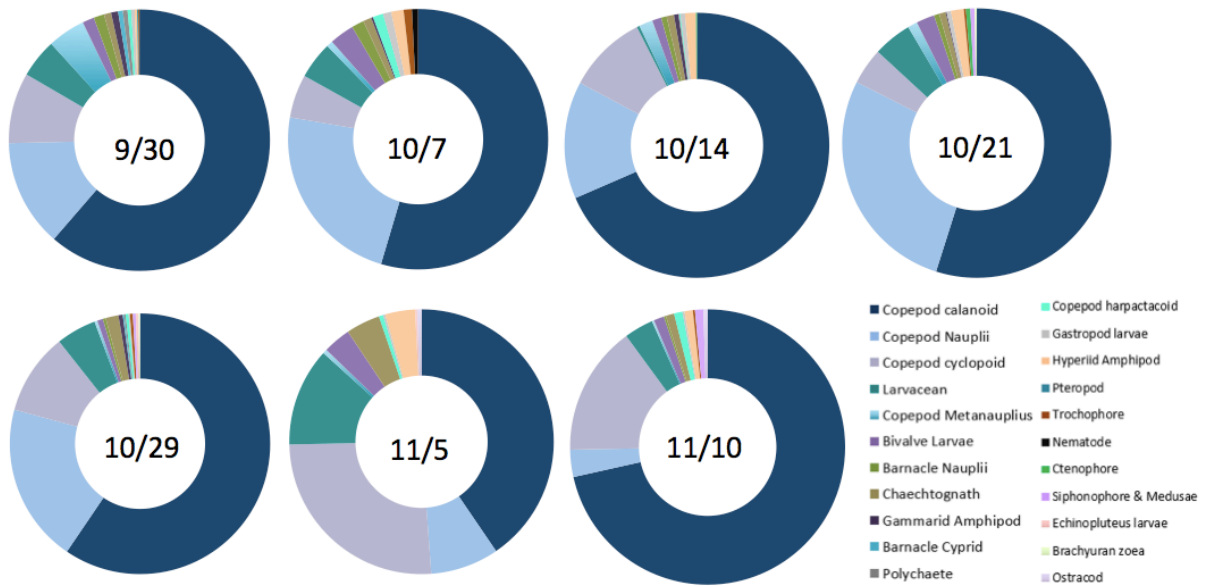


Figure 8. Species composition at South station over fall 2014. Sampling dates are indicated at the center of the charts.

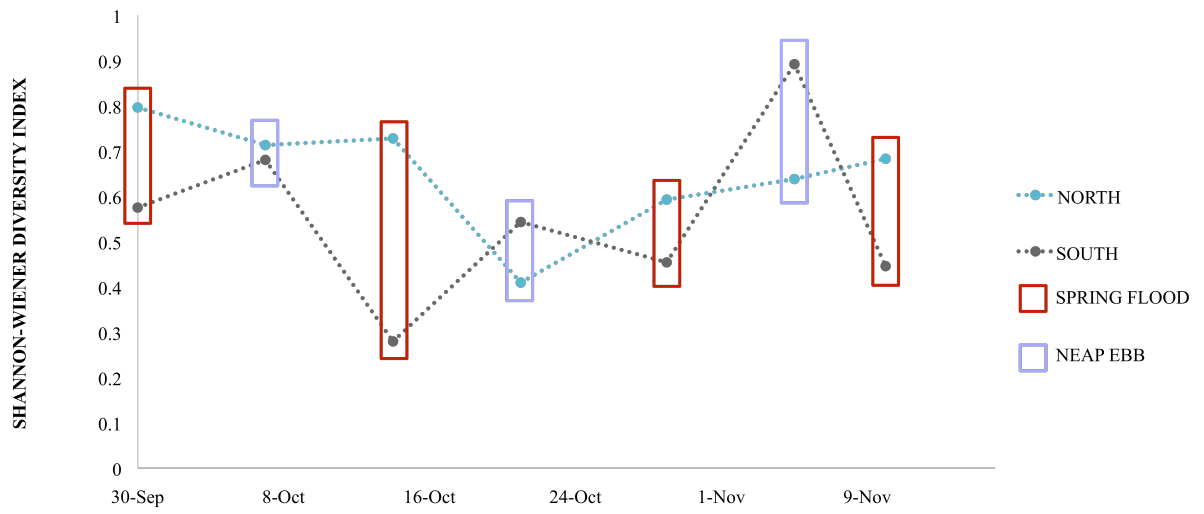


Figure 9. Shannon-Wiener diversity index in the San Juan Channel over fall 2014. Index values range from 0 to 4, where higher values indicate higher species diversity.

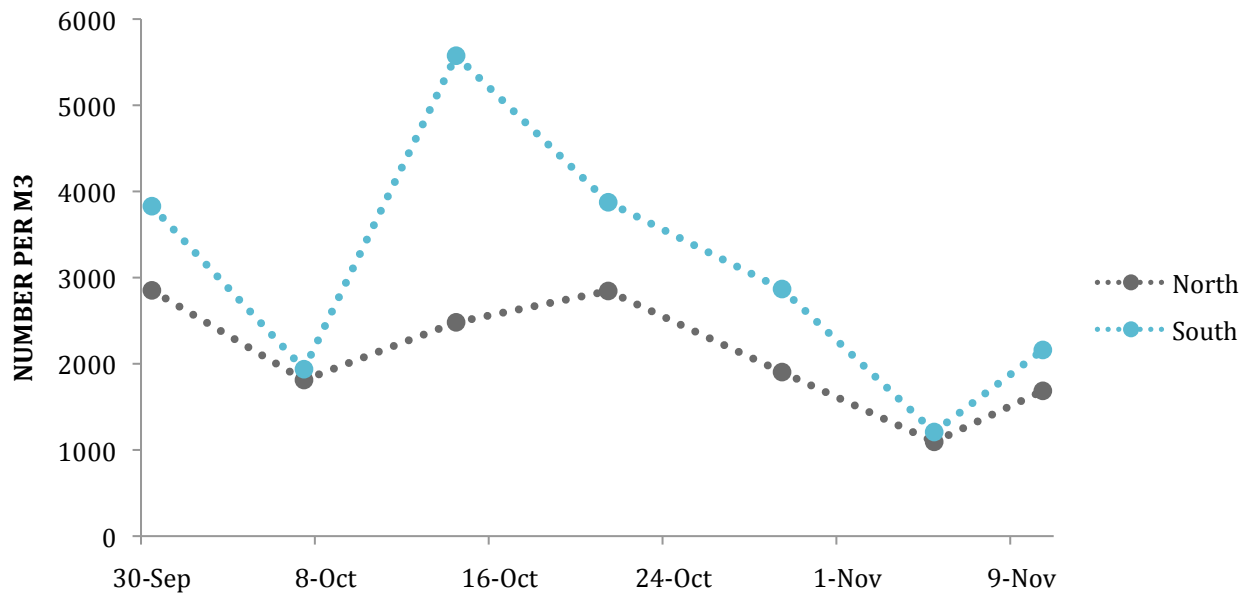


Figure 10. Total calanoid copepod abundance during fall season at North and South stations.

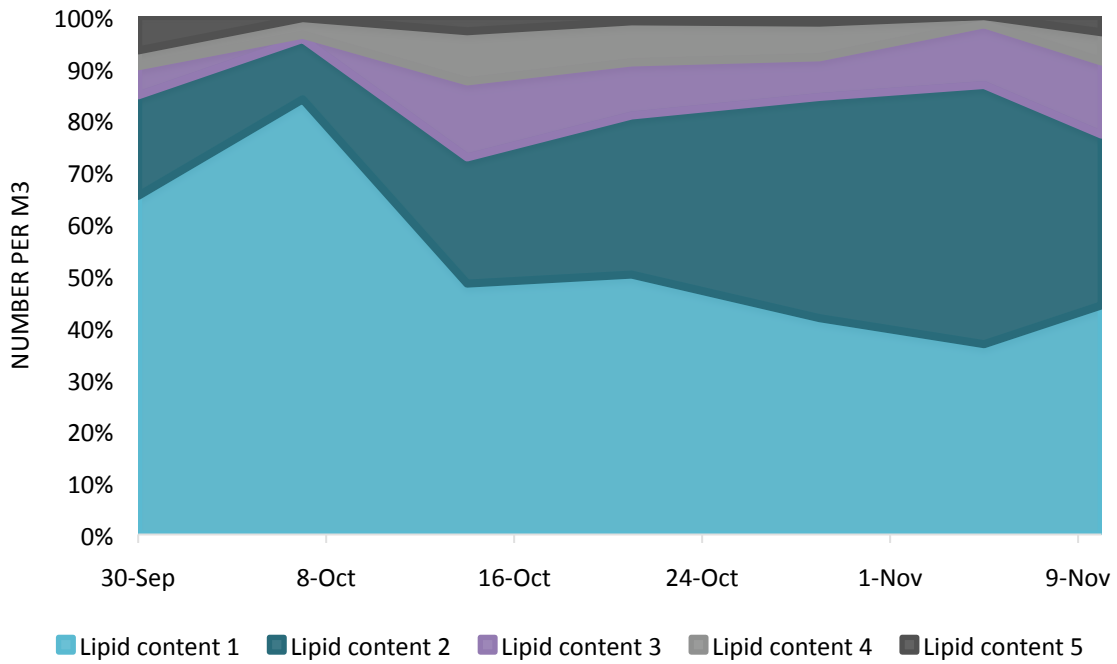
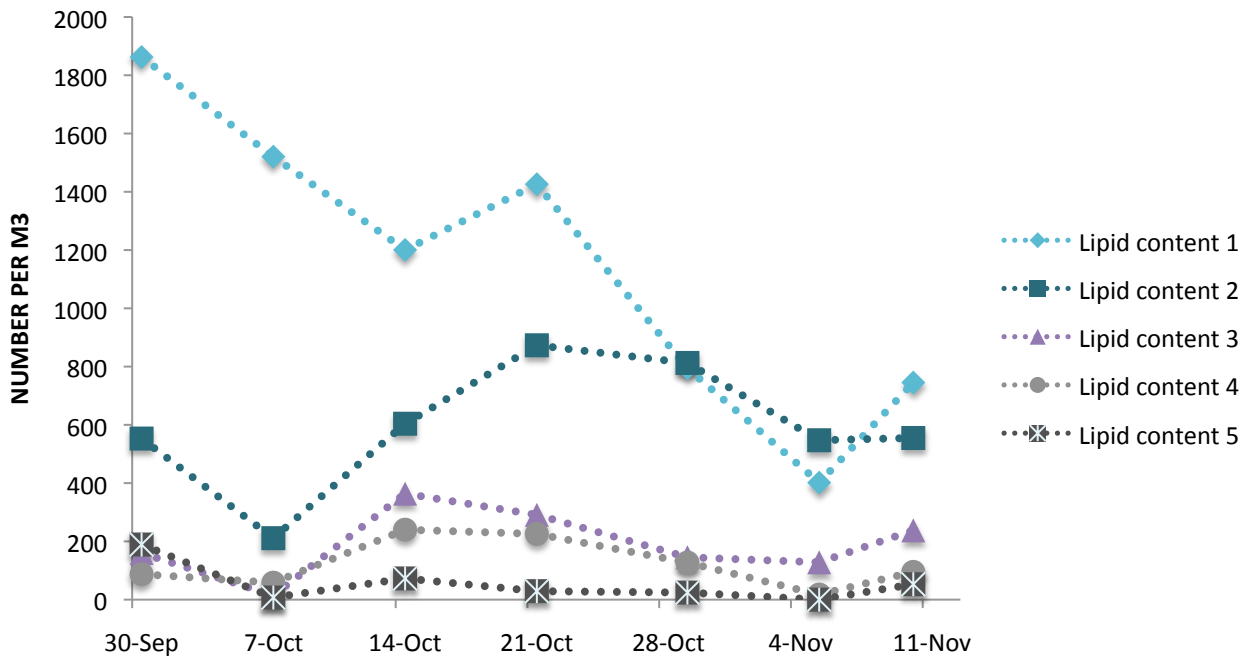


Figure 11. Lipid content in calanoid copepods at North station over fall 2014 (a) & (b).

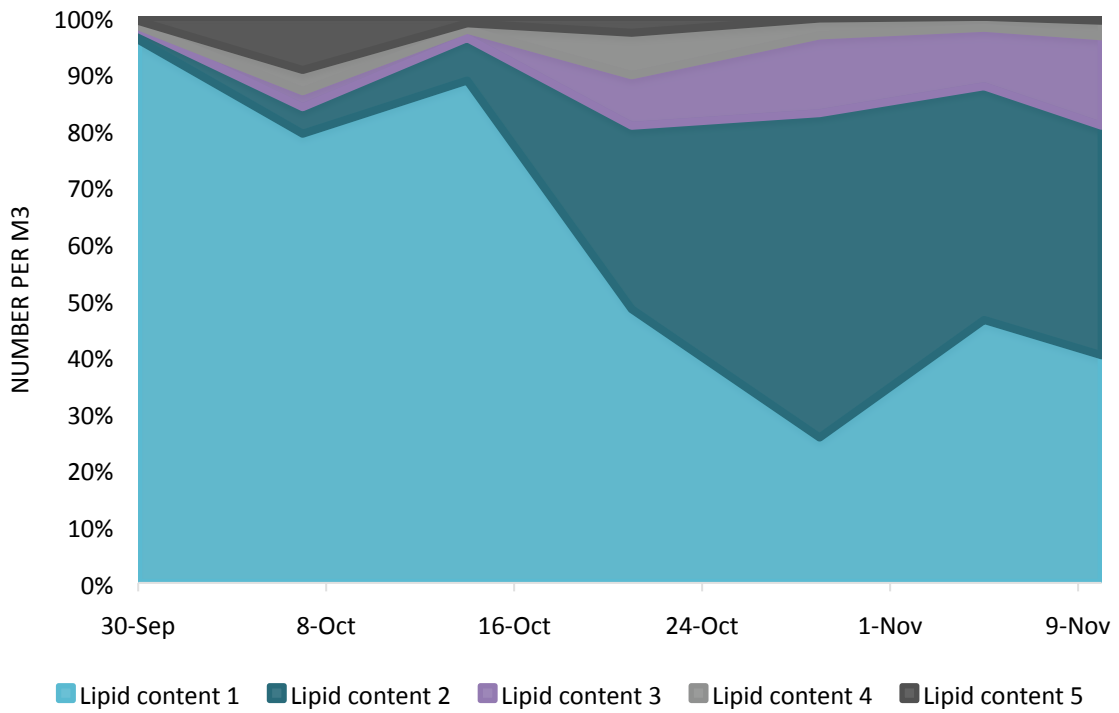
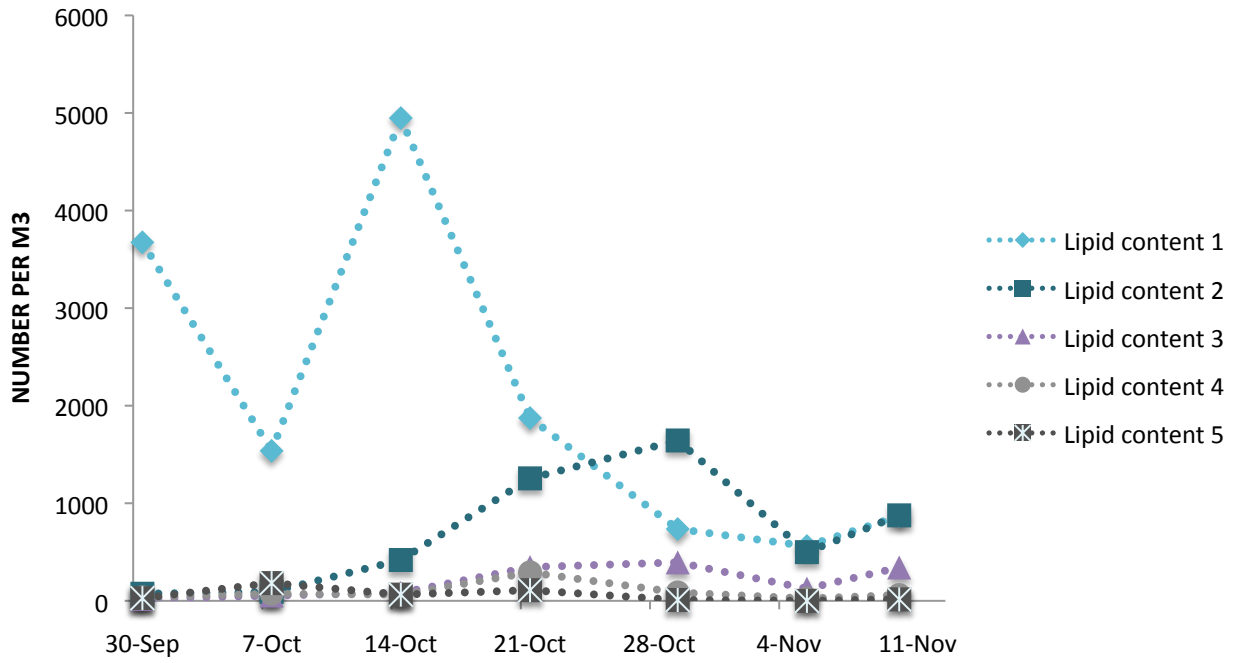


Figure 12. Lipid content in calanoid copepods at South station over fall 2014 (a) & (b).

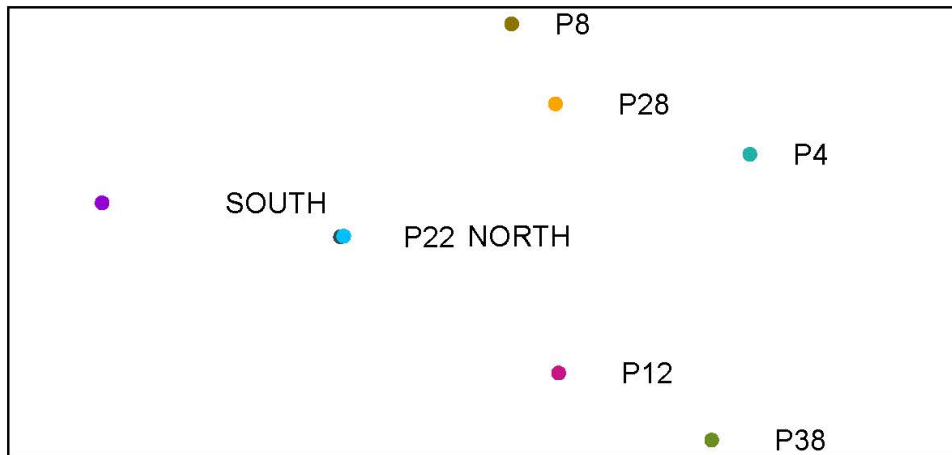
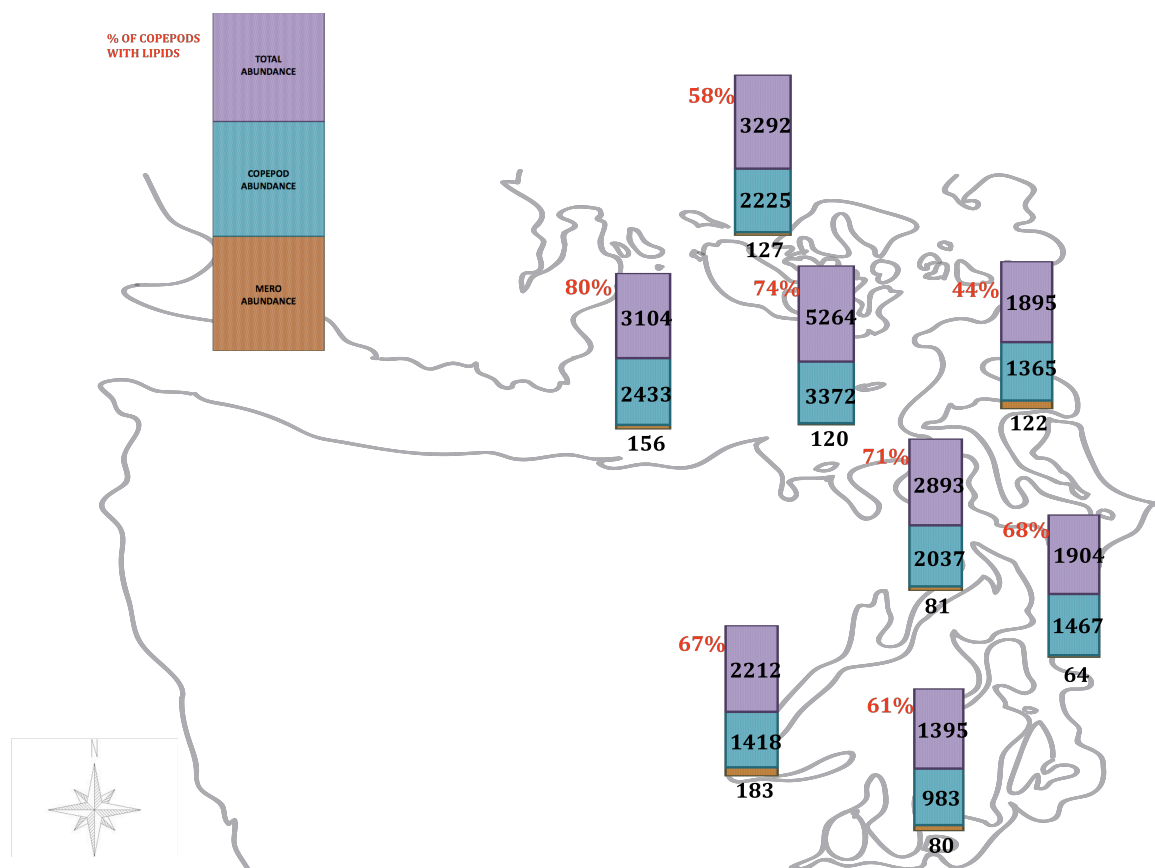


Figure 13. Multidimensional scaling plot depicting spatial patterns in the Salish Sea zooplankton population. Stations closer to each other are more similar in zooplankton species composition.



Figures 14. Map of the Salish Sea with total zooplankton abundance (purple), copepod abundance (blue), meroplankton abundance (brown), and % of copepods with lipid content (red values) for all stations sampled in late October.

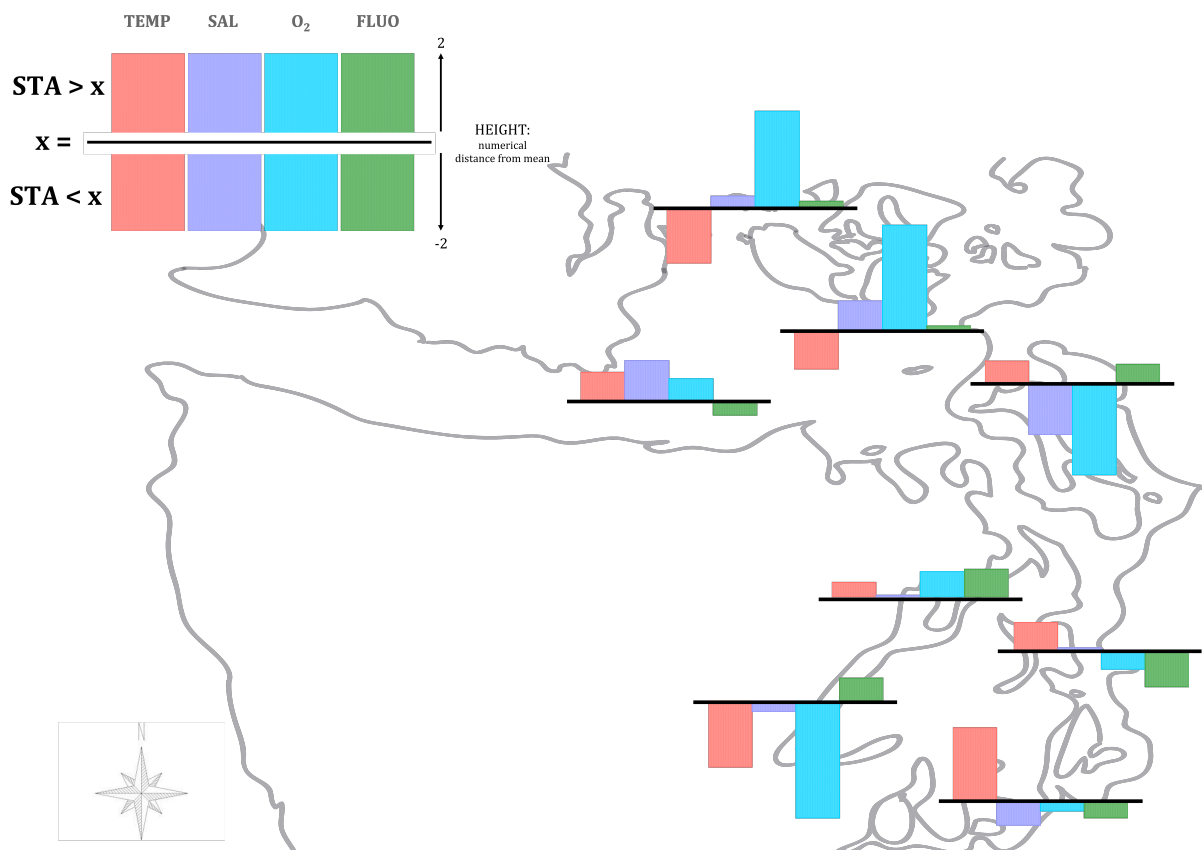


Figure 15. Map of the Salish Sea with temperature (pink), salinity (purple), dissolved oxygen (blue), and fluorescence (green) for all stations sampled in late October.