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Title: Comparing the Hydrography and Copepod Community Structure of the Continental Shelf Ecosystems of Washington and Oregon, USA from 1998 to 2009: Can a Single Transect Serve as an Index of Ocean Conditions over a Broader Area?

Abstract approved:

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Bi-weekly sampling of zooplankton and environmental parameters was conducted along a cross-shelf transect off the coast of Newport, OR, USA (44.65°N) from 1996 to present. Results have demonstrated the feasibility of using copepod community structure as an early indicator of ecosystem response to seasonal and large scale environmental changes in the Northeast Pacific. Spatial surveys of hydrography and zooplankton have also been completed along multiple cross-shelf transects from the central Oregon coast northward to the northwest corner of Washington (45-48°N) every May, June, and September since 1998. Although both sampling programs are located in the productive Northern California Current, questions have arisen as to the spatial comparability of zooplankton data, thus we tested the idea that data from a single transect can

serve as an index of ocean conditions over a much broader area. That is, how feasible is it to make ecosystem forecasts from a single high-frequency data set (Newport) compared to more extensive but less frequent spatial surveys? Comparisons will be made using the environmental parameters (stratification, upwelling strength, chlorophyll concentration) and copepod community structure, including spatial variations and inter-annual variability. Regional analysis of environmental parameters allows insights into the relative importance of spatial variations in environmental variables in shaping copepod community structure and therefore the lower trophic level ecosystem.

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Comparing the Hydrography and Copepod Community Structure of the  
Continental Shelf Ecosystems of Washington and Oregon, USA from 1998 to  
2009: Can a Single Transect Serve as an Index of Ocean Conditions over a  
Broader Area?

by  
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Presented on February 17, 2011.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any other reader upon request.

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Jesse F. Lamb, Author

## TABLE OF CONTENTS

	<u>Page</u>
1. Introduction.....	1
2. Methods.....	8
2.1 Sampling Region (Time and Space) .....	8
2.2 Sampling Protocol.....	9
Hydrography .....	9
Zooplankton Sampling .....	10
2.3 Statistical Analysis .....	11
North versus South Comparisons .....	11
Spatial Methods and Analysis.....	12
3. Results.....	17
3.1 Upwelling, Hydrography, Nutrients, and Chlorophyll.....	17
Upwelling .....	17
Temperature and Salinity .....	17
Stability .....	19
Nutrients.....	19
Chlorophyll .....	21
3.2 Copepods .....	22
General Comparisons .....	22
Comparisons with NH05 .....	24

TABLE OF CONTENTS (Continued)

	<u>Page</u>
Species Comparisons .....	25
Spatial Comparisons .....	27
4. Discussion .....	56
5. Conclusions .....	61
6. References .....	65



## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	BPA Sampling Stations .....	16
2a&b	Mean and cumulative upwelling indices .....	30
3	Mean SST (°C) and mean bottom temperature (°C).....	31
4	Mean bottom temperature (°C) vs. bottom salinity (psu). ....	32
5	South versus north transect stability. ....	33
6a	Silicate (Si(OH) <sub>4</sub> ) and nitrate (NO <sub>3</sub> ) versus SST (°C) and Salinity (psu), June.....	34
6b	Silicate (Si(OH) <sub>4</sub> ) and nitrate (NO <sub>3</sub> ) versus SST (°C) and Salinity (psu), September.....	35
7	Mean surface chl-a (mg). ....	36
8	Mean surface chl-a (mg) versus SST (°C) and salinity (psu) .....	37
9	Mean log abundance and biomass. ....	38
10	Mean biomass to abundance ratio .....	39
11	Mean transect abundance and biomass. ....	40
12	SST (C°) and sea surface salinity (psu) vs. copepod biomass.....	41
13a	NH05 vs. BPA Comparison of mean copepod abundance and biomass, June .....	42
13b	NH05 vs. BPA Comparison of mean copepod abundance and biomass, September .....	43
14	Percent total copepod biomass species comparison. ....	44
15	NH05 vs. BPA comparison of mean copepod biomass of cold and warm water copepods .....	45

LIST OF FIGURES (Continued)

<u>Figure</u>		<u>Page</u>
16	Cross-shelf biomass to abundance by station depth, all copepods .....	46
17	<i>Pseudocalanus</i> spp., all cross-shelf abundance and biomass, by station depth .....	47
18	<i>C. marshallae</i> , all cross-shelf abundance and biomass, by station depth.....	48
19	Cross-shelf biomass to abundance by distance from shore, all copepods.....	49
20	Transect Mean Significant Mantel Correlations.....	50

## LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Standard deviation in SST ( $^{\circ}$ C) and bottom temperature ( $^{\circ}$ C).....	51
2.	Nutrient table: June 1998 – 2009. ....	52
3.	Nutrient Table: September 1998 – 2005 .....	53
4.	Analysis of variance of log copepod abundance and biomass, by year. ....	54
5	Transect Moran's I for log copepod abundance and biomass.....	55



## Introduction

The continental shelves of Washington and Oregon (USA) lie at the northern end of the California Current System (CCS), a fertile, eastern boundary current system in the eastern Pacific Ocean. Eastern boundary current systems are the equatorward flowing arm of the basin scale gyres, with generally weak and meandering flow which near the coast shelf and slope water are driven by alongshore wind stress. When northerly, these winds trigger seasonal upwelling, in spring-summer where deep, nutrient rich water moves to the surface, causing phytoplankton blooms. These blooms are responsible for high chlorophyll concentrations and fuel upper tropic level productivity in continental shelf waters (Hickey, 1998).

As with other eastern boundary current systems, the CCS has latitudinal differences both in the strength and seasonality of equatorward alongshore wind stress which drive coastal upwelling. Northern California ( $\sim 38^{\circ}\text{N}$ ) has year-round, equatorward wind stress, but with seasonality in the strength of the wind stress: weak in the winter and very strong during summer (Huyer, et al., 1979). Central Oregon ( $\sim 45^{\circ}\text{N}$ ) has a defined seasonality, characterized by poleward wind stress during winter, causing downwelling, followed by the “spring transition”, when poleward winds shift to equatorward, causing upwelling during the spring and summer months. Seasonal downwelling and upwelling continues

to be the pattern in waters north of coastal Oregon, however the length of the upwelling season and strength of the winds decrease progressively as one moves to more northern latitudes.

Even though upwelling is more persistent off Northern California with the expectation that productivity is higher, it has been noted that chlorophyll levels in the CCS are highest at latitudes greater than  $45^{\circ}\text{N}$  (Thomas et al., 2001). Satellite data collected from 1997 – 2001 has shown maximum chlorophyll-a concentrations ( $\text{mg m}^{-3}$ ) of the CCS off the Washington shelf (Thomas, et al., 2001). Even during the summer of 2005 when anomalously low chl-a concentrations were seen along the entire CCS (anomalies of  $-1.0$  to  $-2.0 \text{ mg m}^{-3}$ ), the area north of  $45^{\circ}\text{N}$  (especially off Washington) still represented some of the highest values during that period. This was also true of the 1998 El Niño (Thomas and Brickley, 2006).

Ware and Thomson (2005) addressed whether the trophic interactions of the Northeast Pacific, particularly in shelf waters off British Columbia, Washington and Oregon were top-down or bottom up in their assessment of fish production. Using satellite chl-a data along with fish catch data from 1998 - 2003, they found both primary production and fish catch were highest from central Oregon to Vancouver Is., BC. They also found a highly significant correlation between long-term average resident fish yield ( $\text{Metric tons per km}^{-2}$ )

and mean annual chl-a concentration, showing that spatial variability in the annual chl-a concentration accounts for 87% of the spatial variance in the long-term yield in resident fish (Figure 2, Ware and Thompson, 2005). This suggests that the northern portions of the CCS system are controlled by bottom-up interactions.

These observations lead to the question of why the northern end of the CCS is apparently so productive. Hickey and Banas (2008) use the aforementioned examples combined with other studies to show that chl-a concentration, salmon catch data, and even the size of bird colonies are all quite high off the northern end of the CCS (especially the Washington shelf). This region produces the highest mean chl-concentrations in the entire CCS, even though the amount of cumulative upwelling is much lower between 45° – 50°N compared to regions the south. This region is known for sluggish circulation, leading to greater retention of water on the Washington shelf compared to the more southern regions of the CCS, thus they hypothesized that retention of phytoplankton on the Washington shelf is the most significant cause of high biomass. It is also noteworthy that the Washington coastline is slightly concave north to south, with no coastal promontories to cause meanders or jets which could transport shelf waters offshore. Drifters launched in the Juan de Fuca eddy in 2005-2006 largely remained in the shelf region (Hickey and Banas, 2008).

Hickey and Banas (2008) also been noted that chlorophyll concentration was strongly correlated with shelf width along the coast. The Washington shelf is between 50 – 60 km wide and very uniform north to south. South of the Columbia River (46°N), the shelf becomes very narrow off Cape Meares (45.5°N) and Cascade Head (45°N) (~ 20km), eventually widening to > 60km over Heceta Bank, OR, between 44 – 44.6°N. When shelf width and phytoplankton bloom time is compared with equal amounts of wind stress, blooms last only 2 days on a 10km wide shelf as compared to a week on a 60km wide shelf (Lentz, 1992; Hill, et al. 1998). With an annual mean wind stress lower than the rest of the CCS, bloom residence times off the Washington shelf can be even more protracted (Hickey and Banas, 2008).

The studies listed above have included mainly phytoplankton biomass and fish catch, representing the lowest and higher trophic levels. If lower and upper trophic level production is considered higher off the Washington shelf compared to other regions of the CCS, then it is logical to consider the zooplankton, in order to understand the regional differences in production among trophic levels.

Within this region, bi-weekly sampling of zooplankton and environmental parameters has taken place primarily along a cross-shelf transect off the coast of Newport, OR, USA (44.65°N) in the 1970's (Peterson & Miller, 1975) and recently



from 1996 to present ( Peterson, 2009). These studies have demonstrated that copepod communities occupy distinct water masses and strongly reflect basin scale climatic forcing (El Niño/La Niña, PDO phase) along with localized influences, i.e. the seasonal strength and persistence of upwelling or downwelling (Peterson and Keister, 2003; Keister and Peterson, 2003). More specifically, warm water conditions, as seen during downwelling, El Niño, and positive phase PDO have high species diversity due to the presence of both southern neritic and subtropical oceanic copepod species, both of which are relatively small in size and result in low overall biomass off Oregon. Conversely, cold water conditions as seen during upwelling, La Niña, and negative phase PDO exhibit high abundances of relatively large northern boreal species (Hooff and Peterson, 2006).

Data from the Newport time series studies above have been applied as biological indicators in forecasting of adult salmon returns to the Columbia River (Peterson, et. al, 2010). Due to their lower metabolism, these northern boreal copepods are lipid rich in wax esters and triglycerides and fuel a bioenergetically rich food chain for higher trophic levels. Further, the biomass of northern copepods, values of copepod species richness, and the interannual timing of the biological spring transition in the copepod community are all positively correlated with adult Coho survival in Oregon (Peterson, 2009, Peterson et al., 2010). Thus, copepod community structure, biodiversity, and interannual variability can

be used as early biological indicators of ecosystem response to seasonal (upwelling) and large scale (PDO, El Niño) environmental changes in the Northeast Pacific (Peterson and Schwing, 2003).

Another important data set is that generated by the Bonneville Power Administration Salmon Trawl Survey Project. This project has collected data on catch of juvenile salmon, hydrography, nutrients, chlorophyll, and zooplankton on spatial surveys along eight cross-shelf transects from the central Oregon coast (Newport, 44.6°N) north to the northwest corner of Washington (LaPush, 48°N) every May, June, and September since 1998. These spatial surveys have shown the majority of juvenile and adult salmon caught have been primarily on the central to northern coast of Washington (Bi, et. al, 2008, Peterson, et al., 2010).

Given the differences in hydrography and primary productivity off the Washington shelf as compared to the rest of the NCC, it is relevant to ask two questions: (1) whether or not this translates to latitudinal differences in copepod community structure within the region, and if so, how much of a latitudinal dissimilarity is there within the biological parameters mentioned above?, and (2) How feasible is it to make ecosystem forecasts from a high-frequency data set (Newport) as compared to fewer but more extensive spatial surveys (BPA Salmon Project)?

In this paper, we will address these questions through comparisons of the hydrography, chlorophyll, and copepod community structure including spatial and inter-annual variability in relation to the spatial variability in upwelling. Analysis of the spatial and temporal variability within environmental parameters allows for insight into their relative importance in shaping the copepod community structure and therefore the lower trophic level ecosystem. Our findings of the extent of a latitudinal similarity/dissimilarity within the copepod community not only has valuable ecological applications, but could also prove to be beneficial in determining the spatial expanse of future sampling programs within the region in terms of zooplankton sampling.

## Methods

### Sampling Region (Time and Space)

The BPA Salmon project consists of spatial surveys of hydrography, zooplankton, and pelagic fish along multiple cross-shelf transects from the central Oregon coast north to the northwest corner of Washington ( $45^{\circ} - 48^{\circ}\text{N}$ ) every May, June, and September from 1998 to the present (**Fig. 1**). For the present study, our analysis includes data from continental shelf stations along the most frequently sampled transects: La Push (LP), Queets River (QR), Grays Harbor (GH), Willipa Bay (WB), Columbia River (CR), Cape Meares (CM), Cascade Head (CH), and Newport Hydrographic (NH). Spatial separation between sampling stations on each transect was designed to sample similar isobaths between transects, with an emphasis on the near shore. Therefore, inshore stations were 2 – 3nm apart from each other to a station depth around 80m, after which stations were spaced roughly 5nm apart. Our data is constrained in time by the cruises in which zooplankton net samples have been counted: June, 1998 – 2009 and September, 1998 – 2005, for a total of 660 samples.

NH Line project data consist of bi-weekly sampling of zooplankton and environmental parameters along the Newport Hydrographic Line (**Fig. 1**), a cross-shelf transect off the coast of Newport, OR, USA ( $44.65^{\circ}\text{N}$ ), from 1996 to

present. For this study, we used only the NH05 zooplankton samples taken in the same months as the subsequent BPA project samples were taken.

## Sampling Protocol

### Hydrography

The physical characteristics of the water column at each station were measured with a CTD (Sea-Bird 19plus) profiler that was lowered to within 5 m of the sea floor, or to a maximum of 100 m. With this data, we calculated water column stability ( $dp/dz$ ), the change in station density between two depths. Chlorophyll and nutrient samples were collected at 3 m depth using a 3 Liter Niskin bottle. 100 ml water samples were immediately filtered on pre-combusted Whatman™ GF/F filters and the filters stored in 15ml centrifuge tubes for subsequent analysis of chlorophyll-a. The filtrate was saved for nutrient analysis and, along with the filters, kept frozen ( $-20^{\circ}\text{C}$ ) until processed on shore. Total chl-a was determined from GF/F filtered samples, extracted in 90% acetone in the dark at  $0^{\circ}\text{C}$  for 24 hours, and fluorescence measured on a Turner model 10AU fluorometer. Concentration of chl-a was calculated following Strickland and Parsons, 1972.

The concentration of phosphate ( $\text{PO}_4$ ), silicate ( $\text{Si}[\text{OH}]_4$ ), nitrate ( $\text{NO}_3$ ), nitrite ( $\text{NO}_2$ ), and ammonium ( $\text{NH}_4$ ) was determined in nutrient samples by the

University of Washington (Seattle) and Oregon State University Marine Chemistry Laboratory, by K. Kroglund and J. Jennings, using standard methods adapted for Technicon Autoanalyzer (UNESCO 1994).

Upwelling intensity was estimated by calculating the mean for the month previous to the June and September cruises using data from the PFEL website: [http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell\\_menu\\_NA.html](http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html).

### **Zooplankton Sampling**

The plankton net (202 mm mesh) was a half-meter diameter ring net, towed vertically in the water column from 2 m off the bottom, or from a maximum depth of 100 m, to the surface. Flow was measured with a TSK flowmeter. This sampling was designed to examine cross-shelf differences in the abundances of copepods. Once collected, all plankton samples were preserved in 5% buffered formalin. In the laboratory, samples were prepared by first rinsing with fresh water, and then poured into a graduated cylinder to determine a settled volume. The sample was poured into a beaker then diluted to up to 10 times the settled volume, thoroughly mixed with a spatula, and aliquots removed for counting with a 1, 5, or 10 ml Stempel (piston) pipette. Two aliquots were counted, unless more were required to achieve the total of 300 to 500 animals. Copepods were counted as three categories, either copepodite, adult male or adult female,

except for *Calanus marshallae* and *Pseudocalanus* spp. These species were identified and enumerated by individual developmental stages. Prosome lengths were measured on all development stages of *C. marshallae*. Counts were then entered into a Microsoft Access database, which was used to calculate abundance and biomass. Biomass estimates were obtained by multiplying mean dry weight of a stage by abundances ( $n/m^{-3}$ ). Dry weights were obtained from either published data or our unpublished measurements. For all analyses, copepod densities were first summed up for all life history stages, excluding eggs and nauplii.

## **Statistical Analysis**

### **North versus South Comparisons**

Our focus was to examine differences latitudinal differences in the hydrography and copepod community within the whole region, with an emphasis on the Washington continental shelf. Therefore, some analyses of physical and biological data were separated by transects north (LP,QR,GH, and WB) and south (CM,CH, and NH) of the Columbia River. This was done to more easily illustrate difference in hydrography and copepods.

## Spatial Methods and Analysis

Multiple spatial analysis techniques were used in order to locate any north versus south differences in the dispersion between copepod communities from station to station. Here we question whether or not differing effects of upwelling in each region would influence the amount of cross and along shelf spatial similarity within the copepod community. That is, do the advective effects of upwelling determine an increase or decreased amount of spatial clustering in the copepod community between stations?

Spatial autocorrelation measures the extent to which the similarity of samples in spatial locations is dependent upon their geographic distance from one another (Mackas, 1984). We determined spatial autocorrelation using both Moran's I and Mantel correlations.

Moran's I compares the semi-variance of total log copepod abundance between stations to the geographic distance between stations within transects:

$$I = \frac{N}{\sum_{i,j} w_{ij}} \frac{\sum_{i,j} w_{ij} (X_i - \bar{X})(X_j - \bar{X})}{\sum_i (X_i - \bar{X})^2}$$

Where N is the number of spatial units (coordinates) indexed by  $i$  and  $j$ ;  $X$  is the variable of interest;  $\bar{X}$  is the mean of  $X$ ; and  $w_{ij}$  is a matrix of spatial weights.



Spatial weights with a value of 1 ( $w_{ij} = 1$ ) indicates that a pair of samples,  $X_i$  and  $X_j$  are in the same distance class, where a value of 0 indicates all other cases. In this way, only pairs of sites within the stated distance class are taken into account. The expected value of Moran's I under the hypothesis of no spatial autocorrelation is:

$$E I = \frac{-1}{N - 1}$$

Therefore, any value greater than zero is considered autocorrelation. A Moran's I value of +1 is equal to perfect positive correlation; a value of -1 is equal to perfect negative correlation. From here, a two-sided p-value ( $<0.05$ ) is calculated to test for significant differences between the observed and expected values of Moran's I (Moran, 1950; Fortin, et al., 2002). Moran's I is similar to the Pearson product-moment correlation in that the numerator is a covariance comparing all pairs of points in turn while the denominator is the maximum-likelihood estimator of the variance (Legendre & Legendre, 1998).

Mantel correlations differ from Moran's I in that autocorrelation is determined by multivariate data (i.e. individual copepod abundance compared to total copepod abundance used for Moran's I). In our case, Mantel's correlation (Mantel 1967) is computed between a dependent distance matrix of species similarity between stations and a predictor matrix of geographic distance (station

coordinates) ultimately testing for autocorrelation in the dependent matrix

(Legendre & Legendre, 1998):

$$r = \frac{1}{(n-1)} \sum_{i=1}^n \sum_{j=1}^n \frac{(x_{ij} - \bar{x})}{s_x} \cdot \frac{(y_{ij} - \bar{y})}{s_y}$$

Where  $x$  and  $y$  are variables (i.e. species  $x$  and species  $y$ ) measured at locations  $i$  and  $j$ ;  $n$  is the number of elements in the distance matrices (species);  $s_x$  and  $s_y$  are the standard deviations for variable  $x$  and  $y$ . For our analysis, comparisons of the dependent distance matrix (species) were made at binned geographic distances between transect stations of increasing distance, from nearest to farthest. Because we only compared stations within individual transects, correlations are only representative of geographic distances within individual transects.

Because the elements of a distance matrix are not independent, Mantel's test of significance is a permutation test. Rows and columns of the distance matrices are randomly rearranged, with Mantel statistics recomputed for these permuted matrices, and the distribution of values for the statistic is generated via many iterations (Mantel function in R uses 999 permutations for  $\alpha = 0.05$ ). The range of values for Mantel correlations are the same as Moran's  $I$ : +1 is equal to perfect correlation; -1 is equal to perfect negative correlation.

Moran's I and Mantel correlation analyses were conducted between stations within transects for each year. Combining transect stations within regions was not feasible due to distance between transects. Also, station locations between transects run along isobaths, there is uneven spacing between sample stations from one transect to another. Therefore, the geographic distance classes found will be different for each transect found with the Mantel correlations. Finally, due to the fact that we had six or less stations per transect, only the first two geographic distance bins were analyzed, in order to use all samples over all distances. Spatial analysis and all other statistical analysis (means, ANOVA, etc.) were performed using the R statistical software package (<http://www.r-project.org/>).

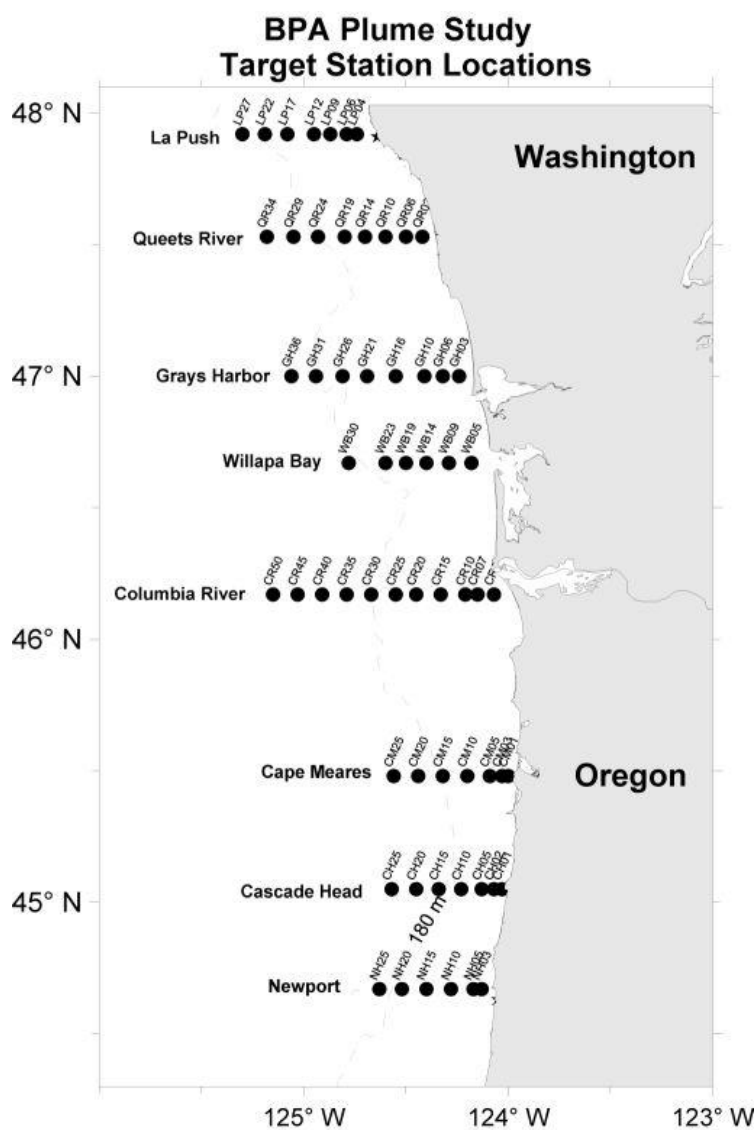


Figure 1. BPA Salmon Project sampling stations, 1998 – Present. For this study, comparisons were made between the continental shelf stations on four northern transects (LaPush, Queets River, Grays Harbor, and Willapa Bay) and the three southern most transects (Cape Meares, Cascade Head, and Newport Hydrographic). Comparisons were also made with the time series taken at the Newport Hydrographic 5 (NH05) station. Dotted line denotes 180m isobaths, the shelf break.

## Results

### Upwelling, Hydrography, Nutrients, and Chlorophyll

#### Upwelling

For the month prior to each cruise, both mean and cumulative upwelling was always greater south (45°N) than to the north (48°N) (**Fig. 2a&2b**). These differences were greater in September than in June. For June sampling years, mean upwelling at 45°N was  $28.53 \pm 8.98 \text{ m}^{-3} \text{ s}^{-1} \text{ 100m}^{-1}$ , compared to  $14.45 \pm 7.26 \text{ m}^{-3} \text{ s}^{-1} \text{ 100m}^{-1}$  at 48°N. In September, mean upwelling was  $36.58 \pm 7.19 \text{ m}^{-3} \text{ s}^{-1} \text{ 100m}^{-1}$  at 45°N, compared to  $11.49 \pm 5.55 \text{ m}^{-3} \text{ s}^{-1} \text{ 100m}^{-1}$ . The cumulative upwelling index from the physical spring transition to October, 1998 – 2009 suggests that upwelling is consistently two to three times stronger at 45°N compared to 48°N (**Fig. 2b**).

#### Temperature & Salinity

**Figure 3** shows mean sea surface temperature (SST (°C)) for continental shelf stations, north and south of the Columbia River transect line for June and September. SST tended to be lower for southern stations compared to the northern stations for 13 of 20 cruises. This difference is greater in September (6 of 8 cruises) compared to June (7 of 12 cruises). SST variability was also consistently higher to the south, with only 3 out of 20 cruises having a higher

standard deviation in SST in the North (**Table 1**). For all years combined, mean SSTs in the north were  $13.43 \pm 0.09$  in June and  $13.44 \pm 0.11$  in September; south mean SSTs were  $12.70 \pm 0.20$  in June and  $11.72 \pm 0.10$  in September.

Similar patterns are seen in mean temperatures 15 meters above the sea floor for continental shelf stations north and south of the Columbia River transect line for both June and September. Again, temperatures were consistently colder to the south (10 of 12 cruises in June and 7 of 8 cruises in September). Standard deviation in bottom temperature were greater in stations north of the Columbia River in 8 out of 12 years in June and 7 out of 8 years in September, which is opposite the variability in SST. For all years combined, as expected from differences in upwelling strength mean bottom temperatures in the north were warmer than in the south:  $8.35 \pm 0.14$  in June and  $8.77 \pm 0.21$  in September; mean bottom temperatures in the south were  $7.93 \pm 0.12$  in June and  $8.25 \pm 0.08$  in September.

Differences in upwelling strength is further reflected in temperature versus salinity plots for data 15 meters off the bottom averaged for all stations north and south (**Fig. 4**). Except for the year 2005, stations south of the Columbia River are consistently colder and saltier than their northern counterparts, regardless of sampling time. Temperatures and salinity values consistently reflect stronger upwelling at stations to the south year after year (except 2005).

## Stability

Stability was calculated for all stations north and south of the Columbia River for June and September as shown in (**Figure 5**) as cross shelf and alongshore differences. Transects are grouped north to south (x-axis), with transect stations listed inshore to offshore (right to left) in the figure. In June, mean transect stability and variability decrease inshore to offshore, except for the NH transect. However, the inshore variability seems to be highest at the two transects closest to the Columbia River (WB and CM). The inshore stability variability decreases as you move both north and south of the Columbia River. In September the region of highest stability was found at stations closest to the Columbia River north to GH and the transects north and south of it (QR and WB). Overall transect stability decreased from June to September at southern transects.

## Nutrients

For all years combined, mean silicate values for northern transects were  $8.49 \pm 0.51$   $\mu\text{M}$  in June increasing to  $16.49 \pm 0.86$   $\mu\text{M}$  in September; mean nitrate values were  $1.38 \pm 0.17$   $\mu\text{M}$  in June increasing to  $3.78 \pm 0.42$   $\mu\text{M}$  by September. To the south, mean silicate values were  $14.40 \pm 0.1.07$  in June increasing to  $17.07 \pm 0.80$  by September; mean nitrate values were  $5.47 \pm 0.73$  in June increasing to  $7.49 \pm 0.71$  by September.

**Figure 6a&b** compares surface nutrients values (silicate and nitrate, both in  $\mu\text{M}$ ) to SST ( $^{\circ}\text{C}$ ) and surface salinity (psu) values per station, respectively. In June, southern stations silicate and nitrate concentrations were higher when SSTs were less than  $11^{\circ}\text{C}$  and salinity greater than 32 psu. To the north, cold salty water was seldom seen at the surface, with the highest silicate and nitrate values found between 11 to  $15^{\circ}\text{C}$  and salinities greater than 31 psu. A summation of June nutrients versus SST and surface salinity ranges can be found in **Table 2**. Red indicates more south stations, grey indicates more north stations. Overall, the highest nutrient values were found to the south at low temperatures and high salinity values, with northern stations having the highest nutrient values at intermediate ranges of both temperature and salinity.

By September (**Fig. 6b**) in the south, higher silicate and nitrate values were found at SSTs less than  $14^{\circ}\text{C}$ , with increasing values at lower SSTs. Higher values were also associated with salinities greater than 32psu. To the north, high silicate values were found at all SSTs, but less than  $14^{\circ}\text{C}$  for nitrate, with increasing values at lower SSTs. There were two peaks of high silicate values to the north, both at salinities less than 31psu and greater than 32psu. High nitrate values were only associated with values greater than 32psu. In some years, mean northern nutrient values increased between June and September, where values decreased to the south. A summation of September



nutrients versus SST and surface salinity ranges can be found in **Table 3**. Again, red indicates more south stations, grey indicates more north stations.

## Chlorophyll

**Figure 7** shows mean surface chl-a ( $\text{mg}/\text{m}^{-3}$ ) for stations north and south of the Columbia River for June and September. More northern stations had higher mean surface chl-a values than southern stations, for both months, for all years sampled. Although surface chl-a trended higher to the north for more years, mean June chl-a for all years sampled was not different between north and south:  $4.15 \pm 0.50$  to the north compared to  $4.01 \pm 0.52$  to the south. In September, mean chl-a for all years sampled was significantly different between north and south:  $6.32 \pm 0.46$  to the north compared to  $4.25 \pm 0.35$  to the south.

Even though the mean values were similar, the overall ranges in chlorophyll values were at times different north to south. Chlorophyll values in June had a range of  $0.001 - 109.56\text{mg}/\text{m}^{-3}$ , with 93% of values less than  $10\text{mg}/\text{m}^{-3}$  to the north; southern values had a range of  $0.17 - 54.24\text{mg}/\text{m}^{-3}$ , with 90% of values less than  $10\text{mg}/\text{m}^{-3}$ . In September northern values had a range of  $0.29 - 39.13\text{mg}/\text{m}^{-3}$ , with 84% of the values less than  $10\text{mg}/\text{m}^{-3}$ ; southern values had a range of  $0.33 - 17.64\text{mg}/\text{m}^{-3}$ , with 90% of values less than  $10\text{mg}/\text{m}^{-3}$ .

**Figure 8** shows mean surface chl-a ( $\text{mg}/\text{m}^{-3}$ ) values versus sea surface temperature ( $^{\circ}\text{C}$ ) and salinity (psu) for north and south stations for June and September. In June, along southern transects mean chl-a ( $\text{mg}$ ) peak at SSTs around  $11^{\circ}\text{C}$  and salinities between 32 to 33, whereas to the north, mean chl-a ( $\text{mg}$ ) peak at SSTs around  $12^{\circ}\text{C}$  and salinities between 31 to 33psu, with only low values ( $< 5\text{mg}/\text{m}^{-3}$ ) at lower salinity values. Values declined between 11 and  $17^{\circ}\text{C}$  in both the north and the south. Low values of chlorophyll were also seen at the lowest temperatures ( $< 9^{\circ}\text{C}$ ). Southern stations had mean surface chl-a values greater than  $5 \text{ mg}/\text{m}^{-3}$  at temperatures less than  $11^{\circ}\text{C}$ , where more northern stations had mean surface chl-a values greater than  $5 \text{ mg}/\text{m}^{-3}$  only at temperatures greater than  $12^{\circ}\text{C}$ . September showed the same overall pattern, with the occasional high surface chl-a values occurring at values greater than  $5 \text{ mg}/\text{m}^{-3}$  at salinity values lower than 31psu.

## Copepods

### General Comparisons

Patterns of copepod abundance and biomass encompassed a great overall variability, ranging in abundance between  $67 - 21800 \text{ n}/\text{m}^3$  and biomass between  $0.29 - 94.09 \text{ mgC}/\text{m}^3$ . For June, mean copepod abundance ( $\text{n}/\text{m}^3$ ) north versus south was within their standard error for all years, except 2005, where both copepod abundance and biomass ( $\text{mgC}/\text{m}^3$ ) were significantly higher to the north (**Fig. 9**). Southern stations had significantly higher log biomass than

northern stations in 2002, 2006, and 2007; by September, mean station abundance and biomass were higher to the north in 2001, 2002, and 2004, but southern stations only had higher abundance and biomass in 2005.

One-way Analysis of Variance was used to test for year to year differences in both log abundance and biomass between northern and southern stations (**Table 4**). This revealed only three of the twenty comparisons showed significant differences where specific species had anomalously high abundances or biomass. In June 2005 there were very high abundances of *Acartia tonsa* north. In September 2004 and 2005 there were much higher abundances of *Acartia tonsa*, *Ctenocalanus vanus*, and *Paracalanus parvus* north.

Additional analysis of mean abundance and biomass values revealed interannual and spatial trends. First, the mean weight of copepods, obtained by dividing mean station biomass by mean station abundance per station, revealed that in most years the biomass for southern stations for both June and September sampling came from larger sized copepods (**Fig. 10**). Except for June 2005, 2008 and September 2001, southern stations have higher biomass per individual copepod. Second, spatial trends in transect comparisons for June (**Fig. 11**), showed a decrease in mean copepod abundance along with an increase in mean copepod biomass from north to south. However, by September, the opposite pattern was seen: transect mean abundance and biomass were both

higher to the north, with a decline in both copepod abundance and biomass as you moved south of Queets River. An exception was the La Push transect where abundance and biomass were always lower than any other transect. Overall copepod abundance and biomass was higher in June than September when analyzed on a species by species basis.

North versus south copepod biomass ( $\text{mgC}/\text{m}^3$ ) was compared to SST ( $^{\circ}\text{C}$ ) and surface salinity (psu) in **Figure 12**. Like **Figures 6&8**, which compared both nutrients and chlorophyll to both SST and surface salinity, the highest values of copepod biomass were found mostly associated with both the coldest temperatures and highest salinity values. However, the majority of biomass values occur at the full range of temperatures (south range:  $8 - 16^{\circ}\text{C}$ , north range:  $11 - 16^{\circ}\text{C}$ ) along with a larger range of salinity ( $31 - 33\text{psu}$ , both regions) compared to nutrients and chlorophyll. Similar to nutrients and chlorophyll, the only stations where values of  $< 31$  psu were found were northern stations

### **Comparisons with NH05**

**Figure 13a&b** show comparisons of mean station abundance and biomass of the time series station NH05 with combined mean station abundance and biomass of northern stations of comparable depths (stations LP06, QR10, GH10, and WB09), by year. Mean abundances for June sampling were slightly higher at the northern stations for many years, yet mean biomass fell on the line of slope = 1. Only two years out of the twelve shown were skewed toward the

northern stations (1999) or NH05 sampling (2008). In 1999, NH05 was sampled only once, where the mean biomass of the northern stations was five times that of NH05. In 2008, NH05 was abundant in *Calanus marshallae*, whose presence increased biomass to twice that of the northern stations, which was relatively lacking in *C. marshallae*. September had more years trending toward the north stations. 2000 had much higher mean abundance and biomass at station NH05, due to higher abundances of *Pseudocalanus* spp to the south.

### Species Comparisons

Seasonal variations in abundance and biomass were seen for the nine most common species for all years combined (**Fig. 14**). *Pseudocalanus* spp., a medium sized copepod (female weight = 14.0  $\mu\text{gC}$ ), represented around 50% of the total copepod biomass per station for both June and September sampling. *Calanus marshallae* (large, female weight = 109.0  $\mu\text{gC}$ ) and *Centropages abdominalis* (medium, female weight = 13.6  $\mu\text{gC}$ ) dropped from a combined 25% total biomass per station in June to roughly 10% in September. This is opposite to three species with low individual biomass (*Acartia longiremis* (female weight = 6.0  $\mu\text{gC}$ ), *Acartia hudsonica* (female weight = 5.0  $\mu\text{gC}$ ), and *Paracalanus parvus* (female weight = 3.5  $\mu\text{gC}$ )), which represented around 15% of the total copepod biomass per station in June, increasing to over 25% total copepod biomass per station in September. *Calanus pacificus* (female weight = 75.0  $\mu\text{gC}$ ) also showed a seasonal increase in total copepod biomass per station: around 2% in

June to 5% in September. *Metridia* spp. (female weight = 47.6 $\mu$ gC) had basically no change of representative biomass from June to September (around 2.5%).

We then plotted combined biomass of species by the water type preference, similar to Hooff and Peterson (2006), they occupy in north south comparison plots, similar to **Figures 13a&b (Fig. 15a&b)**. For both June and September, cold water copepods (*A. hudsonica*, *A. longiremis*, *C. marshallae*, *C. abdominalis*, *Microcalanus pusillus*, *Scolecithricella minor*, and *Tortanus discaudatus*) tended to fall on the 1:1 ratio line, except for 1999 (higher in the north) and 2008 (higher in the south), which is similar to the relationship seen in **Figure 13a&b**. When warm water copepods (*A. tonsa*, *C. pacificus*, *C. anglicus*, *Ctenocalanus vanus*, *Clausocalanus* spp., and *P. parvus*) were present, they were most often found to the north in June than at NH05. By September, there was little difference between their abundances at NH05 and north of the Columbia River.

### **Spatial Comparisons**

Mean cross shelf abundance and biomass by station depth (m) was plotted for total copepod abundance and biomass per station, along with the individual species *Pseudocalanus* spp. and *C. marshallae* (**Fig. 16, 17, & 18**). Mean station abundance and biomass peaked between 20 – 40m depth, gradually decreasing to the deepest stations near the shelf break. Regionally,

northern stations had higher inshore mean abundances in June, while southern stations had higher inshore biomass. By September, both inshore abundance and biomass amounts were similar north and south. Interestingly, there were slight upticks in abundance and/or biomass between 180 – 200m for all regions before a steep decline at the shelf break stations (except the south in September). Similarly, peak mean *Pseudocalanus* spp. abundance and biomass occurred between 20 – 40m, albeit with higher mean abundance and biomass to the south in June. This pattern switched by September, with higher mean *Pseudocalanus* spp. abundance and biomass to the north and a decline in the south. There was also a similar inshore pattern between northern June samples and southern September *Pseudocalanus* spp., where low mean abundance and biomass at the shallowest stations increased to peak abundances at deeper stations.

*C. marshallae* exhibited a greater variety of patterns than the above examples. Similar to *Pseudocalanus* spp., *C. marshallae* exhibited peak mean abundance around stations around 40m followed by a gradual decrease to stations around 120m, followed by both up and down ticks in both mean abundance and biomass at stations greater than 120m in June. Mean *C. marshallae* biomass increased rather gradually from mean minimum values at shallow stations to peak mean biomass around 80m to the south and 110m to the north. Mean peak *C. marshallae* biomass was higher to the south in June as

well. By September, *C. marshallae* mean cross shelf abundance and biomass decreased dramatically compared to June values for both regions, although southern values were slightly higher.

The north to south cross shelf similarities with isobaths become more pronounced when you do the same cross shelf comparison of abundance and biomass versus distance from shore (**Fig. 19**). Southern transects were much narrower than northern transects, and the declines in copepod biomass and abundance were much more pronounced in the south than to the north, which was much more gradual.

We tested for spatial autocorrelation within transects using Moran's I (for total copepod abundance and biomass per station) and Mantel correlations (for species abundance per station), respectively. **Table 5** shows Moran's I calculations for each transect (significant calculations values in yellow) for both log copepod abundance and biomass. Blacked out years indicate when stations either were not sampled, or too few stations (< 3) were sampled to perform the analysis.

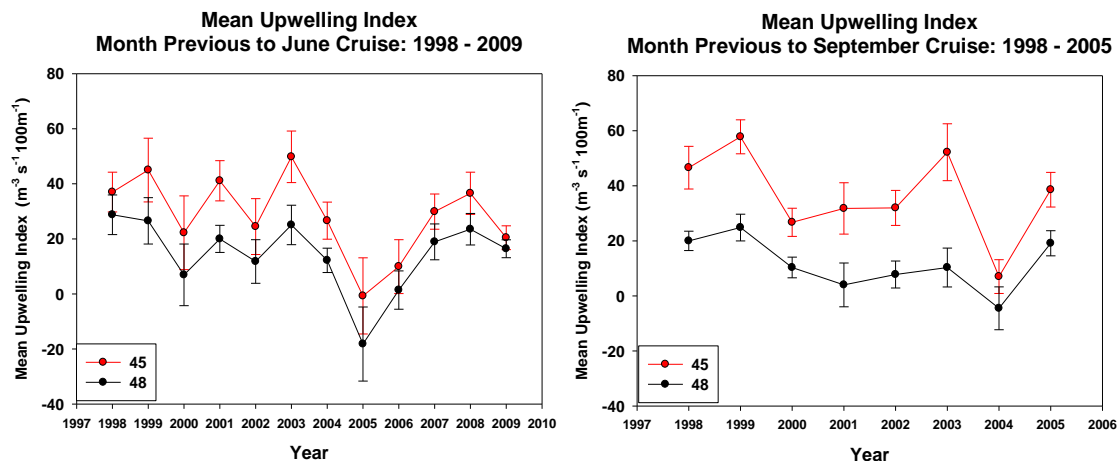
Northern transects showed more significant positive autocorrelation for all years sampled than southern transects. The ratio of north to south transects showing significant positive autocorrelation in log copepod abundance was



around 6:1 in June, decreasing to 2:1 in September. For biomass the north to south June ratio was around 2.5:1, decreasing to 1.5:1 in September. This would indicate a higher amount of station to station similarity to the north in both copepod abundance and biomass in June.

Mantel correlations use multivariate data (in our case individual species log abundance per station within transect) to show the amount of autocorrelation over specific geographic distances (nautical miles) (**Fig. 20**). Most transects sampled fell over the entire range of correlation values, within only the short range correlations of the NH transect in June. There were more significant correlations found year to year at northern transects, similar to the results for Moran's I. In June, the majority of significant Mantel correlation ranged from 0.2 - 0.8 at distances a little less than 3 - 6 nautical miles. Northern transects were correlated between 3.5 - 6nm, with the exception of one GH transect. Southern transects showed significant correlation at two distance classes: one between 2.5 - 4nm, the other from 6 - 7nm, with higher correlation values at shorter distances. September had the same range in correlation values, with the majority of transects over the same distance range found in June. The southern CM transect was found at a very small distance class (around 1.5nm) and three northern transects were found at a second distance class (LP, QR, and GH), between 7.5 - 8nm.

2a:



2b:

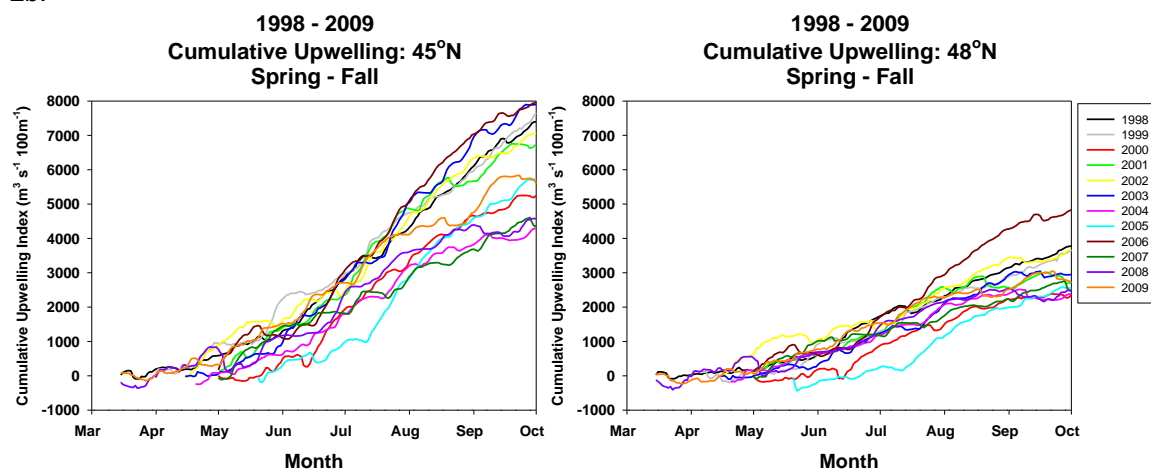


Figure 2. Mean upwelling index ( $\text{m}^{-3} \text{s}^{-1} 100\text{m}^{-1}$ ) at  $45^{\circ}\text{N}$  (red) and  $48^{\circ}\text{N}$  (black) for the month prior to the cruise for June (1998 – 2009) and September (1998 – 2005). Upwelling is continually stronger ( $> 2x$ ) at  $45^{\circ}\text{N}$  compared to  $48^{\circ}\text{N}$ . B. Cumulative upwelling index ( $\text{m}^{-3} \text{s}^{-1} 100\text{m}^{-1}$ ) at  $45^{\circ}\text{N}$  and  $48^{\circ}\text{N}$  from physical spring transition to October, 1998 – 2009. Upwelling is continually stronger ( $> 2x$ ) at  $45^{\circ}\text{N}$  compared to  $48^{\circ}\text{N}$ . Data obtained through the PFEL website: [http://www.pfel.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell\\_menu\\_NA.html](http://www.pfel.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html)

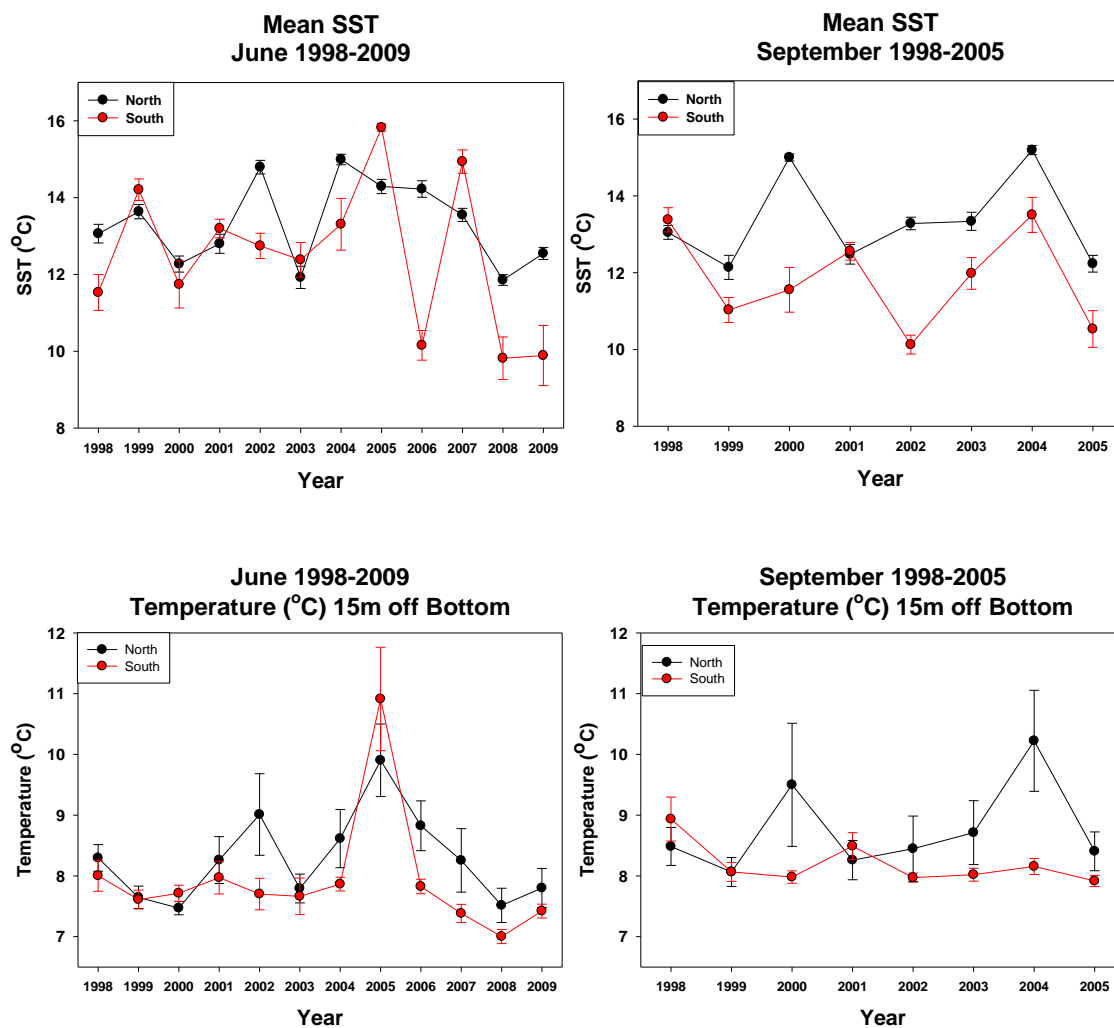


Figure 3. Mean sea surface and bottom temperature ( $^{\circ}\text{C}$ ) for continental shelf stations, north (black) and south (red) of the Columbia River transect line for June (1998 – 2009) and September (1998 – 2005).

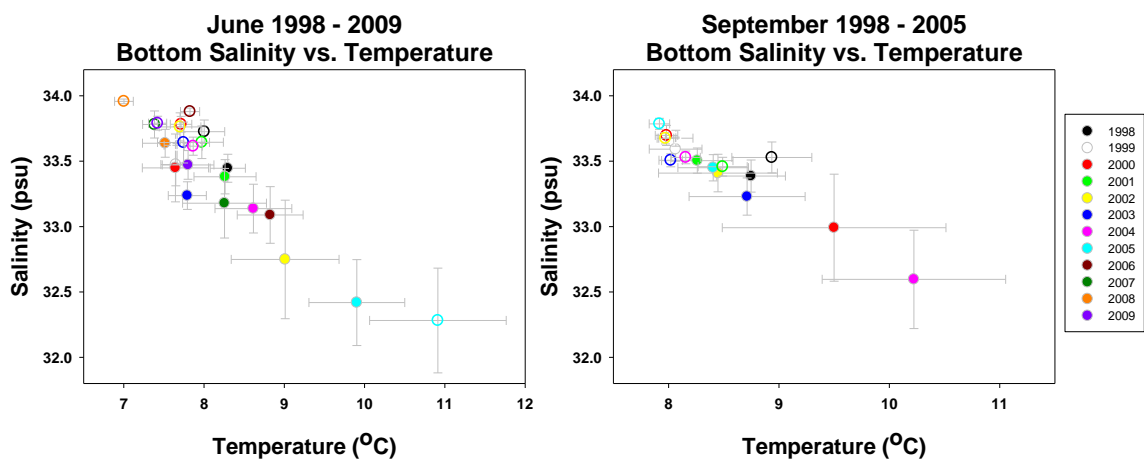


Figure 4. Mean bottom temperature ( $^{\circ}\text{C}$ ) versus mean bottom salinity (psu) for all stations north (filled circles) and south (open circles) of the Columbia River for June (1998 – 2009) and September (1998 – 2005). Southern stations were predominately colder and saltier than northern stations for most years.

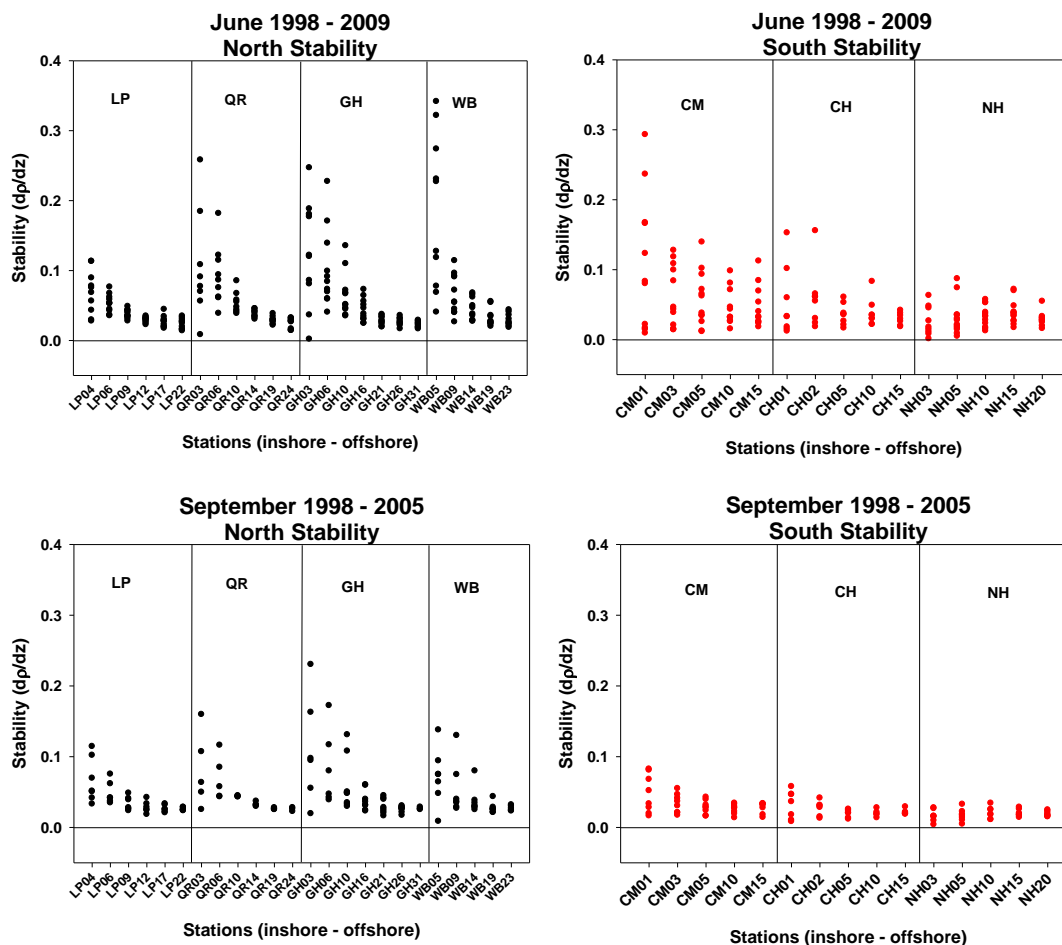


Figure 5. Cross-shelf stability (change in water density ( $\sigma_t$ ) over the change in water depth ( $m$ )) for all transects north and south of the Columbia River for June and September. X-axis represents inshore to offshore stations (left to right) of each transect, with each transect separated by a vertical line. Stability measurements were consistently highest inshore of the northern WB, GH, and QR transects, in both June and September.

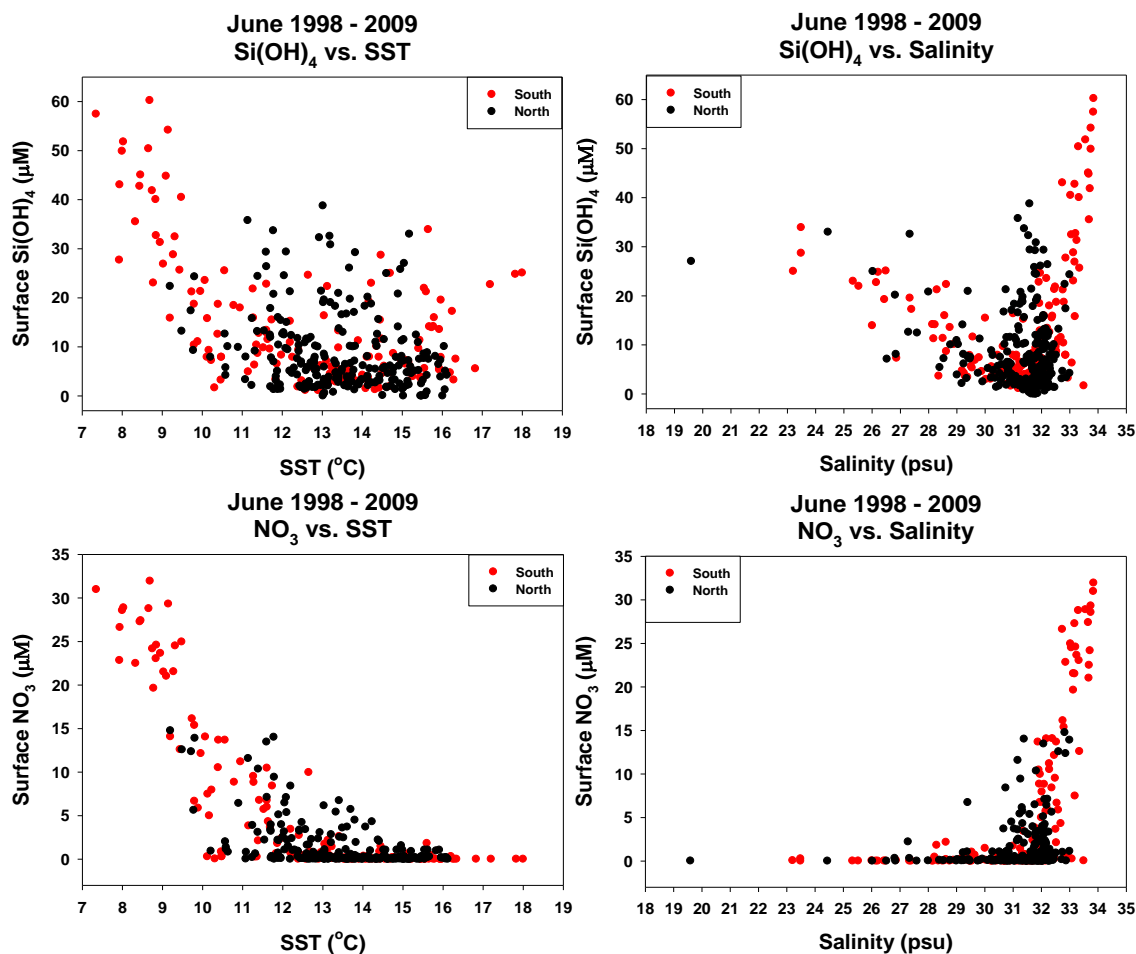


Figure 6a. Silicic acid ( $\text{Si(OH)}_4$ ) and nitrate ( $\text{NO}_3$ ) values versus sea surface temperature ( $^\circ\text{C}$ ) and salinity (psu) for all north (black) and south (red) stations, June 1998 – 2009. To the south, higher  $\text{Si(OH)}_4$  and  $\text{NO}_3$  values are found at SSTs less than  $11^\circ\text{C}$  and salinities less than 30 psu (for  $\text{Si(OH)}_4$ ) or greater than 32 psu (for both). To the north, higher  $\text{Si(OH)}_4$  and  $\text{NO}_3$  values are found between 11 to  $15^\circ\text{C}$  and salinities less than 30psu (for  $\text{Si(OH)}_4$ ) or between 31 to 32 psu (for both). Most northern values in the above ranges have  $\text{Si(OH)}_4$  values less than  $10\mu\text{M}$  and  $\text{NO}_3$  values around  $0\mu\text{M}$ .

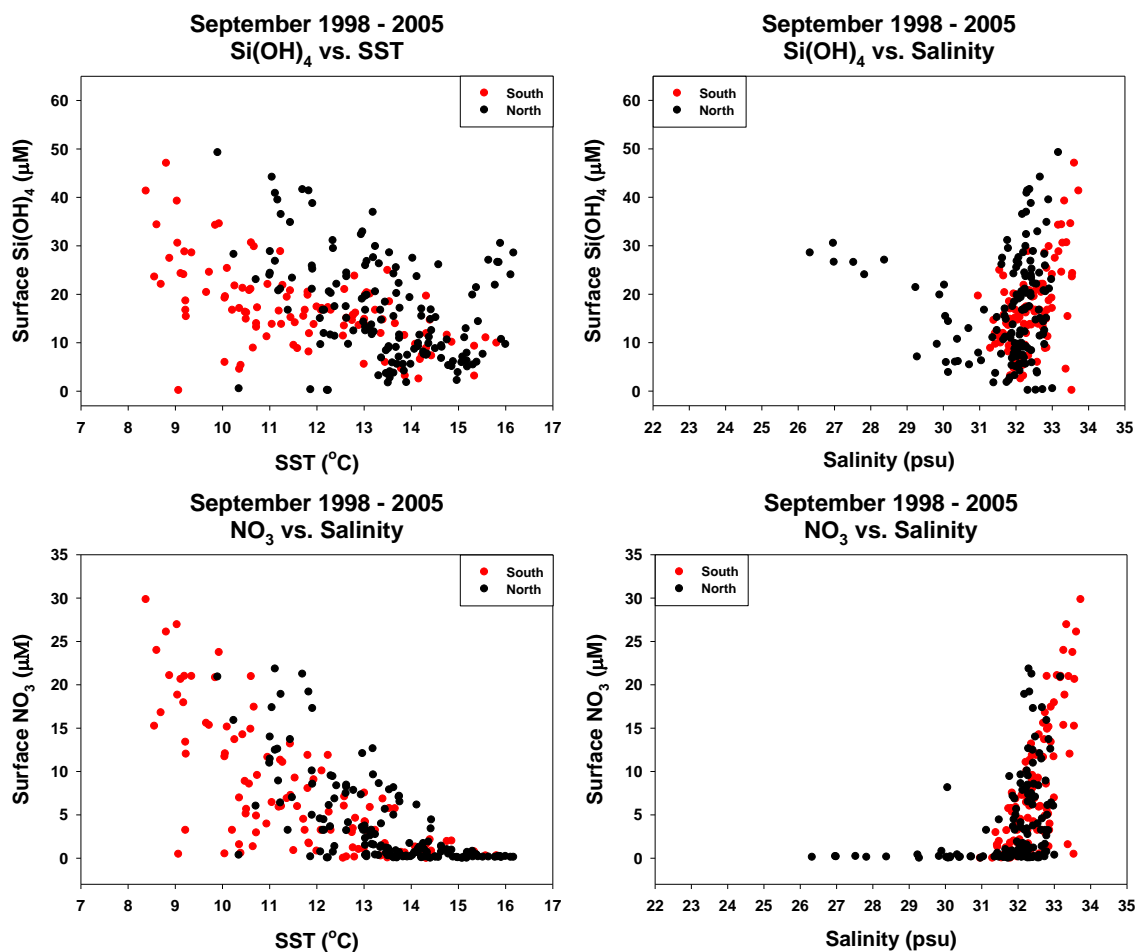


Figure 6b. Silicic acid ( $\text{Si(OH)}_4$ ) and nitrate ( $\text{NO}_3$ ) values versus sea surface temperature ( $^{\circ}\text{C}$ ) and salinity (psu) for all north (black) and south (red) stations, September 1998 - 2005. To the south, higher  $\text{Si(OH)}_4$  and  $\text{NO}_3$  values were found at SSTs less than  $14^{\circ}\text{C}$ , with increasing values at lower SSTs. Higher values were also associated with salinities greater than 32 psu. To the north, high  $\text{Si(OH)}_4$  values were found at all SSTs and less than  $14^{\circ}\text{C}$  for  $\text{NO}_3$ , with increasing values at lower SSTs. There were two peaks of high  $\text{Si(OH)}_4$  values to the north, both at the lowest and highest salinity values. High  $\text{NO}_3$  values were only associated with values greater than 32 psu. Also note more northern stations had  $\text{Si(OH)}_4$  values greater than  $30\mu\text{M}$  in September compared to June.

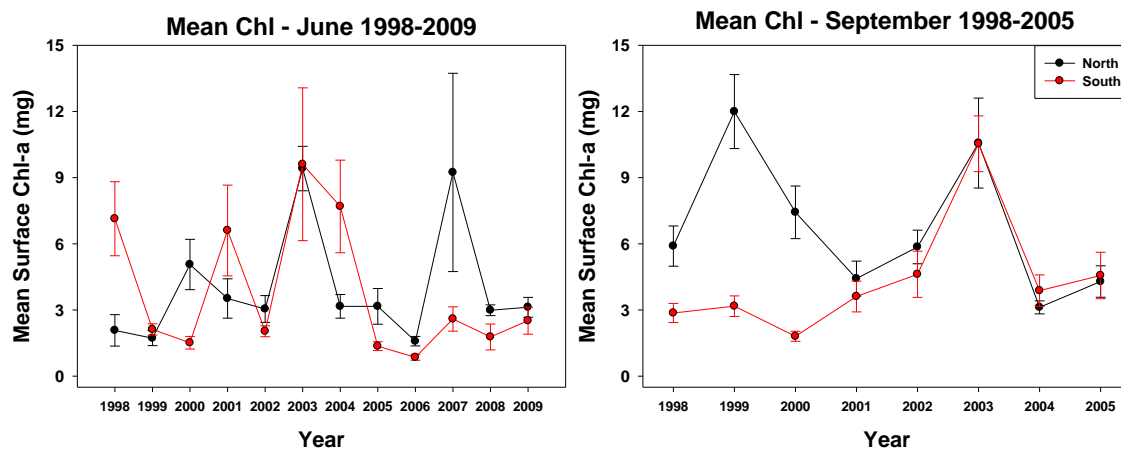


Figure 7. Mean surface chl-a (mg) for stations north (black) and south (red) of the Columbia River for June (1998 – 2009) and September (1998 – 2005). Northern stations have higher mean surface chl-a values (not within a standard error) than southern stations, for both months, for all years sampled.



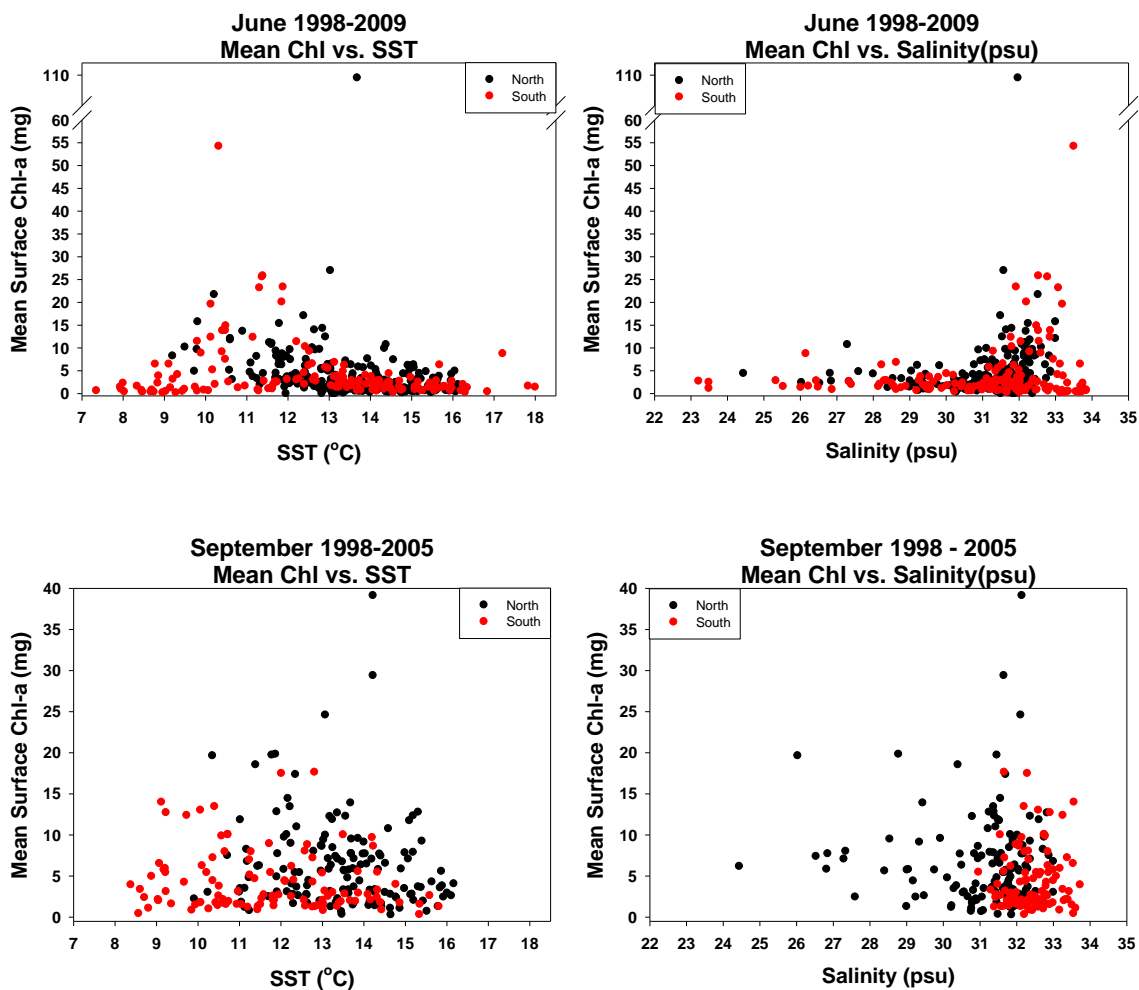


Figure 8. Mean chlorophyll values (mg) versus sea surface temperature ( $^{\circ}\text{C}$ ) and salinity (psu) for all north (black) and south (red) stations, for June and September. In June, the highest chlorophyll values fall around  $11^{\circ}\text{C}$  and 32 psu, similar to the highest nutrient values. September was more variable, yet peak chlorophyll was still found around  $11^{\circ}\text{C}$  and 32 psu. Isolated high chlorophyll values were found at lower salinity values, also similar to  $\text{Si}(\text{OH})_4$ .

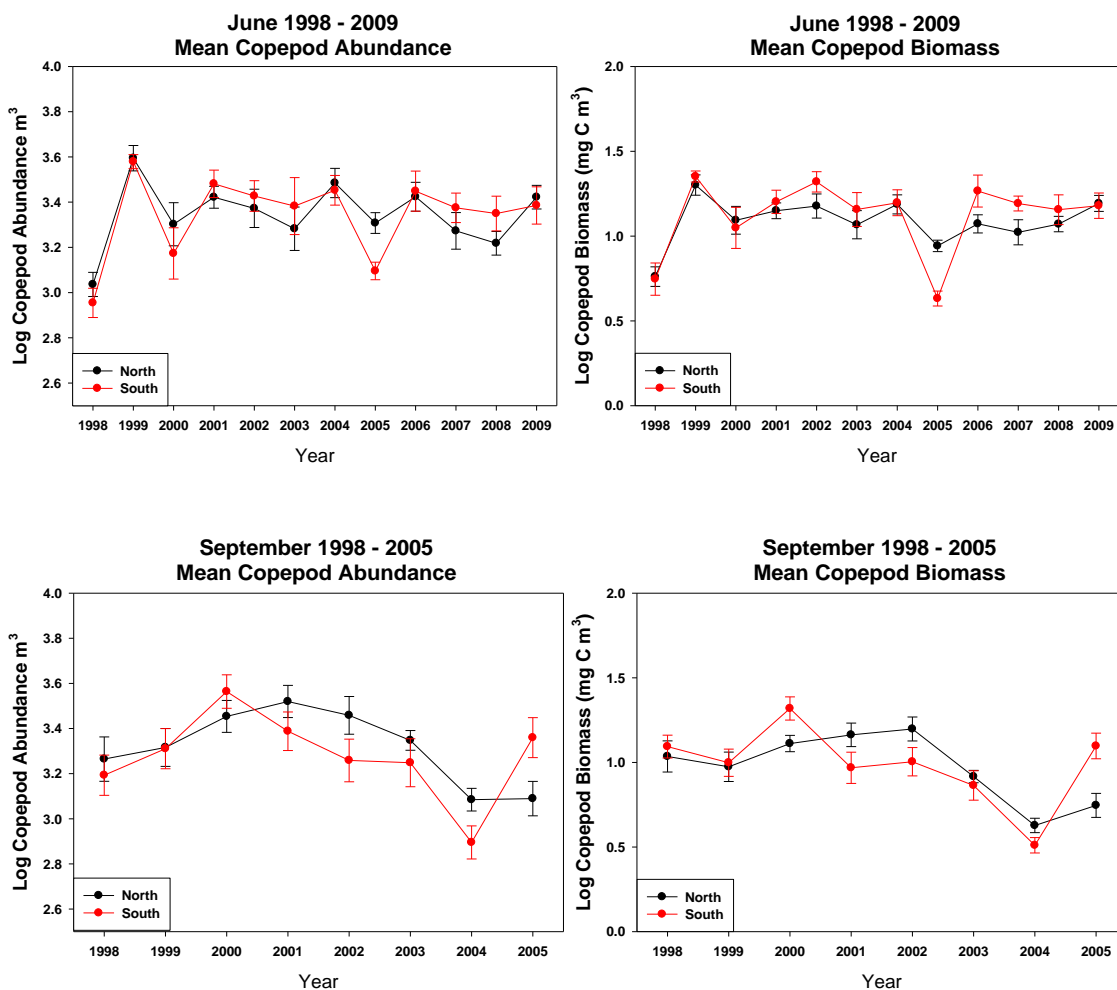


Figure 9. Log copepod abundance and biomass for stations north (black) and south (red) of the Columbia River for June and September. In June, log abundance for stations north and south are within their standard error for all years, except 2005. Southern stations have higher log biomass in 2002, 2006, and 2007. North stations have higher log biomass and abundance in 2005. In September, northern stations have higher abundance and biomass in 2001, 2002, and 2004. Southern stations only have higher abundance and biomass in 2005.

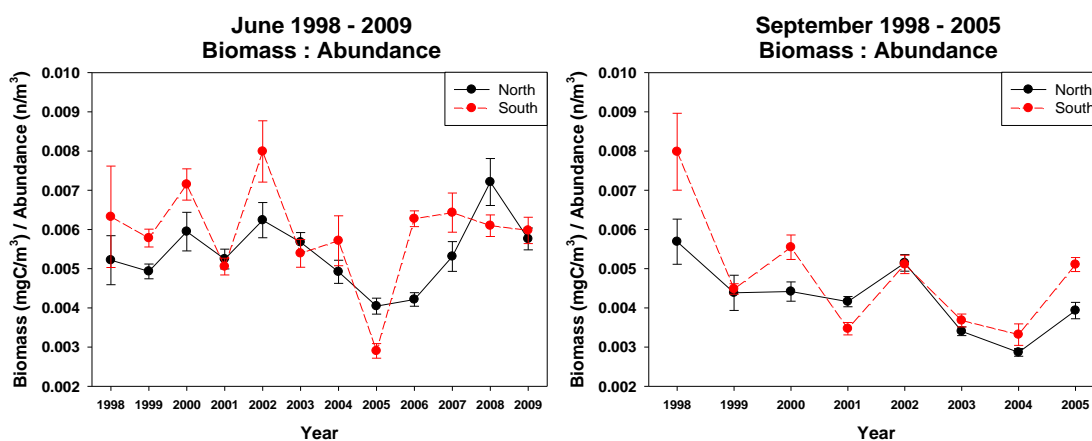


Figure 10. Mean copepod biomass ( $\text{mgC}/\text{m}^3$ ) divided by abundance ( $\text{n}/\text{m}^3$ ) per station for all stations north (black) and south (red) of the Columbia River for June and September. Except for June 2005, 2008, and September 2001, southern stations have higher biomass per individual copepod sampled.

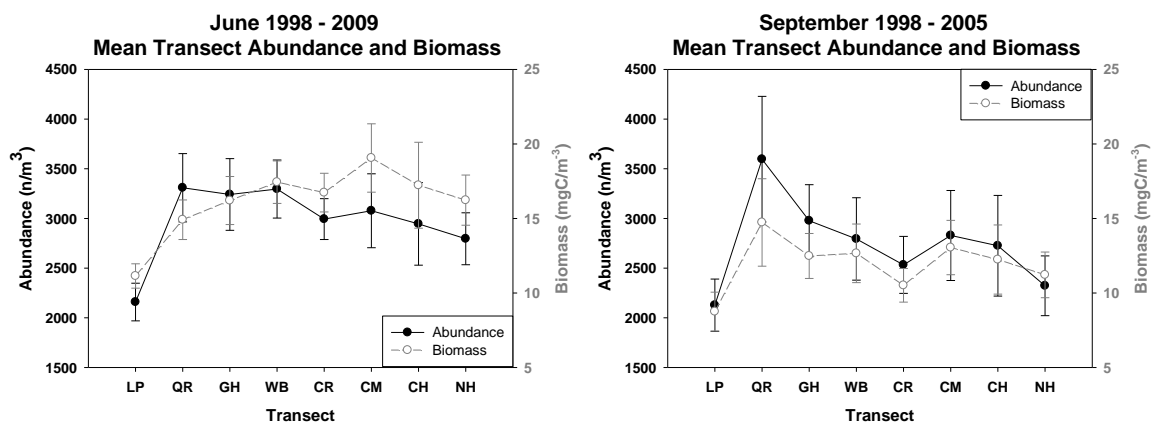


Figure 11. Mean abundance (black) and mean biomass (grey) for sampled transects for June and September. In June, transects north of the Columbia River (QR, WB, and GH) have higher densities and lower biomass than stations south of the Columbia River (CM, CH, and NH). In September, both transect densities and biomass tended to be higher in the north than the south. The LaPush transect (LP) consistently have the lowest transect density and biomass for both months, all years.

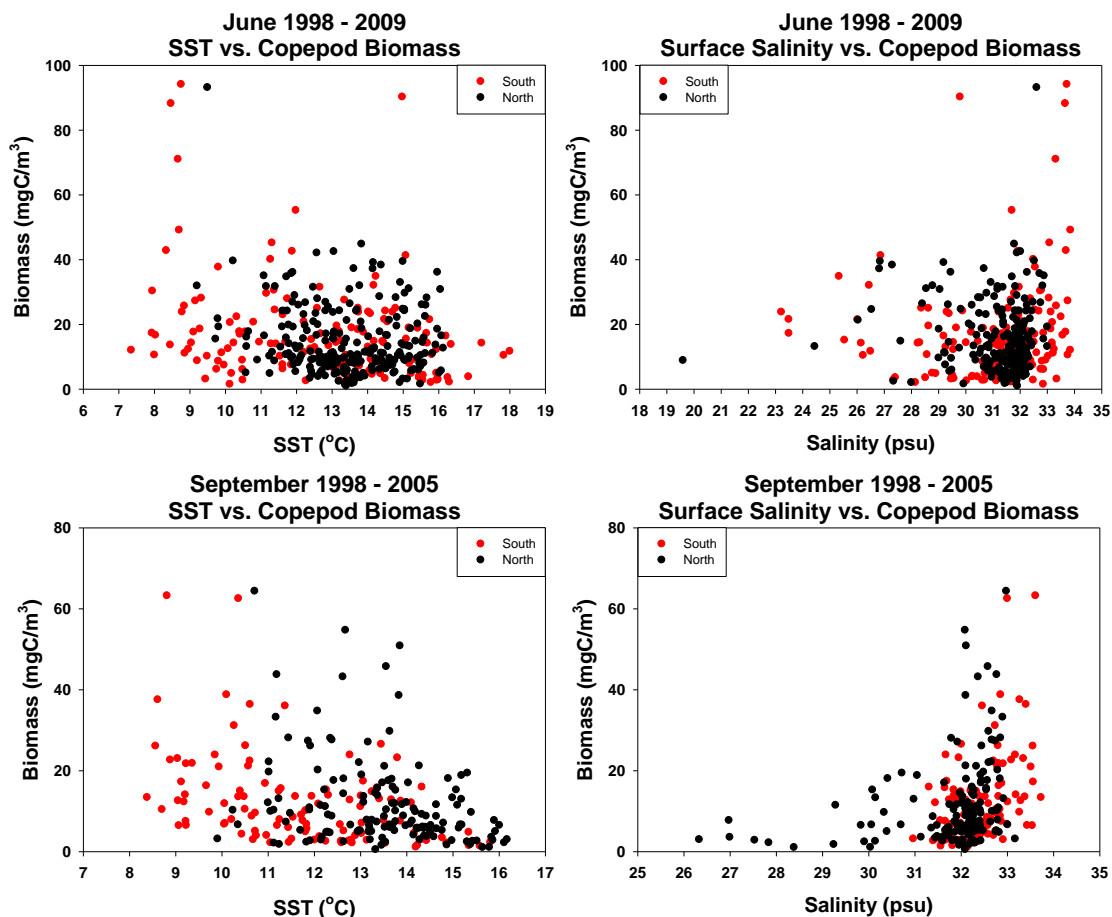


Figure 12. Copepod biomass ( $\text{mgC/m}^3$ ) values versus sea surface temperature ( $^{\circ}\text{C}$ ) and salinity (psu) for all north (black) and south (red) stations, June 1998 – 2009. To the south, biomass values are found at the full range of SST and salinity values, with the most extreme values found at the lowest temperatures and highest salinities, regardless of month. To the north, biomass values are also found within the full range of SST and salinity values, with higher biomass values found at times during September.

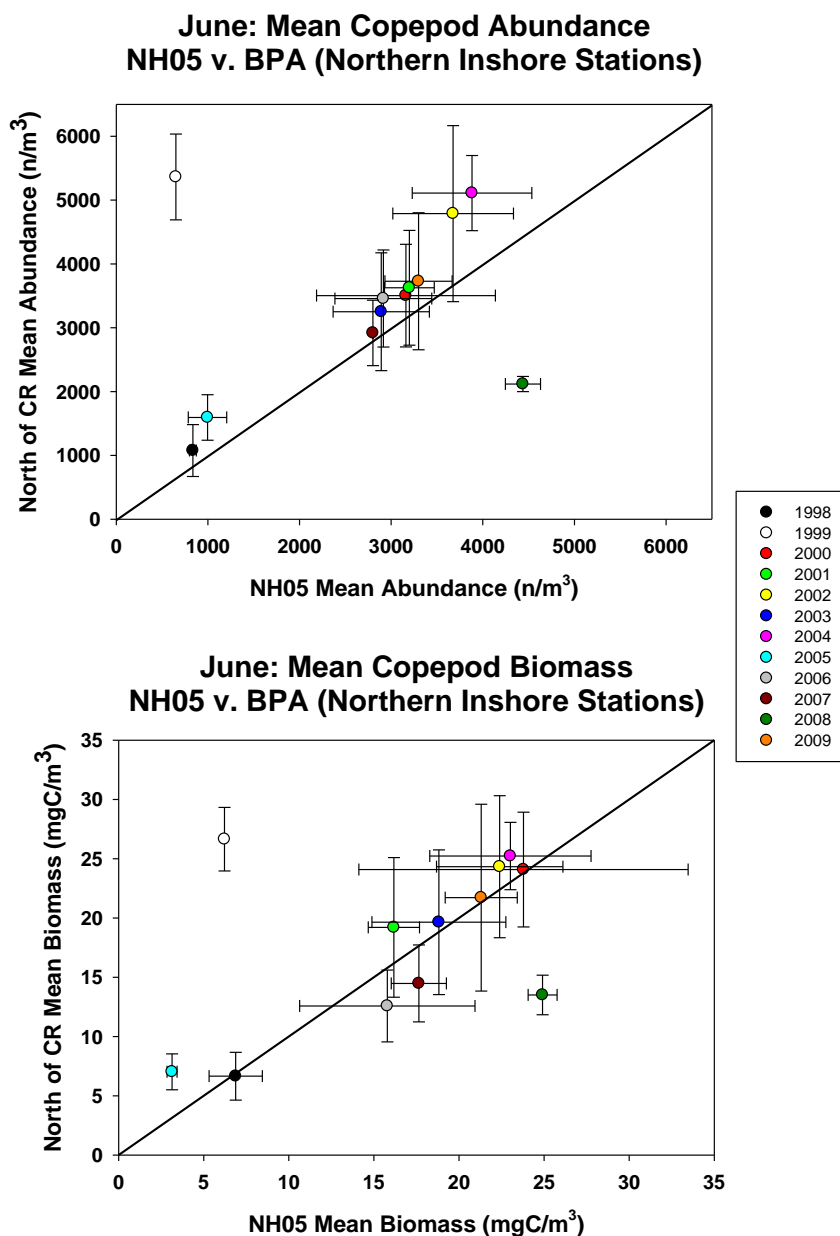


Figure 13a. Mean copepod abundance and mean biomass comparison for NH05 samples (NH Line time series, x-axis) four stations of similar depth (60m) north of the Columbia River (BPA Project, y-axis) for June 1998 – 2009. Line represents a 1:1 ratio. BPA stations have slightly higher mean densities, where mean biomass was closer to 1:1 for most years. Much higher mean density/biomass ratios were found in 1999 (North of CR) and 2008 (NH05), respectively.

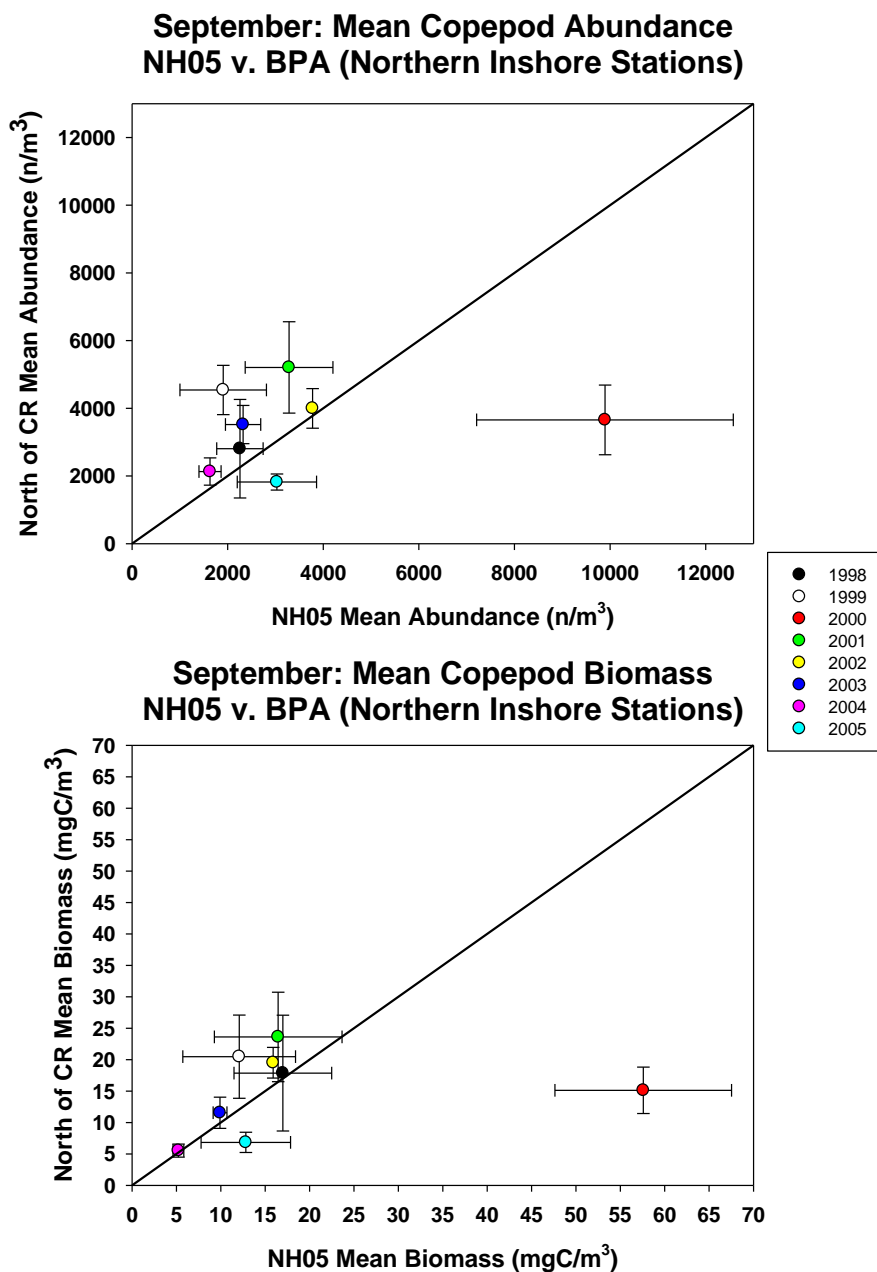


Figure 13b. Mean copepod density and biomass comparison for NH05 samples (NH Line time series, x-axis) to four stations of similar depth (60m) north of the Columbia River (BPA Project, y-axis) for September, 1998 - 2005. Line represents a 1:1 ratio. BPA stations have slightly higher mean density/biomass ratios for all years except 2000 and 2005.

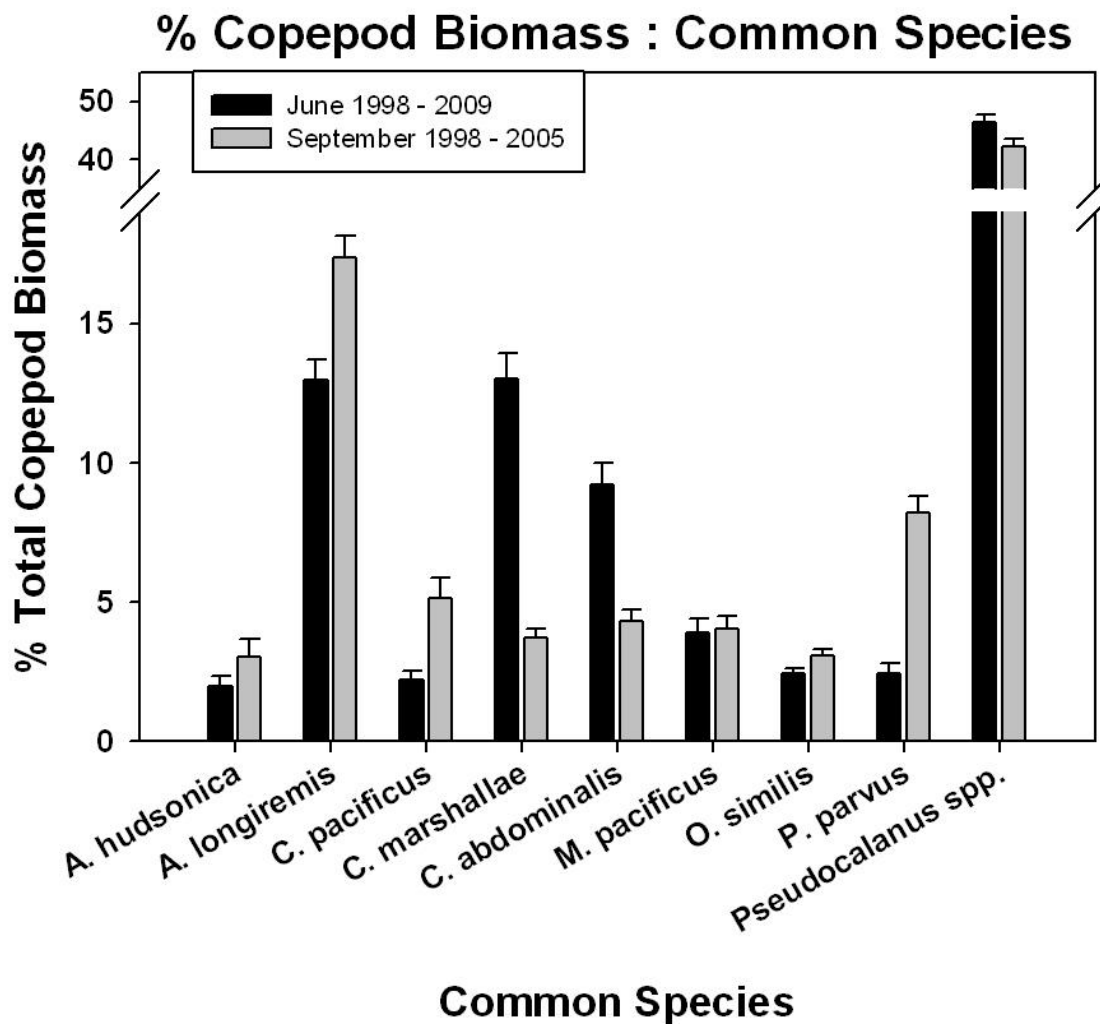


Figure 14. Comparison of the percent total copepod biomass for common species for June, 1998 – 2009 (black) and September 1998 – 2005 (grey). Smaller copepods (*A. hudsonica*, *P. parvus*) represent a higher percent biomass in September compared to June, while for medium/larger copepods *C. abdominalis* and *C. marshallae*, the opposite is true. *Pseudocalanus spp.* represents 50% of the total copepod biomass for both sampling periods.



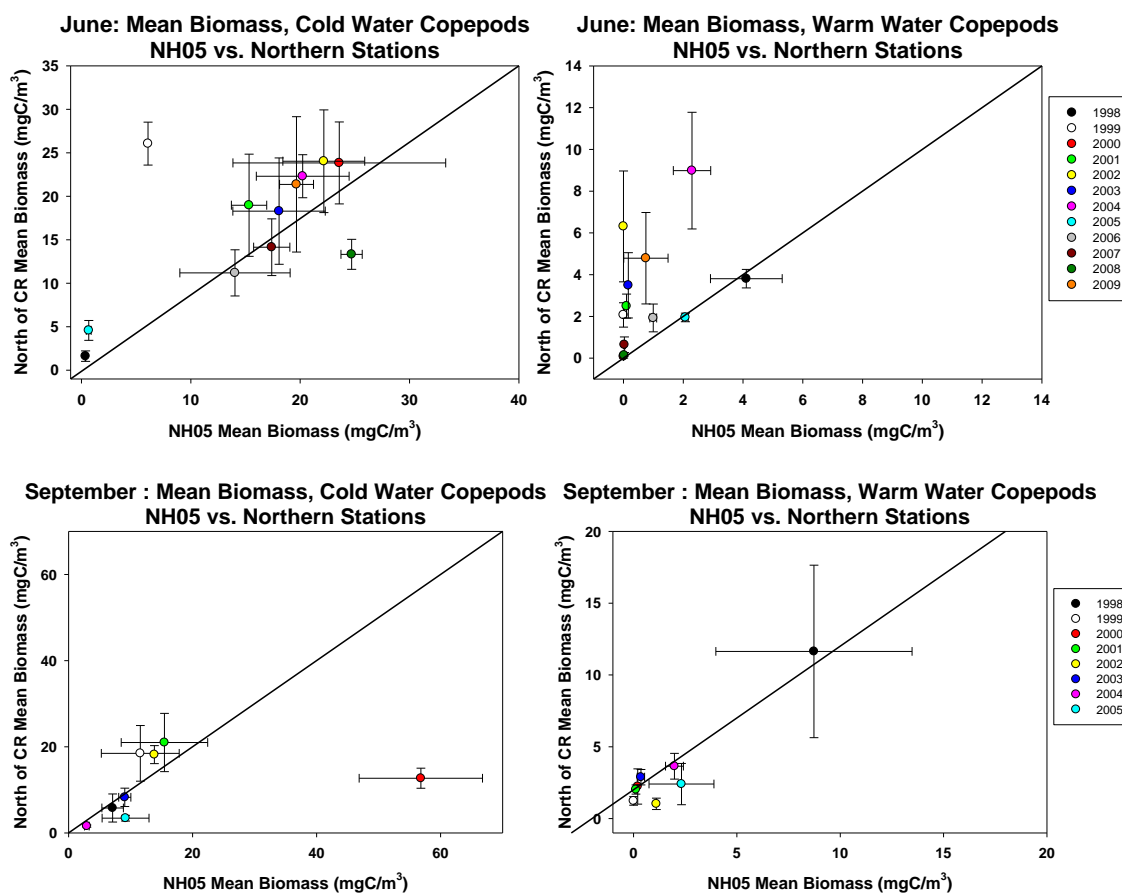


Figure 15. Mean copepod abundance and mean biomass comparison for NH05 samples (NH Line time series, x-axis) four stations of similar depth (60m) north of the Columbia River (BPA Project, y-axis) for June 1998 – 2009, for warm and cold water copepods. Line represents a 1:1 ratio. Warm water copepods were found predominately at northern stations in June.

## All Copepods

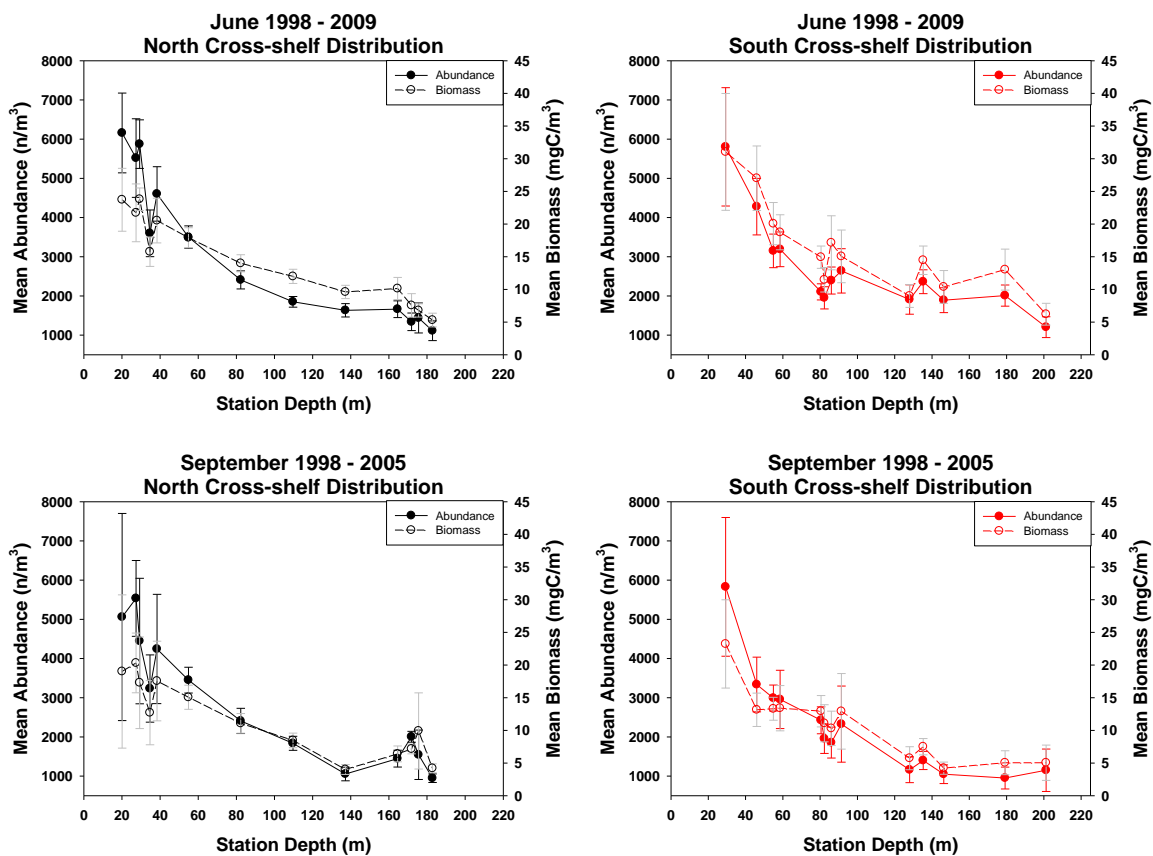


Figure 16. Mean copepod cross-shelf abundance (n/m<sup>3</sup>) and biomass (mgC/m<sup>3</sup>) for stations north and south of the Columbia River for June and September. Note the decrease in both abundance and biomass with increasing station depth, regardless of location.

### *Pseudocalanus* spp.

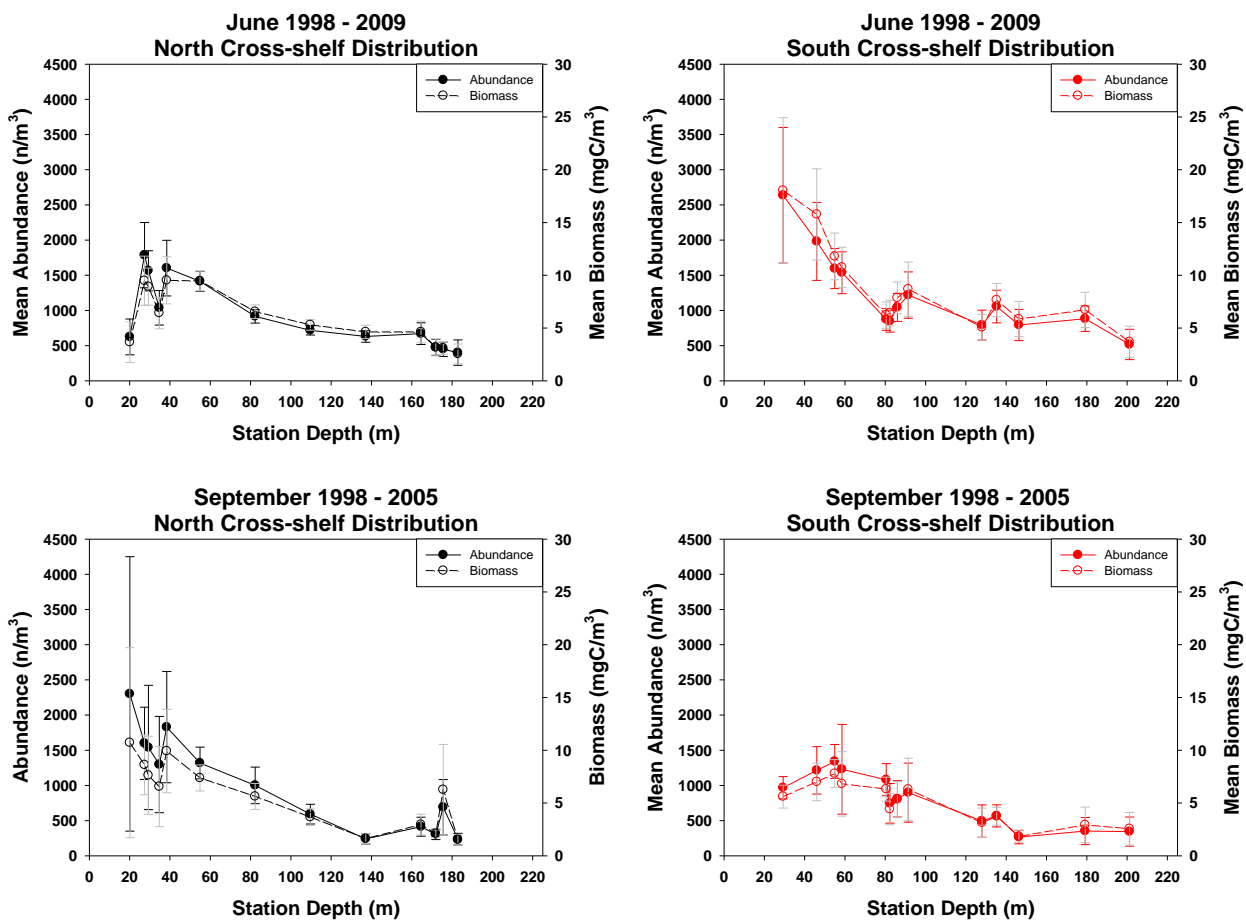


Figure 17. Mean *Pseudocalanus* spp. cross-shelf abundance (n/m<sup>3</sup>) and biomass (mgC/m<sup>3</sup>) for stations north and south of the Columbia River for June and September. Both abundance and biomass peak inshore between 20 – 40m, then slowly decreasing with increasing station depth. There were higher inshore abundance and biomass to the south in June, with higher inshore abundance and biomass to the north in September.

### *Calanus marshallae*

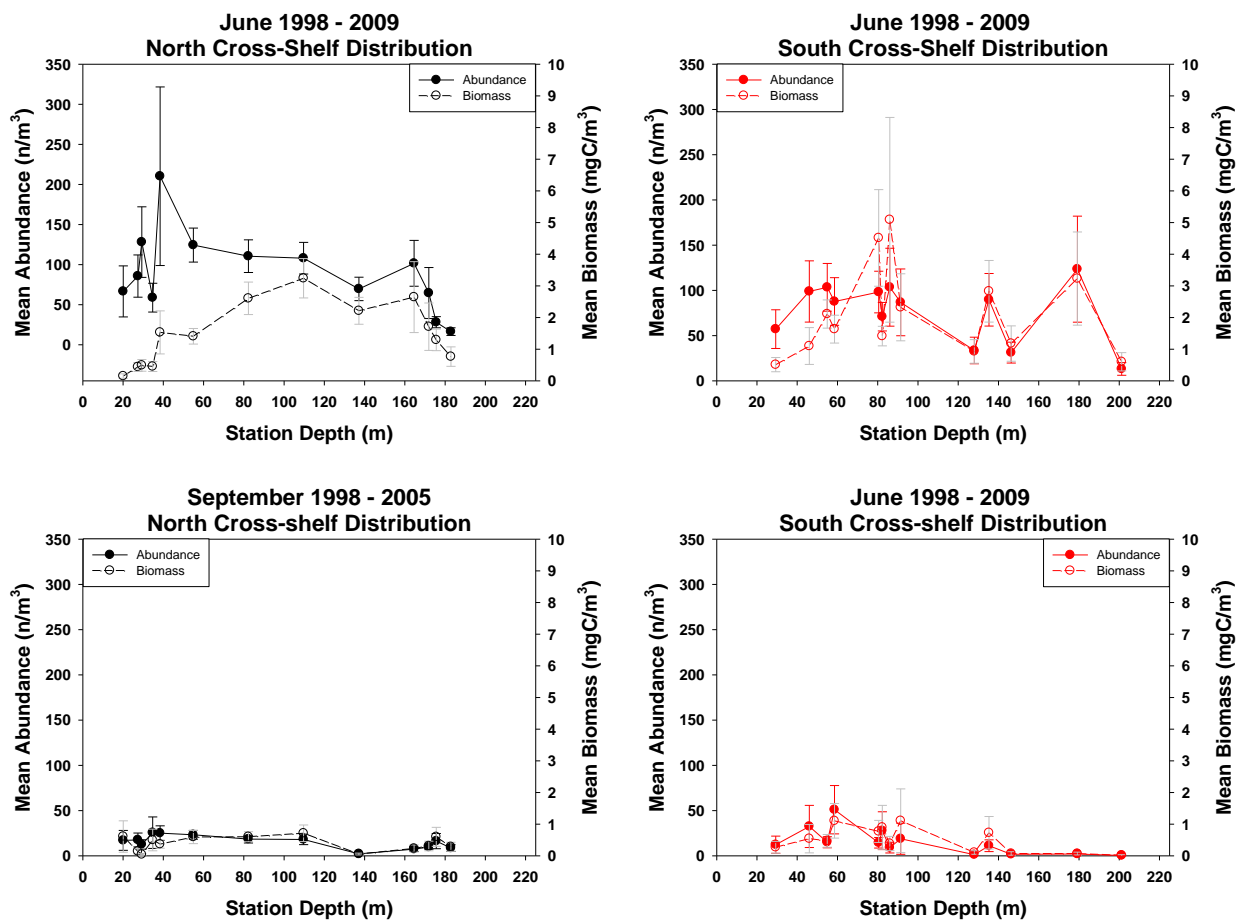


Figure 18. Mean *Calanus marshallae* cross-shelf abundance (n/m<sup>3</sup>) and biomass (mgC/m<sup>3</sup>) for stations north and south of the Columbia River for June and September. Abundance initially increases and levels off with increasing depth, while biomass increases at a slower rate, peaking at station depths between 80 – 100m. Note the decrease in both abundance and biomass in September.

## All Copepods

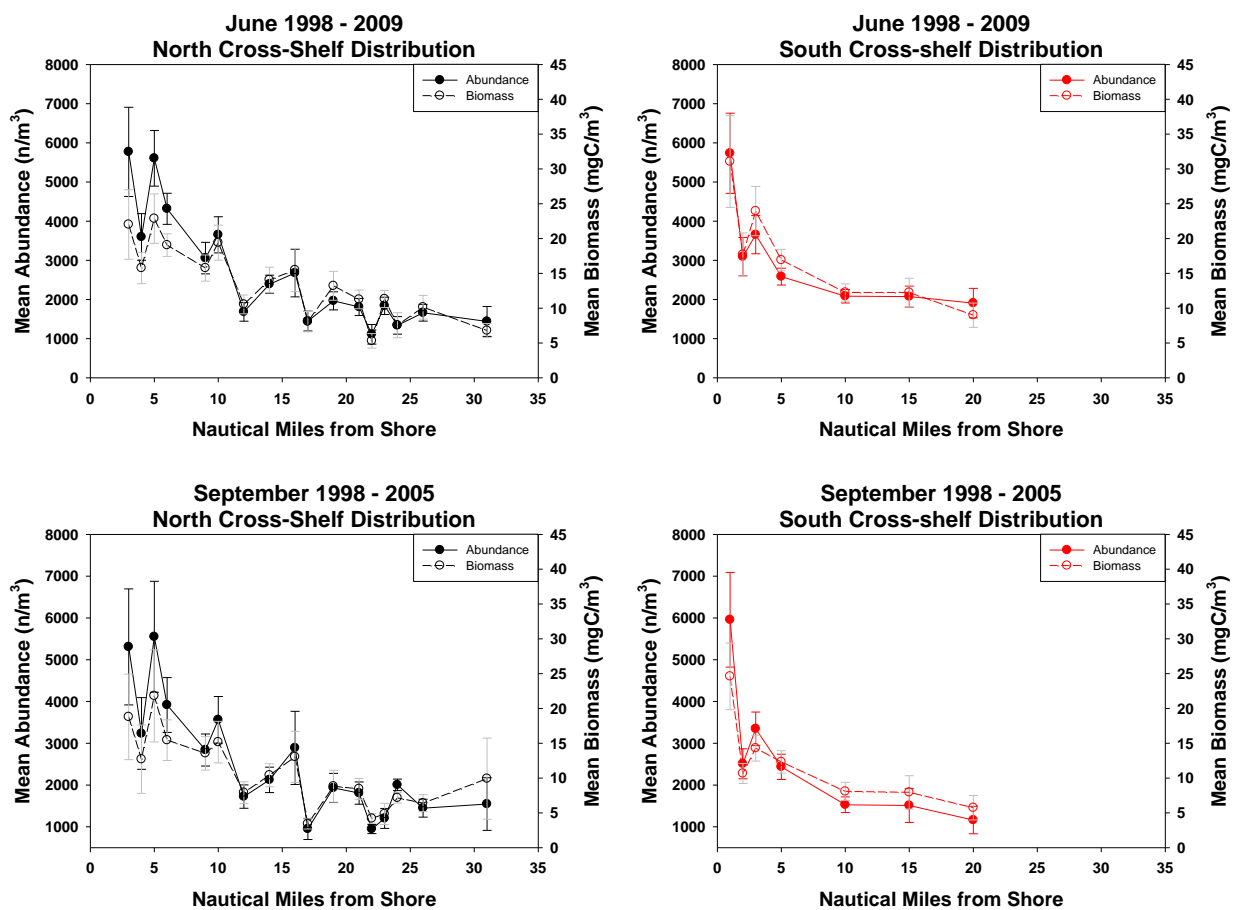


Figure 19. Mean copepod cross-shelf abundance (n/m<sup>3</sup>) and biomass (mgC/m<sup>3</sup>) for stations north and south of the Columbia River for June and September. Note the steep declines in both abundance and biomass to the south, compared to more gradual cross shelf declines to the north.

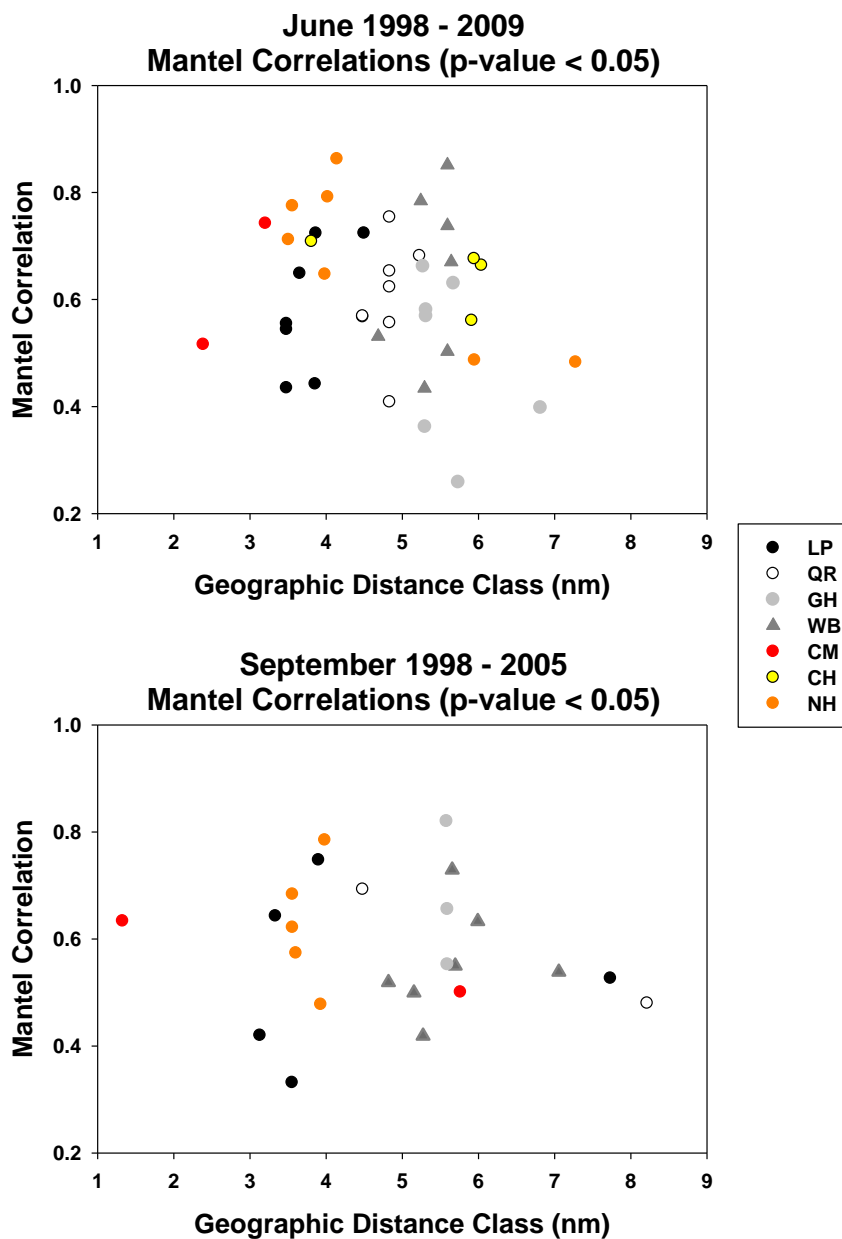


Figure 20. Geographic distance (nm) versus mean significant Mantel correlations for June and September sampling. In June, significant autocorrelation between transect stations occurred from 3 and 6 nm at a range of 0.2 to 0.8 to the north; from 2.5 and 7 nautical miles at a range of 0.5 to just over 0.8 to the south. By September, the range in autocorrelation decreased to between 1.5 to 6 nm in the south.

Table 1. Standard deviation of sea surface (SST) and bottom temperature ( $^{\circ}\text{C}$ ) for stations north and south of the Columbia River for June and September. SST was more variable to the south, while bottom temperature was more variable to the north. Regions are labeled (north = gray, south = red) by the location with higher standard deviation.

Year	SD of SST				SD of Bottom Temperature			
	June		Sept		June		Sept	
	North	South	North	South	North	South	North	South
1998	0.64	1.62	0.61	1.13	0.58	0.72	0.94	1.31
1999	0.80	1.21	0.87	1.31	0.55	0.51	0.83	0.54
2000	0.61	1.82	0.30	2.02	0.16	0.40	2.68	0.29
2001	1.29	0.96	1.23	1.19	1.45	0.89	1.25	0.86
2002	0.92	1.70	0.92	1.17	2.69	0.82	2.22	0.26
2003	1.38	1.72	1.11	1.28	0.95	0.95	1.90	0.28
2004	0.62	2.86	0.64	1.70	1.97	0.36	3.53	0.40
2005	0.92	0.39	1.06	1.85	2.53	2.69	1.36	0.26
2006	1.03	1.50			1.69	0.38		
2007	0.89	1.03			2.39	0.47		
2008	0.67	1.82			1.32	0.37		
2009	0.81	2.48			1.51	0.34		

Table2. Count of stations falling within ranges of nutrients ( $\text{Si(OH)}_4$  and  $\text{NO}_3$  (in  $\mu\text{M}$ )) and environmental parameters (temperature ( $^\circ\text{C}$ ) and salinity (psu)) for stations north and south of the Columbia River, June 1998 – 2009. Red indicates more south stations in a specific range; grey indicates more north stations within a specific range.

Silicate		$\text{Si(OH)}_4 > 10\mu\text{M}$		$\text{Si(OH)}_4 > 20\mu\text{M}$	
		North	South	North	South
Temperature	$<11^\circ$	6	35	2	26
	$>11^\circ - <16^\circ$	69	33	23	10
	$> 16^\circ$	1	4	0	3
Salinity		$\text{Si(OH)}_4 > 10\mu\text{M}$		$\text{Si(OH)}_4 > 20\mu\text{M}$	
		North	South	North	South
Salinity	$<30.5\text{psu}$	14	23	7	10
	$>30.5 - <32\text{psu}$	40	7	14	3
	$>32\text{psu}$	20	41	4	26
Nitrate		$\text{NO}_3 > 5\mu\text{M}$		$\text{NO}_3 > 10\mu\text{M}$	
		North	South	North	South
Temperature	$<11^\circ$	6	36	4	31
	$>11^\circ$	15	9	4	1
Salinity		$\text{NO}_3 > 5\mu\text{M}$		$\text{NO}_3 > 10\mu\text{M}$	
		North	South	North	South
Salinity	$<30.5\text{psu}$	1	0	0	0
	$>30.5\text{psu}$	20	45	8	32



Table3. Count of stations falling within ranges of nutrients ( $\text{Si(OH)}_4$  and  $\text{NO}_3$  (in  $\mu\text{M}$ )) and environmental parameters (temperature ( $^\circ\text{C}$ ) and salinity (psu)) for stations north and south of the Columbia River, September 1998 - 2005. Red indicates more south stations in a specific range; grey indicates more north stations within a specific range.

Silicate		$\text{Si(OH)}_4 > 10\mu\text{M}$		$\text{Si(OH)}_4 > 20\mu\text{M}$	
		North	South	North	South
Temperature	$<11^\circ$	3	38	3	24
	$>11^\circ$	93	49	49	9
Salinity		$\text{Si(OH)}_4 > 10\mu\text{M}$		$\text{Si(OH)}_4 > 20\mu\text{M}$	
		North	South	North	South
Salinity	$>31.5\text{psu}$	76	83	44	33
	$<31.5\text{psu}$	17	4	8	0
Nitrate		$\text{NO}_3 > 5\mu\text{M}$		$\text{NO}_3 > 10\mu\text{M}$	
		North	South	North	South
Temperature	$<11^\circ$	3	33	2	19
	$>11^\circ$	37	23	6	0
Salinity		$\text{NO}_3 > 5\mu\text{M}$		$\text{NO}_3 > 10\mu\text{M}$	
		North	South	North	South
Salinity	$<30.5\text{psu}$	1	0	2	0
	$>30.5\text{psu}$	40	56	8	19

Table 4. Analysis of variance (ANOVA) testing for north versus south differences in log copepod abundance ( $n/m^3$ ) and log biomass ( $mgC/m^3$ ) by year. Significant values ( $p < 0.05$ ) coded in yellow. Years with significant north south differences due to high values in individual species.

Year	June				September			
	Log Density		Log Biomass		Log Density		Log Biomass	
	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
1998	0.52	0.483	0.05	0.821	0.29	0.57	0.28	0.603
1999	0.00	0.970	0.62	0.440	0.00	0.966	0.05	0.828
2000	1.25	0.277	0.23	0.635	0.00	0.966	0.05	0.828
2001	0.69	0.412	0.43	0.517	1.35	0.253	2.99	0.093
2002	0.23	0.635	2.18	0.150	2.48	0.124	2.58	0.117
2003	2.28	0.140	2.21	0.147	1.06	0.313	0.53	0.471
2004	0.01	0.912	0.20	0.659	4.88	0.033	3.04	0.089
2005	10.54	0.003	33.35	0.000	5.39	0.027	11.42	0.002
2006	0.05	0.818	3.69	0.062				
2007	0.59	0.449	2.09	0.158				
2008	1.91	0.176	0.90	0.351				
2009	0.14	0.710	0.02	0.876				

Table 5. Table of Moran's I values (1 = perfect correlation, -1 = perfect anticorrelation) calculated from log copepod station densities and biomass values per transect. Values in yellow are significant ( $p < 0.05$ ); values in black are either transects not sampled or transects without enough stations for calculation. More northern stations had significant spatial autocorrelation than southern stations in June. Fewer transects overall were found to be autocorrelated in September.

<b>June</b>								<b>Biomass</b>							
Abundance	North Stations				South Stations			LP	North Stations			South Stations			
	LP	QR	GH	WB	CM	CH	NH		LP	QR	GH	WB	CM	CH	NH
1998			-0.38	-0.25		-0.25		1998			-0.36	-0.54		-0.44	
1999	0.08		0.12		-0.08	-0.40	-0.50	1999	0.06		0.09		0.07		-0.54
2000	0.04		0.22		0.18		-0.34	2000	-0.13		0.19		0.17		-0.35
2001	0.02	0.07	0.05	-0.01	0.00	0.08	0.19	2001	-0.06	-0.05	0.05	0.06	-0.04	0.07	0.20
2002		0.17	-0.26	0.12	-0.33	-0.11	-0.43	2002		0.06	-0.21	0.14	-0.12	-0.30	-0.46
2003	0.20	0.13	-0.13	0.05	-0.04		0.10	2003	0.14	0.10	-0.10	0.05	-0.26		0.23
2004	0.08	0.19	0.25	0.04	-0.21	-0.07	-0.47	2004	0.11	0.16	0.14	-0.26	-0.11	-0.03	-0.21
2005	-0.40	0.11	-0.06	-0.28	-0.48	-0.06	-0.31	2005	-0.40	-0.16	-0.37	-0.32	-0.11	-0.22	-0.45
2006	0.14	0.08	0.16	0.02	-0.38	-0.15	-0.06	2006	0.03	0.10	0.01	-0.04	-0.33	-0.15	0.00
2007	0.23	0.11	-0.18	-0.46	-0.29		-0.15	2007	0.21	0.03	-0.15	-0.12	-0.27		-0.18
2008	-0.07	-0.14	0.07	-0.15	-0.28		-0.19	2008	-0.24	-0.36	-0.27	-0.37	-0.22		0.06
2009	0.04	-0.17	-0.02	0.02	-0.20		-0.16	2009	-0.14	-0.31	-0.20	-0.01	-0.15		-0.06

<b>Sept</b>								<b>Biomass</b>							
Abundance	North Stations				South Stations			LP	North Stations			South Stations			
	LP	QR	GH	WB	CM	CH	NH		LP	QR	GH	WB	CM	CH	NH
1998	-0.31		-0.36	-0.14	0.01			1998	-0.20		-0.45	-0.08	-0.20		
1999	-0.02		-0.12	-0.22	0.09	-0.24	-0.39	1999	-0.44		-0.03	-0.42	0.13	-0.26	-0.43
2000	0.03		0.23	-0.22	-0.32		-0.11	2000	-0.04		0.10	-0.42	-0.30	-0.26	-0.35
2001	0.18	0.23	-0.15	0.11	-0.18	0.09	0.18	2001	0.14	0.21	-0.28	0.12	-0.17	0.10	0.11
2002	0.08	-0.01	0.29	0.03	-0.18	0.11	0.05	2002	0.10	-0.01	0.21	-0.02	-0.17	0.08	0.19
2003	0.00	-0.19	0.03	0.05	-0.03		0.06	2003	0.13	-0.29	-0.03	-0.01	-0.14		0.09
2004	-0.36	-0.05	-0.04	-0.01	0.01	0.12	0.02	2004	-0.33	0.11	-0.04	-0.26	-0.28	0.09	0.02
2005	0.24		-0.08	0.06	0.14	0.01	-0.39	2005	0.05		-0.15	0.03	0.16	0.03	-0.35

p-value < 0.05

## Discussion

Over our sampling period, upwelling was consistently stronger off central Oregon compared to the northern Washington. This was evident in both our finding of colder sea surface and bottom temperatures, along with the higher salinity values more often to the south, especially during June. June nutrient data revealed that the coldest, saltiest water to the south at intermediate values of SST yielded the highest nutrient values, but also that the northern region yielded higher nutrient values compared to the south at a distinct range SST and salinity values as well. Surface chlorophyll values were variable year after year in June, with the highest chlorophyll values seeming to occur at surface temperature and salinity values associated with higher nutrient content both in the north and south (11 – 12°C, 31 – 32 psu). Mean surface chlorophyll for the entire sampling period was similar in both regions.

In September, upwelling strength, SST, bottom temperature, and salinity profiles all reflected the same north and south patterns that were found in June. However, there was an increase in mean nutrient values in both regions, especially a doubling in mean silicate to the north. There was a small increase in mean surface chlorophyll along with a 9% increase in the amount of chlorophyll values found above 10mg m<sup>-3</sup> to the north from June to September compared with virtually no change at all in the south during the same period.

One interesting finding was the moderately high silicate values associated with low salinity water found in the entire region in June and only north in September. These values ( $< 30$ psu) are characteristic of a fresh water influence. This could also be the cause of the high inshore stability values seen off the WB, GH, and QR transects in both June and September, along with the CM transect in June, which are closest to Columbia River plume water. It is unclear whether or not this silicate-rich fresh water influence is related to the increase in mean surface chlorophyll across the northern study area in September from our data set, but it bears noting. In 2006, Hickey et al. (2009) found that low inshore salinity values ( $< 30$  psu) were due to a lagged forcing from previous northern (downwelling) or southern (upwelling) wind events. Also, low salinity water found inshore to the north could also come from both Willapa Bay and/or Grays Harbor, although the salinity signals of those estuaries are higher than the lower salinities attributed to the Columbia River plume water, which dominated their time series.

Relatedly, even though northern nutrients levels never reach the extremes we saw south of the Columbia River, it has been argued that upwelling winds push relatively fresh nutrient-rich water from the Strait of Juan de Fuca down the Washington continental shelf, making up for the difference in the lack of nutrients that would be produced if upwelling in that region was stronger (Hickey and Banas, 2009, Hickey et al., 2009). Also, Mackas (1992) noted seasonally increasing nutrient and phytoplankton biomass on the inner shelf of southwest

British Columbia for the entire summer through September, similar to our findings.

The copepod data revealed albeit few, if any real differences between the two regions. Analysis of overall year-to-year mean abundance and biomass revealed less than one quarter of the cruises had differences in mean abundance or biomass. Comparisons with samples taken at NH05 with northern samples taken at the same isobath at the same time were different again only less than one quarter of the cruises. Spatially, total copepod cross shelf abundance and biomass had very similar patterns both north and south, with the highest abundances found around the 20m isobath followed by a steep, then gradual decline to the outer shelf. The same was also true of both *Pseudocalanus* spp. and *C. marshallae*, which exhibited differing individual species patterns but similar seasonal north versus south patterns, especially concerning *C. marshallae*. The regional cross isobath similarities to abundance and biomass became more apparent when making the same cross shelf comparisons to transect distance, where southern, narrower transects had a much steeper decline in both measures.

Differences were seen when looking at the spatial and seasonal aspects of both abundance and biomass. Southern stations more often had copepods with a higher individual biomass. There was also an inverse relationship

between biomass and abundance seen from north to south between transects in June, with northern stations having higher abundance, yet low biomass. The relationship was gone by September, where biomass decreased to the south. This decrease in biomass could be due to the shifting species composition from June to September, most notably the decline of *C. marshallae*. Change in species composition June to September could also reflect seasonal differences in abundance among different species. In a thirteen year study of the seasonal cycle of the zooplankton of southwestern British Columbia, Mackas (1992) found a decrease of both *C. marshallae* and *Pseudocalanus* spp. by midsummer, which was followed by an increase of the smaller *A. longiremis*, reflecting a similar pattern.

There could also be a regional preference with certain species. In the north vs. NH05 comparison, warm water species were more often found to the north in June. The majority of the warm water species are relatively smaller in size compared to the copepod community as a whole. As said previously, a strong case has been made for retention on the Washington shelf (Hickey and Banas, 2008; Hickey, et al, 2009). Retention could benefit these and other smaller, neritic species found within the region, such as *A. longiremis* and *Pseudocalanus* spp., which have been shown to occupy the upper layers of the water column (Lamb and Peterson, 2005). In an examination of both spatial and vertical sampling, Keister et al.( 2008) suggested a gradient in the effects of

offshore advection on neritic copepod distributions from the smallest taxa to the largest, where relatively small and mid-sized taxa were most susceptible to strong off shelf advection within an upwelling filament off Cape Blanco, OR in 2000.

Spatial analysis with both Moran's I and Mantel correlations revealed more significant autocorrelation year to year in the north, suggesting perhaps a more consistent degree of patchiness between northern stations. Again, this could be due to the differences in shelf width and differing retentive properties from north to south, where the decline in cross shelf abundance and biomass happens over a much broader area at northern transects. However, it should be understood that the sample design for the BPA Salmon project was intended for maximum spatial coverage in the shortest period of time, which is not ideal for the spatial analysis above. In a study of spatial autocorrelation of zooplankton on a continental shelf, Mackas (1984) suggested that sample spacing be closer perpendicular to isobaths than parallel to them in order to detect significant dissimilarity in the cross-shelf copepod community.



## Conclusions

Our findings would indicate that there were no great differences found in chlorophyll concentrations between the two regions even though there were significant differences in both strength of upwelling and in nutrient content. Hickey and Banas (2008) stated that “seasonally average chlorophyll concentrations increased fivefold from northern California to southern Vancouver Is...” never explicitly stating differences between the continental shelves of Washington and British Columbia to the rest of the CCS. Also, published chlorophyll values from satellite observations are averaged from the coastline seaward to 100km, in an effort to capture much of the seasonal variability (Landry et al., 1989; Henson and Thomas, 2007). Thomas et al., 2009 stated that disadvantages of the 100 km average include a possibly biased view of total coastal chlorophyll when the shelf and/or upwelling area is either significantly less than 100 km or significantly wider. Shelf width of our southern transects are around 27 km for both Cape Meares and Cascade Head and around 56 km for Newport. Therefore, perhaps there is an underestimation of satellite surface chlorophyll content in these areas. The proper comparison would be chlorophyll averaged only for shelf waters. In terms of area, the larger shelf width and retentive properties of the Washington shelf having higher total chlorophyll content as argued in Hickey and Banas (2008) still hold true.

In spite of these observations, our spatial sampling is but a snapshot of the current surface chlorophyll content, and does not reflect the amount of retentive/advective properties or the patchiness of phytoplankton blooms of each region, which would be better served by a different sampling approach.

The intent of this study was to test for latitudinal differences within the copepod community structure in the region. Throughout this paper, we have shown that there are few strong differences within the copepod community both spatially and temporally. These findings extend to other aspects within the region as well. In a study of the same region during the RISE project, Shaw et al., 2009 found no significant evidence of latitudinal differences in the egg production rates of *C. marshallae* or *C. pacificus*, as was hypothesized. In fact, they found that egg brood sizes by the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* were actually higher to the south, again the opposite of what was hypothesized.

Given that the distances along which we sampled were not great, one might initially suspect that there would not be a gradient in copepod community composition. Other studies have shown similar findings from even larger expanses. In a biodiversity study of the North and Central Chilean upwelling region, Hildalgo et al. (2010) found no differences in abundance and found both common and rare species in two study areas over 16° latitude apart. In a review

of 37 years of sampling off Peru, Ayon et al., (2004) divided the coastal sampling into three regions spanning a total of 14° latitude, due to their differing oceanographic properties. Even though the decadal decrease in zooplankton biovolumes from the 1960's to the 1980's between the three regions were different, the difference between regions was only 15% over the entire expanse (65 – 70% in the north and south regions; 55% in the central region). These two studies would suggest that for some coastal upwelling areas, the scale of uniformity in zooplankton communities in terms of biomass can be tens of degrees in latitude. Unfortunately we cannot make such a comparison for the California Current because species data for shelf stations are only available from transects ranging in latitude from 41 to 50°N.

In conclusion, perhaps the only true differences between the central Oregon and Washington continental shelf are in how each region obtains nutrients, where the Oregon shelf represents the classic upwelling system, and the Washington shelf represents a system with a unique combination of nutrient sources (Strait of Juan de Fuca and Columbia River) leading to its productivity. Regardless, our study found no striking spatial, seasonal, or year to year differences within the copepod community between the two regions, suggesting an increased spatial range in the ability to use data from the Newport Line in the forecasting of salmon. That being said, our sampling covered only brief time periods in the middle (June) and end of the summer (September) within the

region. Even though we had no solid indications of some sort of temporal difference within the regions, there were a few hints that such a disparity (however small or insignificant) could exist. Only temporal sampling of a similar nature to the NH transect line off of the central WA coast could clarify any differences in copepod species abundance or biomass on a seasonal or interannual basis.

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