

MACROZOOPLANKTON COMMUNITY DYNAMICS
IN RELATION TO ENVIRONMENTAL VARIABLES
IN WILLAPA BAY, WASHINGTON, USA

By

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A thesis submitted in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE IN ENVIRONMENTAL SCIENCE

WASHINGTON STATE UNIVERSITY VANCOUVER
School of Earth and Environmental Science

AUGUST 2008

To the faculty of Washington State University:

The members of the Committee appointed to examine the thesis of
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Chair

ACKNOWLEDGEMENTS

I would like to thank A. Helms, J. Quenette, I. McComas, L. Marko, J. Breckenridge, L. Friedenberg, K. Olsen, and J. Duerr for their help in the field, and O. Kalata and L. Marko for identification assistance. Additionally, special thanks to D. Gewant and R. Hooff for assistance with multivariate techniques. Finally, thanks to S. Bollens, G. Rollwagen-Bollens, C. Schultz, and B. Tissot for their comments on early versions of the manuscript.

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Abstract

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August 2008

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Willapa Bay is a large, economically and ecologically important estuary on the Washington coast, USA, for which the zooplankton community has not previously been studied. Thus, in 2006 and 2007, six stations within Willapa Bay were sampled biweekly for macrozooplankton, chlorophyll, and various abiotic variables to elucidate the processes underlying community composition and dynamics. Non-metric multidimensional scaling identified water temperature and upwelling values as major factors defining two distinct temporal communities. Winter was marked by high abundances and a community of mainly oceanic species (*Calanus pacificus*, *Centropages abdominalis*), while summer was dominated by estuarine species (Palaemonidae, *Clevelandia ios*). Subsequent groupings were classified by variation in chlorophyll *a* concentration and salinity, and were marked by the presence of other taxa (Mysidae, *Neotrypaea californiensis*). These results point to the importance of physical processes, in particular interactions with the coastal ocean, in structuring the macrozooplankton in Willapa Bay.

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CHAPTER 1

Introduction

Estuaries are complex ecosystems characterized by rapidly fluctuating conditions, where inputs from both river freshwater and oceanic coastal water can alter the environment as often as every tidal cycle. Although the environment of estuaries can be stressful to organisms due to the large fluctuations in water conditions, organisms that can tolerate such changes thrive because of high productivity levels created by enriched nutrient concentrations (Correll 1978; Cole and Cloern 1987; Howarth 1988). Macrozooplankton, classified in this study by a size larger than 500 μm , are intermediate consumers found in most productive aquatic ecosystems. This group consists of both holoplanktonic and meroplanktonic taxa that consume a large proportion of primary productivity and act as intermediaries between primary producers and higher trophic levels (Gewant and Bollens 2005). This productivity is an important resource for many fish species that utilize these rich systems during larval and juvenile stages, when food availability is paramount to survival (Gunderson et al. 1990; Houde and Rutherford 1993; Beck et al. 2001).

In estuaries around the world plankton communities have been found to correlate with various abiotic factors. In a study of several estuaries on the coast of Texas (USA), Holt and Strawn (1983) found that significant differences in macrozooplankton community composition between warm and cool seasons were distinguished by salinity, due to river flow, and temperature. Soetaert and Van Rijswijk (1993) observed that salinity explained most of the variance within a mesozooplankton community while temperature played a much lesser role in the estuarine reaches of the Schelde River (Belgium and the Netherlands). The macrozooplankton and micronekton community composition in San Francisco Bay (USA) was correlated with season and proximity to the mouth of the estuary (Gewant and Bollens 2005).

Season, as defined by temperature, also played a major role in describing two distinct mesozooplankton communities in a Southern California estuary (USA) (Elliott and Kaufmann 2007).

Willapa Bay, an estuary on the southern coast of Washington state (USA), is part of a network of estuaries along the west coast of North America connected through coastal hydrographic processes (Emmett et al. 2000). In Willapa Bay, where more than half of the surface area and volume of the estuary are drained at low tide (Roegner et al. 2002; Banas et al. 2007), conditions may be highly influenced by coastal processes due to the large exchange of water with the coastal oceans. Other inputs to Willapa Bay include the Willapa and Naselle rivers, which drain largely undeveloped watersheds, a rarity in coastal systems (Secord and Cohen 2001). Although the relatively small drainage may provide some input into the system, the effect of this input may be superceded by the large tidal influence (Banas et al. 2007).

The California Current System drives the coastal oceans of the eastern Pacific; during the spring and summer it is dominated by the southward California Current while the northward Davidson Current prevails during the fall and winter (reviewed in Emmett et al. 2000; Hickey and Banas 2003). Coastal upwelling and downwelling events occur annually prevailing during the summer and winter, respectively (Hickey 1989). In the summer, southerly winds favor upwelling which brings colder, more saline, and nutrient-enriched water as close as a few kilometers from shore, while northerly winds generate downwelling conditions that force warmer, less saline, and nutrient-reduced water onshore (Hickey and Banas 2003; Banas et al. 2004). In Oregon and Washington, northerly winds also force the Columbia River plume back onshore at which point it can enter Willapa Bay (Roegner et al. 2002; Hickey and Banas 2003; Banas et al. 2004).

Willapa Bay supports commercial fisheries for Dungeness crab (*Cancer magister*), English sole (*Parophrys vetulus*) and the Pacific oyster (*Crassostrea gigas*). The oyster fishery is a large source of income to the region and produces between 10 and 25% of the commercially harvested oysters in the USA (Emmett et al. 2000; Feldman et al. 2000; Ruesink et al. 2006). The oyster fishery is facing major changes in its pest management procedures as new regulations are forcing the fishery to phase out the use of carbaryl (1-naphthol n-methylcarbamate) in its management of burrowing shrimp (Pulkkinen 2003). These endemic pests, the ghost shrimp *Neotrypaea californiensis* and the mud shrimp *Upogebia pugettensis*, burrow into the substrate, compromise the sediment stability, and allow oysters to sink and suffocate (Feldman et al. 2000; Dumbauld et al. 2001). Without a viable alternative for pest control, the oyster fishery may suffer, causing regional economic problems and decreasing national oyster supply.

Because Willapa Bay plays a major role in both the economic and ecologic health of the region, it is imperative to document its current biological status. Due to biological invasions (Bollens et al. 2002; Wonham and Carlton 2005; Ruesink et al. 2006), aquaculture activity (Ruesink et al. 2003), and pesticide use (Dumbauld and Wyllie-Echeverria 2003; Pulkkinen 2003), the estuary is changing. Macrozooplankton are sensitive to changes in many abiotic factors, natural or anthropogenic (Holt and Strawn 1983; Soetaert and Rijswijk 1993; Gewant and Bollens 2005) and therefore is a good candidate to analyze in conjunction with variation in environmental conditions. Additionally, currently no studies have examined the macrozooplankton community in Willapa Bay. For these reasons, the current status of Willapa Bay, its plankton community, and the mechanisms affecting their dynamics are important to understand.

This study examined the macrozooplankton community of Willapa Bay with two objectives. The first was to measure the composition, distribution, and abundance of macrozooplankton in Willapa Bay over two consecutive years. The second objective was to correlate community variations to biotic and abiotic factors, including chlorophyll *a* (chl-*a*) concentration, other community members, salinity, temperature, upwelling indices, and tidal fluctuations. The larger goal was to elucidate the relationships between species and their environment within Willapa Bay as well as to provide insights into estuarine zooplankton dynamics more generally.

CHAPTER 2

Materials and Methods

Study Site

Willapa Bay is a shallow estuary located between the mouth of the Columbia River to the south and Grays Harbor to the north (Fig. 1). The drowned-river valley drains a relatively small watershed of 2,900 km² (Emmett et al. 2000; Hickey and Banas 2003) and has an area of nearly 350 km², half of which is intertidal (Roegner et al. 2002). The estuary is aligned along a north-south axis and is connected to the ocean by a relatively small opening in the northwest corner. One major channel runs south from the mouth connecting with the Naselle River while another runs east from the mouth to the Willapa River (Banas et al. 2004). Tidal speed and influence vary over the length and width of the estuary and over the tidal cycle (Banas et al. 2004).

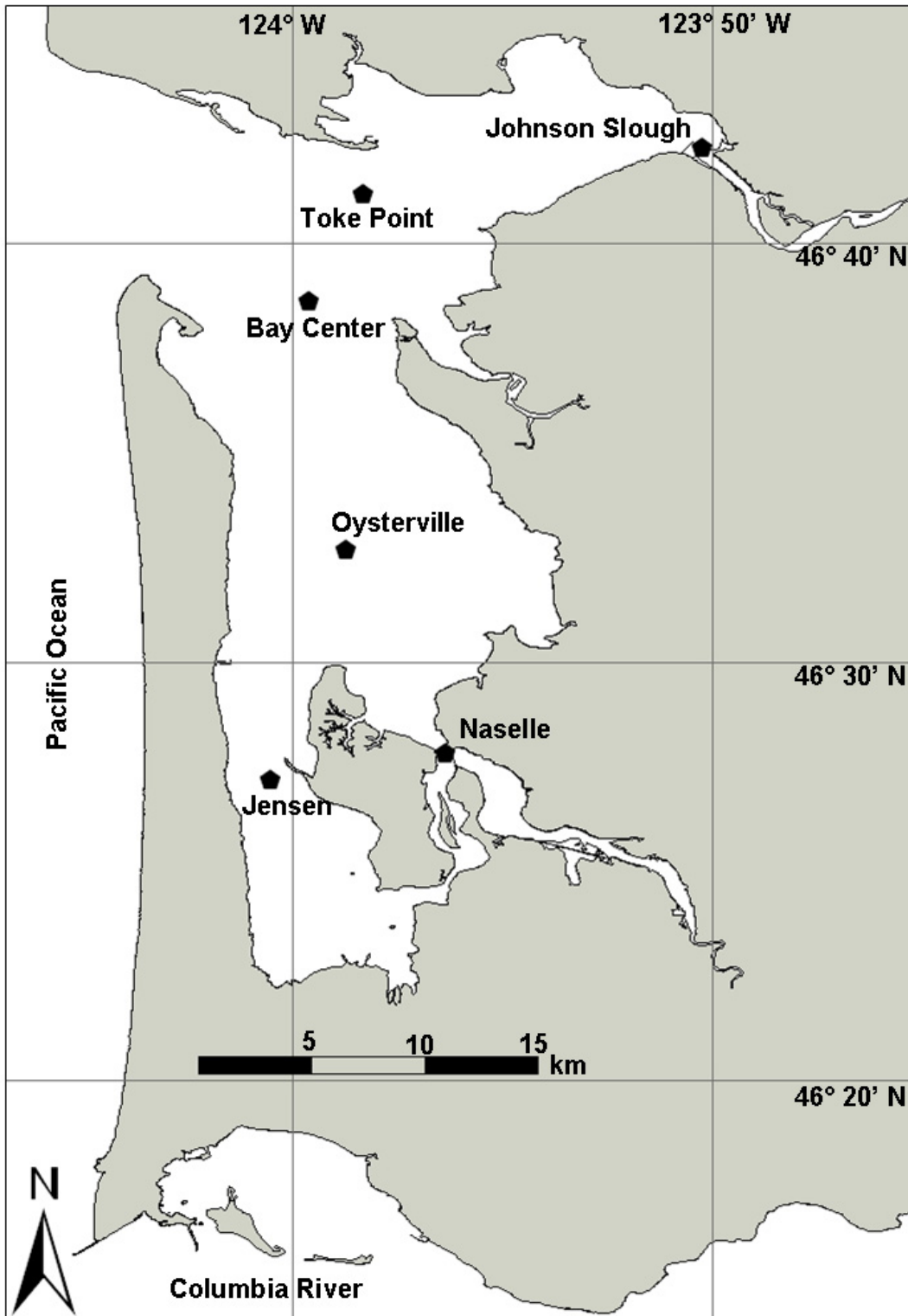


Figure 1. Map of Willapa Bay, Washington, USA.

Field Sampling

We selected six sampling stations within Willapa Bay (Fig. 1) to cover the spatial extent of the bay and both major river channels, in addition to proximity to Washington State Department of Ecology monitoring buoys. We sampled January 2006 through December 2007 on a biweekly schedule, corresponding with neap tides. The number of stations sampled varied due to weather conditions and accessibility but all sampling occurred between 10am and 4pm and was completed independently of the daily tidal cycle. At each station, samples for macrozooplankton and chlorophyll were collected and environmental conditions were recorded.

Macrozooplankton was collected using a 500 μm mesh, 1 m diameter hoop net deployed from a passively moving vessel to approximately 2 m above the bottom and vertically hoisted at a rate of 10-15 m min^{-1} . The net was equipped with a General Oceanics 2030 Flowmeter outfitted with a low-speed rotor. Samples were preserved onboard in 10% buffered formalin. In the laboratory, all specimens in each sample were identified and enumerated to the most specific possible taxonomic classification.

Surface water was collected using a bucket and 100 mL was filtered onboard onto Whatman 47 mm glass fiber filters and frozen for chl-a analysis via fluorometry (Holm-Hansen and Riemann 1978) using a Turner Designs 10-AU fluorometer.

Water column profiles of temperature, salinity and dissolved oxygen (DO) were collected at each station using a SBE25 Sealogger CTD. CTD data were processed and averaged into 1 m bins (SeaTerm Software) and then water column averages were calculated. Average daily temperature, salinity and chl-a measurements were compiled from the Washington Department of Ecology (WA DOE) mooring station at Bay Center (WPA 13) located at 46.6 °N 124.0 °W (http://www.ecy.wa.gov/programs/eap/mar_wat/moorings_what.html). Meteorological

conditions and tidal times and height were collected from the National Oceanic and Atmospheric Administration's (NOAA) Tides and Currents database (<http://tidesandcurrents.noaa.gov>) for the Toke Point Station (ID: 9440910) located at 46.7 °N 123.9 °W, adjacent to our Toke Point sampling station. River flow data were obtained from the US Geological Survey (USGS) for the Willapa and Naselle rivers (<http://waterdata.usgs.gov/WA/nwis/current/?type=flow>).

In addition to environmental variables collected in the bay, we also compiled data on coastal processes and indices. Daily coastal upwelling index values for 45 °N were collected from NOAA's Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov). These provide an index of the strength of wind forcing on the ocean based on Ekman's theory of mass transport due to wind stress. In addition to sampling date values, we averaged daily values over 7, 15, 30, and 60 days prior to sampling dates. We also obtained monthly values for the Multivariate El Niño/Southern Oscillation Index (MEI) from NOAA's Earth Systems Research Laboratory (www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html) and the Pacific Decadal Oscillation (PDO) from the Joint Institute for the Study of Atmosphere and Ocean (<http://jisao.washington.edu/pdo>). Because these indices are based on oceanographic measurements of the tropical Pacific, we lagged the data between zero and six months. Spring and fall transition dates for the California Current System were collected from University of Washington's Columbia Basin Research website (http://www.cbr.washington.edu/data/trans_data.html). Two sets of transition dates were obtained; the biological transition dates that are based on the arrival or disappearance of cold-water copepods (Peterson et al. 2006) and the physical transition dates that are determined when there is a 10-day directional switch in upwelling and sea level (Logerwell et al. 2003).

Statistical Analyses

Macrozooplankton counts were converted to abundance (individuals m^{-3}). Rare species, defined as those found in less than 3% of the samples, are reported but not included in the statistical analyses. All data were $\log_{10}(x+1)$ transformed. Kruskal-Wallis (χ^2), a nonparametric analysis of variance (Zar 1999), was used to explore spatial variation in individual parameters including total abundance, temperature, salinity, chl-a, and specific taxa. To examine spatial patterns in community composition Kendall's coefficient of concordance (W), a nonparametric multisample rank-correlation statistic, was used to test for spatial difference between pairs of stations. A lack of significant correlation was interpreted as an absence of concordance indicating a substantial difference in zooplankton communities. This test compiled averages of the 14 most abundant species and compared their rank abundance at each station. This analysis was run twice: once compiling all of the sample dates and a second time analyzing the cold and warm seasons separately. All univariate statistics were completed using SAS v 9.1 for Windows.

Nonmetric Multidimensional Scaling (NMDS) ordination was used to examine relationships between zooplankton community and environmental characteristics within the groups identified by the cluster analysis. Sorenson's (Bray-Curtis) distance measure was used and the ordination that most adequately described the data was chosen based on the final stress (a measure of the goodness-of-fit between the data and the final ordination) in relation to the dimensionality. Pearson correlation coefficients (r) were used to evaluate the relationships between the ordination axes and environmental variables. Cluster analysis was used to identify groups of samples based on similarity of zooplankton community composition. The dendrogram was generated using Sorenson's (Bray-Curtis) distance measure with the flexible beta linkage method. The number of groups defined was based on a balance between maximizing the number

of significant indicator values (see below; Dufrêne and Legendre 1997) and biological interpretability. Indicator Species Analysis (ISA) further examined these groups and determined which taxa had the strongest affiliations to each group. This technique evaluates each species against a perfect indicator that would faithfully and exclusively occur in a particular group; each species is assigned an indicator value for each group based on the degree of faithfulness and exclusiveness (Dufrêne and Legendre 1997). Indicator values were determined statistically significant via Monte Carlo randomization. All multivariate analyses were conducted in PC-ORD for Windows 5.10 (McCune and Mefford 1999). To determine which environmental variables were correlated with individual species, *a posteriori* Spearman rank correlation coefficients (r) were calculated between the dominant environmental variables and indicator species (SAS v 9.1).

CHAPTER 3

Results

Macrozooplankton Abundance

A total of 35,468 individuals representing 76 taxa were identified in 184 samples collected over 41 cruises between January 2006 and December 2007 (Table 1). Abundance patterns varied between the two years although not significantly ($\chi^2 = 0.33$, $p = 0.57$). The spring peak in March was twice as high in 2006 than 2007 (Fig. 2). Abundances in June and July of 2006 were much lower than those seen in 2007. Finally, the autumn and winter abundances in 2007 were higher than in 2006.

Total macrozooplankton abundance varied spatially ($\chi^2 = 18.17$, $p < 0.01$). In general, stations closer to the mouth supported larger abundances than stations farther up-estuary with a trend of decreasing abundance as distance from the mouth increased. The largest differences in abundance between upper and lower sites were found during months with peak abundances (Fig. 2).

Table 1. List of macrozooplankton species identified during the study ranked in terms of total numbers. Number of Samples = number of samples in which taxon was present, total number = number collected, percentage = percent of total catch. *Taxa that were found in less than 3% of the samples and not included in statistical analyses.

Taxon	Number of Samples	Total Number	Percentage
<i>Calanus pacificus</i>	86	10,500	29.6
<i>Centropages abdominalis</i>	123	7,836	22.1
<i>Neotrypaea californiensis</i>	96	2,904	8.19
Pinnotheridae	128	2,085	5.88
Mysidae	58	2,076	5.85
Hydrozoa	74	2,021	5.70
<i>Crangon</i> spp	77	1,379	3.89
<i>Cumella vulgaris</i>	70	1,224	3.45
Amphipod	70	705	1.99
Syllidae	86	488	1.38
<i>Lamprops quadriplicata</i>	59	443	1.25
<i>Podon</i> sp.	38	393	1.11
<i>Pseudocalanus</i> sp.	54	370	1.04
Bivalve larvae	37	354	1.00
Hippolytidae	64	264	0.74
<i>Epilabidocera longipedata</i>	52	238	0.67
<i>Clevelandia ios</i>	38	210	0.59
Barnacle nauplii	28	206	0.58
<i>Acartia</i> spp	41	202	0.57
<i>Eurytemora americana</i>	19	189	0.53
<i>Daphnia</i> sp.	17	169	0.48
Palaemonidae	26	156	0.44
Paguridae	12	147	0.41
<i>Tortanus discaudatus</i>	34	136	0.38
<i>Caprella</i> sp.	60	127	0.36
<i>Sagitta</i> sp.	29	84	0.24
Majidae	19	56	0.16
Lithodidae	24	51	0.14
<i>Nippoleucon hinumensis</i>	30	45	0.13
Osmeridae	18	45	0.13
<i>Leptocottus armatus</i>	21	36	0.10
<i>Eucalanus</i> sp.	5	27	0.08
Xanthidae	8	22	0.06
Grapsidae	8	19	0.05
Larval fish	8	16	0.05
<i>Cancer</i> sp.	8	16	0.05
<i>Oithona</i> sp.	5	16	0.05
<i>Clausidium vancouverae</i>	11	15	0.04
Barnacle cyprid	6	14	0.04
<i>Hemicyclops</i> sp.	8	12	0.03
Isopod	8	11	0.03
Porcellanidae	5	9	0.03
<i>Pleurometes isolepis</i>	5	6	0.02
Total Collected	184	35,468	100.00

**Armandia brevis*, calanoid copepod, *Cancer* sp. megalope, caridean, copepod, crab zoea, Ctenophora, cumacean, cyclopoid copepod, decapod megalope, Diogenidae, ephyra, *Errex zachirus*, *Evadne* sp., fish, harpacticoid copepod, Hemigrapsidae, Hippidae, Liparidinae, *Macropsis* sp., megalope, *Mesolamprops* sp., Ostracod, Pandalidae, *Parophrys vetulus*, *Platichthys stellatus*, polychaete, sea lice, shrimp, snail, *Synghathus leptorhynchus*, *Temora* sp.

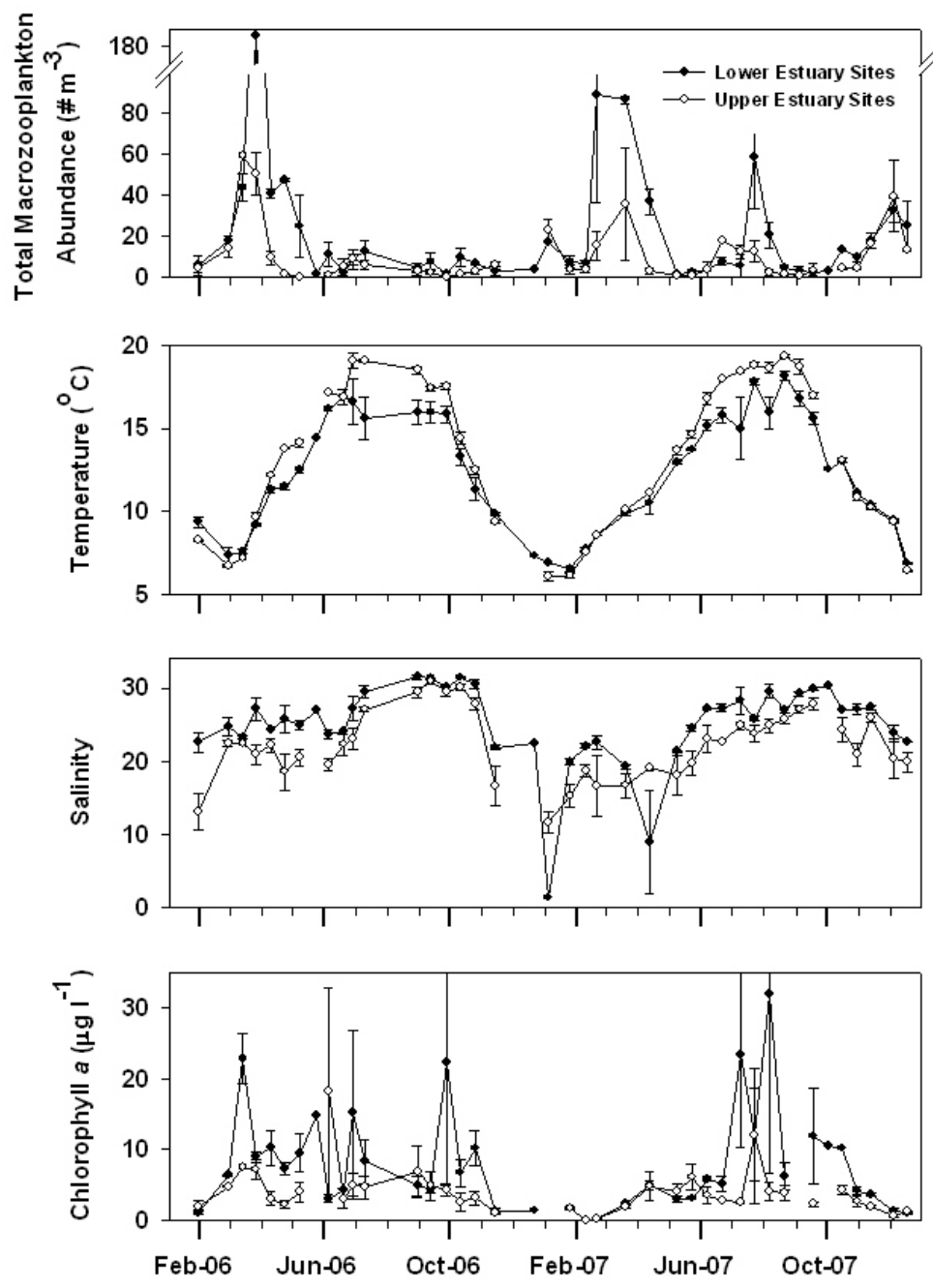


Figure 2. Regional means (\pm SE) of total macrozooplankton abundance ($\# \text{ m}^{-3}$) and water column means (\pm SE) for temperature, salinity, and chlorophyll *a* in Willapa Bay, 2006-2007. Closed symbols denote means at lower estuary sites (Bay Center, Oysterville and Toke Point); open symbols denote means at upper estuary sites (Jensen, Johnson Slough and Naselle).

Hydrography and Chlorophyll a

Temperatures varied by 10 °C between winter lows and summer highs. The coldest months of February and March had temperatures close to 6 °C while July and August, the warmest months, had temperatures up to 19 °C (Fig. 2). The magnitude and timing of the changes in temperature were similar between 2006 and 2007 ($\chi^2 = 0.67$, $p = 0.41$). There were no spatial differences in average water column temperatures among the stations ($\chi^2 = 3.88$, $p = 0.57$) although more variation was seen between lower and upper estuary stations during the summer months (Fig. 2).

The temporal pattern in salinity was less clear, ranging from below 10 in early January 2007 to over 30 on several dates during the summer months of 2006 (Fig. 2). Overall, 2007 had lower salinities than 2006 ($\chi^2 = 12.12$, $p < 0.01$). There was also spatial variation in salinity among the stations ($\chi^2 = 31.33$, $p < 0.01$). As with total macrozooplankton abundance, the stations closer to the mouth of the bay had higher salinity than those upriver, with a trend of decreasing salinity as distance from the mouth increased. The difference in salinity between upper and lower estuary sites was fairly consistent throughout the sampling period (Fig. 2).

Variation in chl-a was high, particularly on dates with peak measurements (Fig. 2). However, seasonal trends were consistent with trends recorded at the WA DOE mooring station. Overall, 2007 had significantly lower chl-a than 2006 ($\chi^2 = 15.78$, $p < 0.01$). Spatially, higher concentrations were found at stations closer to the mouth of the bay ($\chi^2 = 31.07$, $p < 0.01$), with the highest chl-a occurring in the Willapa River channel stations (Toke Point and Johnson Slough).

The transition dates for the California Current System varied between the years (Table 2). In 2007, both the spring and fall transition dates were a month earlier than in 2006. Downwelling

conditions, determined by negative upwelling values, prevailed October through April of both years. Similarly, upwelling conditions prevailed May through October.

Table 2. Transition dates for the California Current System (CCS) based on Logerwell et al. (2003) for physical transition dates. North and south denote the prevailing direction of the CCS.

	2006	2007
January	North	North
February	North	North
March	North	March 15
April	April 22	South
May	South	South
June	South	South
July	South	South
August	South	South
September	South	September 27
October	October 31	North
November	North	North
December	North	North

Macrozooplankton Community Analysis

NMDS ordination of samples allowed for a visual comparison of similarities within the community composition, where points that are closer together represent samples that contain more similar community compositions versus points that are farther apart. NMDS resulted in a 3-dimensional solution, with a final stress of 18.07 after 225 iterations, explaining 73.0% of the variance in the macrozooplankton community (Fig. 3). While this is considered a “fair” level of stress, the large number of sample units partly explains the high value and justifies continued analysis (Kruskal & Wish 1978; McCune & Grace 2002). The solution was found to be statistically different from a randomized solution using a Monte Carlo test ($p = 0.01$). Axis 1 explained 29.1% of the total variation and axis 3 explained 20.5% (Fig. 3), creating gradients along both axes that illustrate the separation of groups due to temperature (axis 1, Pearson’s $r = 0.817$) and chl-a and/or salinity (axis 3, chl-a: $r = -0.427$, salinity: $r = -0.420$). Axis 2 explained 23.5% of the variability, but because it lacked strong associations with any of the environmental variables it was left out of the analysis (all $r < 0.229$).

Cluster analysis revealed four distinct macrozooplankton community groups at a 15% dissimilarity level. These four groups were first classified into two seasons: Warm and Cold. Warm samples were collected roughly between April-October and had an average temperature of 15.91 °C (± 0.24) and cold samples were collected between October-April with an average temperature of 9.27 °C (± 0.25) (Table 3). Overlaying the groupings on the NMDS ordination showed that the two did not overlap, suggesting that this 2-dimensional plot (circles vs triangles, Fig. 3) was a good representation of the cluster analysis.

The secondary split in the cluster analysis defined each of the primary seasons (Warm and Cold) into two subgroups (Fig. 3). Cold 1 contained samples collected mostly in December-

February of both years and represented the samples collected in the coldest conditions and low chl-a and salinity values (Table 3); Cold 2 contained samples collected throughout October-April in a wider temperature range and a slightly higher chl-a and salinity range. Samples collected throughout both Cold groups contained markedly higher abundances than samples from the Warm groups, and Cold 2 had the highest abundances. Warm 1 contained samples from May through September, which were collected in the warmest conditions and over a narrow and high range of chl-a and salinity (Table 3). These samples contained higher overall abundances than the remaining warm samples. The remaining Warm samples were not analyzed as a group because the high variability and low species abundances among them did not illustrate any clear trends (Fig. 3).

Indicator Species Analysis (ISA) was used to identify which of the 43 species included in the ordination were indicative of the groups identified by the cluster analysis (Table 4). Of those, 29 were abundant enough to be statistically significant indicators and only two taxa were commonly found in both temperature groups: a decapod family, Pinnotheridae, and an amphipod, *Caprella* sp. In the cold season, 14 taxa were common including the calanoid copepods *Calanus pacificus* and *Centropages abdominalis*, and a cumacean, *Cumella vulgaris*. Only one taxon, the mysid family, Mysidae, identified the Cold 1 group, while eight taxa were indicative of the Cold 2 group. The strongest indicator species for the Cold 2 group included the calanoid copepod *Epilabidocera longipedata*, a marine cladoceran, *Podon* sp., and bivalve larvae. Conversely, only a few species were associated with one or both of the warm groups. Two taxa were common across the entire Warm season: the larval zoea stages of shrimp from the Palaemonidae family and the larval stage of the arrow goby, *Clevelandia ios*. The Warm 1 group was classified by the presence of larval zoea I stage of the ghost shrimp, *N. californiensis*.

An ordination of species depicted the relationships between indicator species and environmental variables, and further defined the important environmental variables for several groups (Fig. 4). The relative space between the indicator species for the Cold season (*C. pacificus*, *C. abdominalis*, *C. vulgaris*) and the Cold 2 group (*Podon* sp., *E. longipedata*, bivalve larvae) indicate Cold 2 was represented by species found in slightly higher temperatures and chl-a and salinity. Mysidae, the indicator for Cold 1, was plotted at low temperatures and low chl-a and salinity. Palaemonidae and *C. ios*, the indicators for the whole Warm season, were related to temperature, whereas *N. californienses*, the indicator of Warm 1, was more strongly correlated with high chl-a and salinity. Pinnotheridae and *Caprella* sp., the two ubiquitous species, were found in the center of the ordination.

Although the NMDS ordination showed that only two indicator taxa were related to distance from the mouth of the estuary (*C. vulgaris*, Palaemonidae), we also examined community composition. Over the two year sampling period, only one station near the mouth of the bay, Bay Center, was found to have a different community composition than both Jensen ($W = 0.38$, $p = 0.06$) and Naselle ($W = 0.34$, $p = 0.09$), the two stations farthest inland. During the cold season a similar trend was seen: the community at Bay Center was different from Jensen ($W = 0.34$, $p = 0.09$) and Naselle ($W = 0.32$, $p = 0.11$). Additionally, Toke Point, the other station closest to the mouth of the bay, also had a different community than Jensen ($W = 0.38$, $p = 0.06$). During the warm season, only Toke Point and Jensen ($W = 0.35$, $p = 0.09$) had differing zooplankton communities. Although results of these concordance analyses indicate some spatial variation within the community, all of the groups defined by the cluster analysis contained samples from all stations.

Table 3. Mean values (\pm SE) for major environmental variables for each group identified in Fig 3.

	Primary Groups		Secondary Groups		
	Cold	Warm	Cold 1	Cold 2	Warm 1
<i>Temperature</i>	9.27 (0.25)	15.91 (0.24)	7.30 (0.22)	10.27 (0.26)	16.43 (0.31)
<i>30 d Upwelling</i>	-42.24 (4.61)	31.94 (2.09)	-50.25 (9.39)	-38.15 (5.03)	44.11 (3.03)
<i>Chlorophyll a</i>	4.39 (0.57)	7.28 (1.07)	1.90 (0.36)	5.52 (0.78)	15.76 (2.56)
<i>Salinity</i>	21.71 (0.64)	25.95 (0.40)	18.13 (1.05)	23.53 (0.68)	28.03 (0.43)

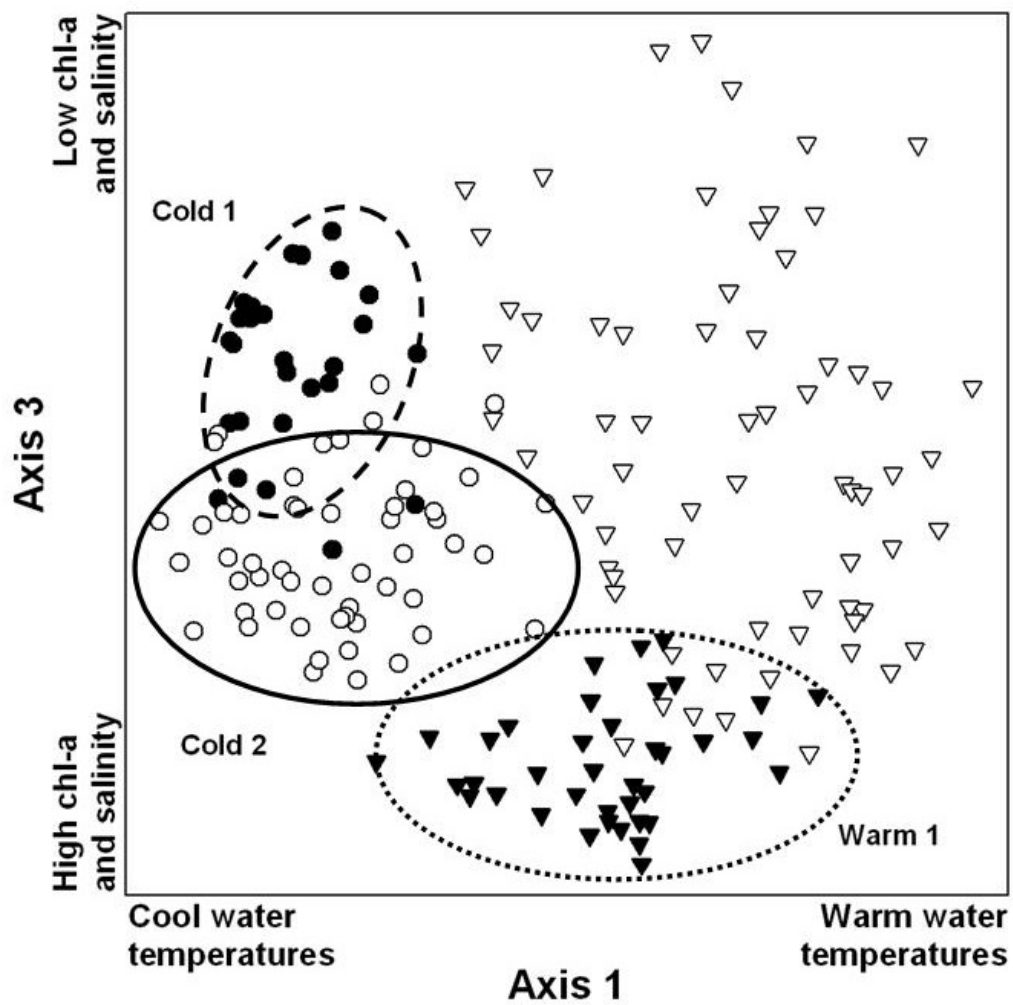


Figure 3. Non-metric Multidimensional Scaling Ordination of the 184 samples collected during the study. Circles indicate the cold season: closed circles indicated Cold 1 and open circles indicate Cold 2. Triangles indicate the warm season: closed triangles indicated Warm 1. Axis 1 ($r^2 = 0.291$) is associated with temperature ($r = 0.817$) and upwelling values ($r = 0.716$). Axis 3 ($r^2 = 0.205$) is associated with chlorophyll *a* concentration ($r = -0.427$) and salinity ($r = -0.420$).

Table 4. Indicator values (IV) for taxa with significant Monte Carlo p-values. Clusters are those groups identified in Fig 3. Bold indicates a good IV for the cluster (IV >5x higher than that for any other cluster).

	Primary Groups		Secondary Groups		
	Cold	Warm	Cold 1	Cold 2	Warm 1
<i>Cold Season Species</i>					
Primary Groups					
Amphipod	54	2	17	34	6
<i>Calanus pacificus</i>	91	0	16	75	0
<i>Centropages abdominalis</i>	80	6	14	67	3
<i>Crangon</i> spp	62	2	28	33	3
<i>Cumella vulgaris</i>	58	2	15	42	2
<i>Eurytemora americana</i>	22	0	5	17	0
<i>Lamprops quadriplicata</i>	41	3	9	30	4
<i>Leptocottus armatus</i>	22	0	6	17	0
<i>Nippoleucon hinumensis</i>	20	2	18	5	3
Osmeridae	23	0	22	6	0
<i>Pseudocalanus</i> sp.	45	2	13	31	2
<i>Sagitta</i> sp.	33	0	18	16	0
Syllidae	45	9	3	44	9
<i>Tortanus discaudatus</i>	36	0	11	25	0
Secondary Groups					
<i>Acartia</i> spp	35	1	4	33	0
Barnacle Nauplii	26	0	0	35	0
Bivalve Larvae	29	1	2	28	2
<i>Epilabidocera longipedata</i>	37	2	1	45	2
Hydrozoa	54	3	1	62	1
Lithodidae	20	1	0	24	0
Mysidae	67	0	77	11	0
Paguridae	12	0	0	18	0
<i>Podon</i> sp.	20	3	0	28	2
<i>Warm Season Species</i>					
Primary Groups					
<i>Clevelandia ios</i>	0	33	0	0	15
Palaemonidae	0	24	0	0	1
Secondary Groups					
<i>Daphnia</i> sp.	0	14	0	0	25
<i>Neotrypaea californiensis</i>	12	43	1	8	51
Grapsidae	0	6	0	0	7
Xanthidae	0	6	0	0	14
<i>Ubiquitous Species</i>					
<i>Caprella</i> sp.	15	17	0	15	24
Pinnotheridae	26	44	1	22	59

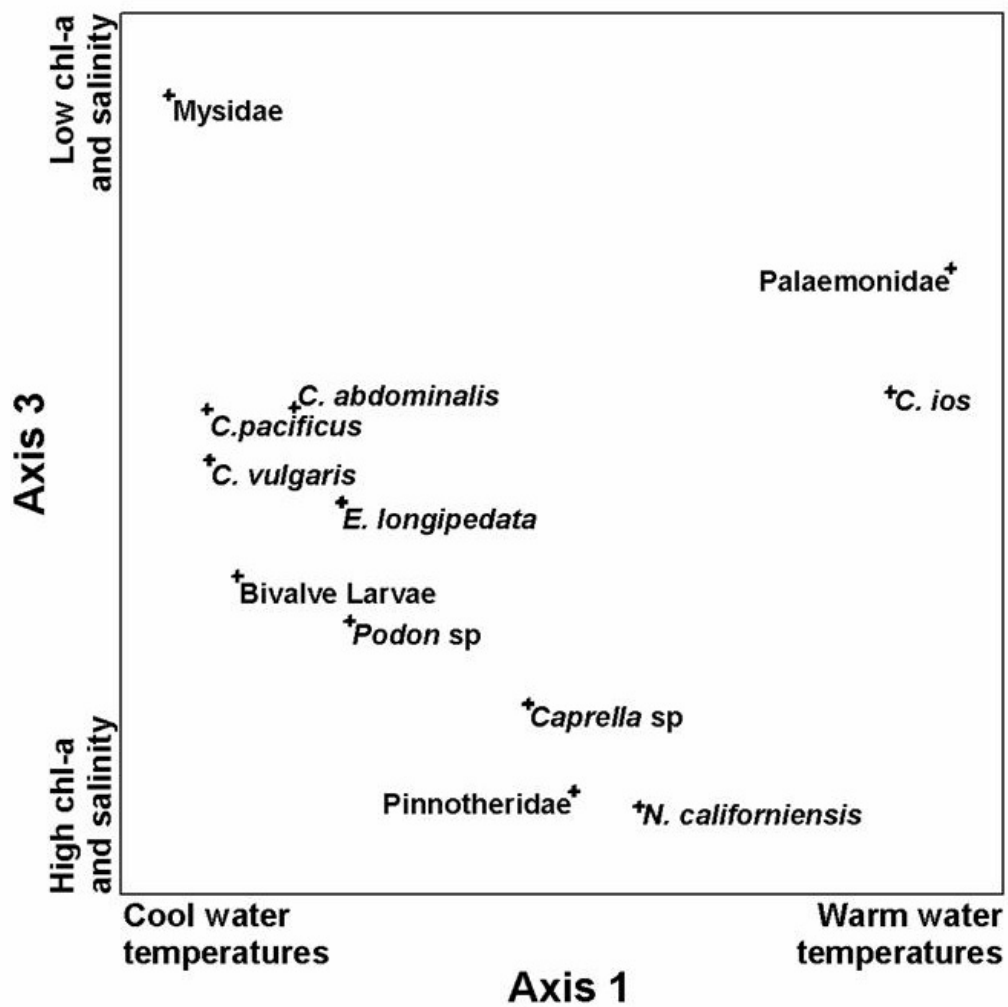


Figure 4. Non-metric Multidimensional Scaling Ordination of the 43 most abundant macrozooplankton, important species derived from the Indicator Species Analysis are identified.

Abundance Patterns and Environmental Associations of Individual Taxa

Three of the species indicative of the cold season (*C. pacificus*, *C. abdominalis*, *C. vulgaris*) all had major peaks in March of both years in addition to elevated abundances in other winter months (Fig. 5). *C. pacificus* was mostly absent from the plankton during summer months; however, *C. abdominalis* and *C. vulgaris* were seen in low abundances sporadically throughout the year. Both *C. pacificus* and *C. abdominalis* were highly correlated with all the environmental variables associated with axis 1, and most strongly associated with the 30-day upwelling average (Table 5). *C. vulgaris* was similarly associated with all the variables on axis 1, and most strongly associated with the 7-day upwelling average. On axis 3, *C. pacificus* was most strongly associated with salinity, *C. abdominalis* was not associated with any of the variables, and *C. vulgaris* was only associated with distance from the mouth of the bay. Despite these marked differences, all three were plotted in close vicinity on the ordination, suggesting very similar abundance patterns (Fig. 4).

Mysidae (Cold 1) were found in high abundance in the winter months of both years, with peak abundances occurring in January 2007 (Fig. 6). The location of this taxon on the species ordination suggests strong correlation with low temperature and low chl-a and salinity (Fig. 4). Spearman rank-correlations indicate a strong correlation with all of the environmental variables associated with both axes except for distance from the mouth of the estuary (Table 5). The strongest relationships for each axis, both negative, were with temperature and salinity.

Three of the indicator species for Cold 2 (*Podon* sp., *E. longipedata*, bivalve larvae) had peak abundances in spring of both years (Fig. 6). Despite correlations with different environmental variables, all three taxa were plotted in the ordination at mid-range chl-a and salinity and cooler water temperatures (Fig. 4). On axis 1, *Podon* sp. was only correlated with

temperature, and with salinity and chl-a on axis 3 (Table 5). *E. longipedata* was also most strongly associated with temperature, but additionally associated with several of the upwelling averages on axis 1. On axis 3 unlike *Podon* sp., *E. longipedata* was most strongly related to chl-a. Bivalve larvae were most strongly related to the 60-day averaged upwelling values and were not associated with any of the major variables on axis 3.

The two taxa associated with the warm season, *C. ios* and Palaemonidae, were not found in the plankton in winter months and increased in abundance during summer months (Fig. 7). Both taxa were highly related to all the variables on axis 1 and most strongly correlated with temperature (Table 5). As illustrated by the position in the ordination (Fig. 4), these taxa were associated with the highest temperatures. On axis 3, *C. ios* was not associated with any of the variables and Palaemonidae was positively associated with distance from the mouth of the bay.

N. californiensis, the indicator species for the Warm 1 group, had increased abundances in the spring and sustained elevated abundances through September (Fig. 7). *N. californiensis* was most strongly associated with temperature on axis 1 and only associated with chl-a on axis 3 (Table 5). Its position in the ordination suggests that *N. californiensis* was the taxon associated with the highest chl-a concentrations (Fig. 4).

The two ubiquitous taxa in the plankton community, Pinnotheridae and *Caprella* sp., were both found throughout the year. Abundances for both taxa were variable; Pinnotheridae appeared to peak in summer, while *Caprella* sp. showed no distinguishable peaks (Fig. 8). Both taxa were most associated with the 60-day upwelling average on axis 1 (Table 5). On axis 3, Pinnotheridae was strongly related to both salinity and chl-a, while *Caprella* sp. was only related to salinity.

Although only two taxa were correlated with distance from the mouth of the estuary in the NMDS ordination, several more were determined to have some spatial variability in abundance. Taxa associated with cold groups showed similar spatial variation. *C. abdominalis* ($\chi^2 = 12.01$, $p = 0.03$), *E. longipedata* ($\chi^2 = 12.83$, $p = 0.02$) and bivalve larvae ($\chi^2 = 20.85$, $p < 0.01$) all varied with increasing abundance at stations closer to the mouth of the estuary. Spatial gradients varied among species associated with the warm season. *C. ios* ($\chi^2 = 14.07$, $p = 0.02$) and Palaemonidae ($\chi^2 = 19.93$, $p < 0.01$) abundances increased with increasing distance from the mouth of the bay while the highest *N. californiensis* abundances were at the two stations closest to the mouth ($\chi^2 = 24.28$, $p < 0.01$). Similar to *N. californiensis*, Pinnotheridae abundances were also highest at stations closest to the mouth and decreased at stations farther inland ($\chi^2 = 38.10$, $p < 0.01$).

Table 5. Spearman rank correlation coefficients for major environmental variables for the ordination axes and indicator species for the primary and secondary groups. Bold indicates the highest correlated variable for each species on each axis; single underline $p < 0.05$, double underline $p < 0.01$.

	Axis 1					Axis 3		
	Temperature	60d Up- welling	30d Up- welling	15d Up- welling	7d Up- welling	Chl <i>a</i>	Salinity	Distance to Mouth of Bay
Cold Species								
<i>C. pacificus</i>	-0.7649	-0.7348	-0.7867	-0.7357	-0.5340	-0.1754	-0.3989	0.0607
<i>C. abdominalis</i>	-0.5394	-0.5113	-0.6132	-0.5732	-0.4042	-0.0075	-0.1271	0.0133
<i>C. vulgaris</i>	-0.2238	-0.2243	-0.1739	-0.1811	-0.2390	0.0998	-0.0297	0.1527
Cold 1								
Mysidae	-0.7488	-0.6657	-0.6555	-0.6035	-0.5929	-0.5555	-0.5824	0.0601
Cold 2								
<i>Podon</i> sp.	0.1534	0.1277	0.1177	0.0880	0.1293	0.1529	0.2261	-0.0682
<i>E. longipedata</i>	0.2303	0.1526	0.1241	0.1384	0.1900	0.2252	0.2158	-0.0011
Bivalve Larvae	-0.1637	-0.2242	-0.1876	-0.1380	-0.1395	0.0428	-0.0624	-0.0935
Warm Species								
<i>C. ios</i>	0.4296	<u>0.2959</u>	<u>0.3768</u>	<u>0.3525</u>	<u>0.2703</u>	0.0184	0.0008	0.0475
Palaemonidae	0.2970	<u>0.2353</u>	<u>0.2417</u>	<u>0.2483</u>	<u>0.2091</u>	0.0258	0.0920	0.2737
Warm 1								
<i>N. californiensis</i>	0.2993	0.0846	<u>0.1480</u>	<u>0.1867</u>	<u>0.1998</u>	0.3903	0.1380	0.0314
Ubiquitous Species								
Pinnotheridae	<u>0.1996</u>	0.2605	0.1400	0.1093	0.1362	<u>0.3823</u>	0.5106	-0.0476
<i>Caprella</i> sp.	0.1119	0.1784	0.0756	0.0309	-0.0206	0.0148	0.1584	0.0326

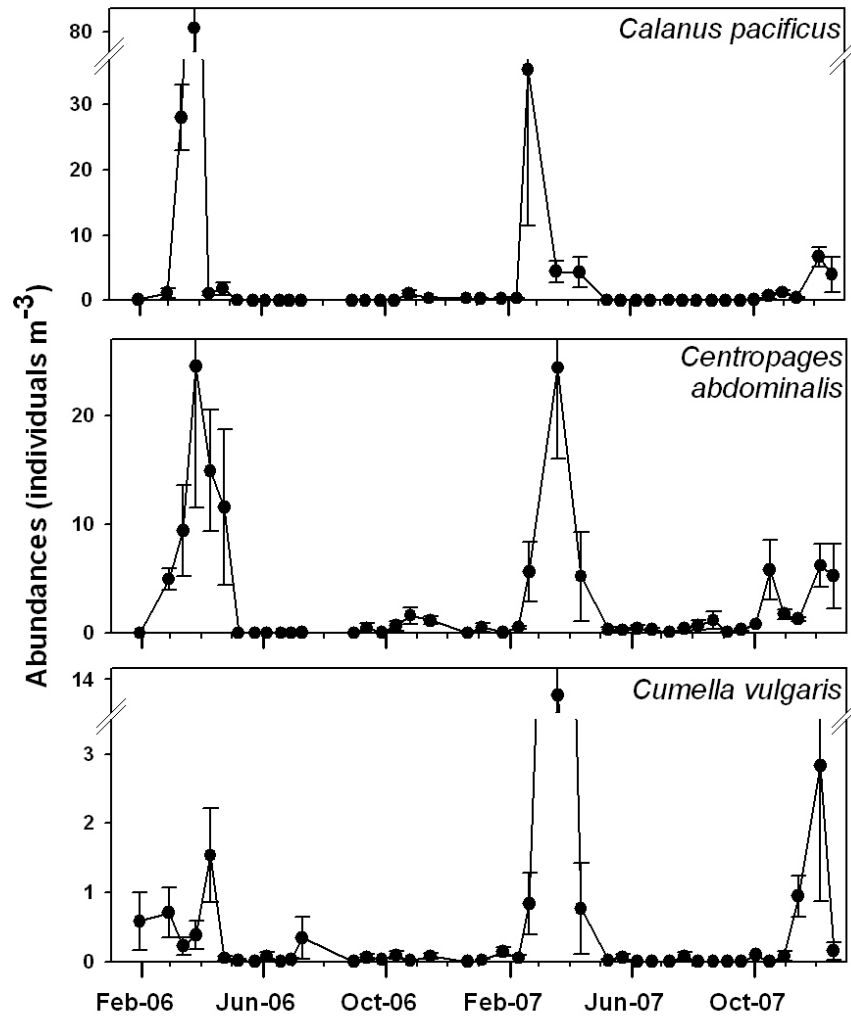


Figure 5. Bay-wide mean (\pm SE) abundances ($\# \text{ m}^{-3}$) of *C. pacificus*, *C. abdominalis*, and *C. vulgaris* in Willapa Bay, 2006-2007.

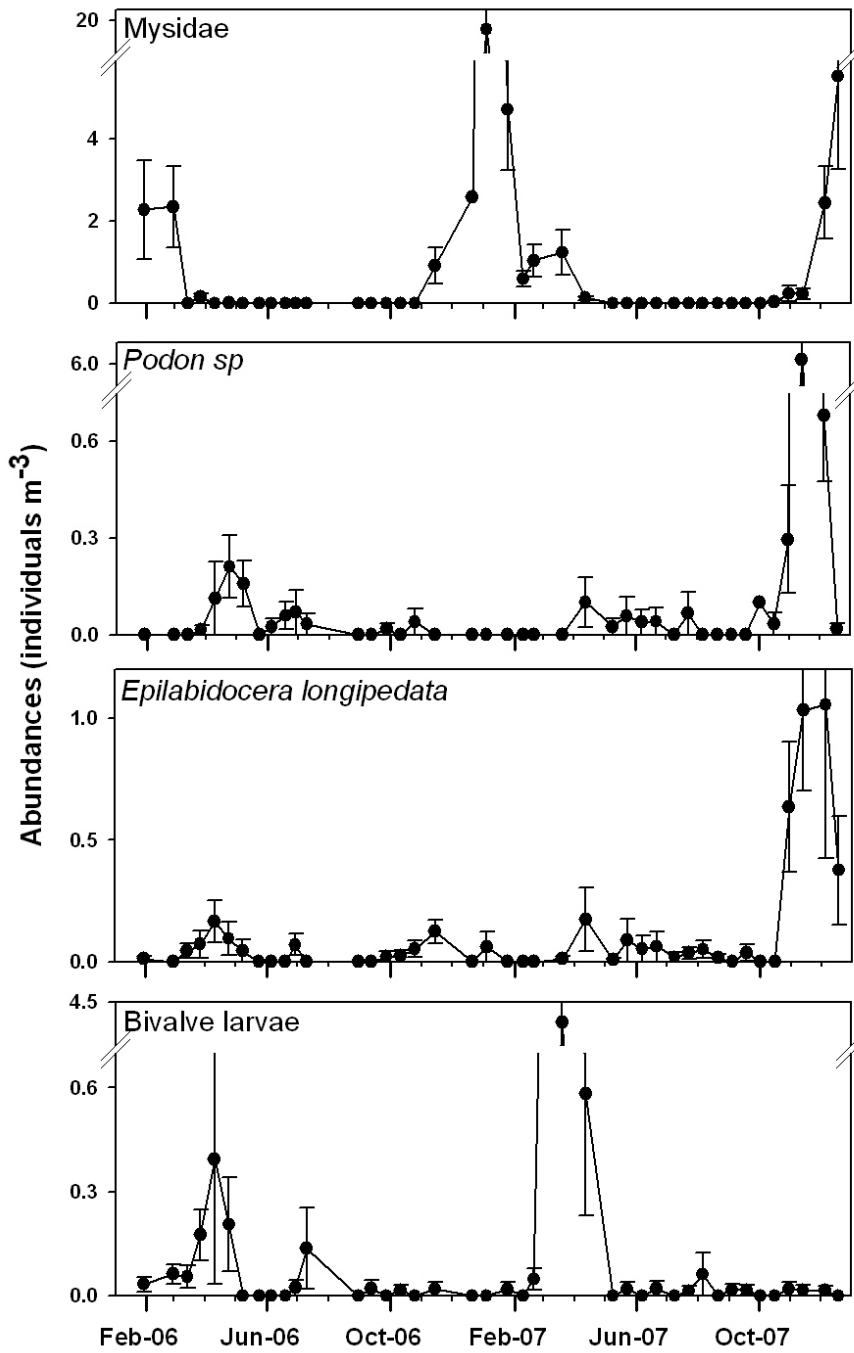


Figure 6. Bay-wide mean (\pm SE) abundances ($\# \text{ m}^{-3}$) of Mysidae, *Podon* sp., *E. longipedata*, and bivalve larvae in Willapa Bay, 2006-2007.

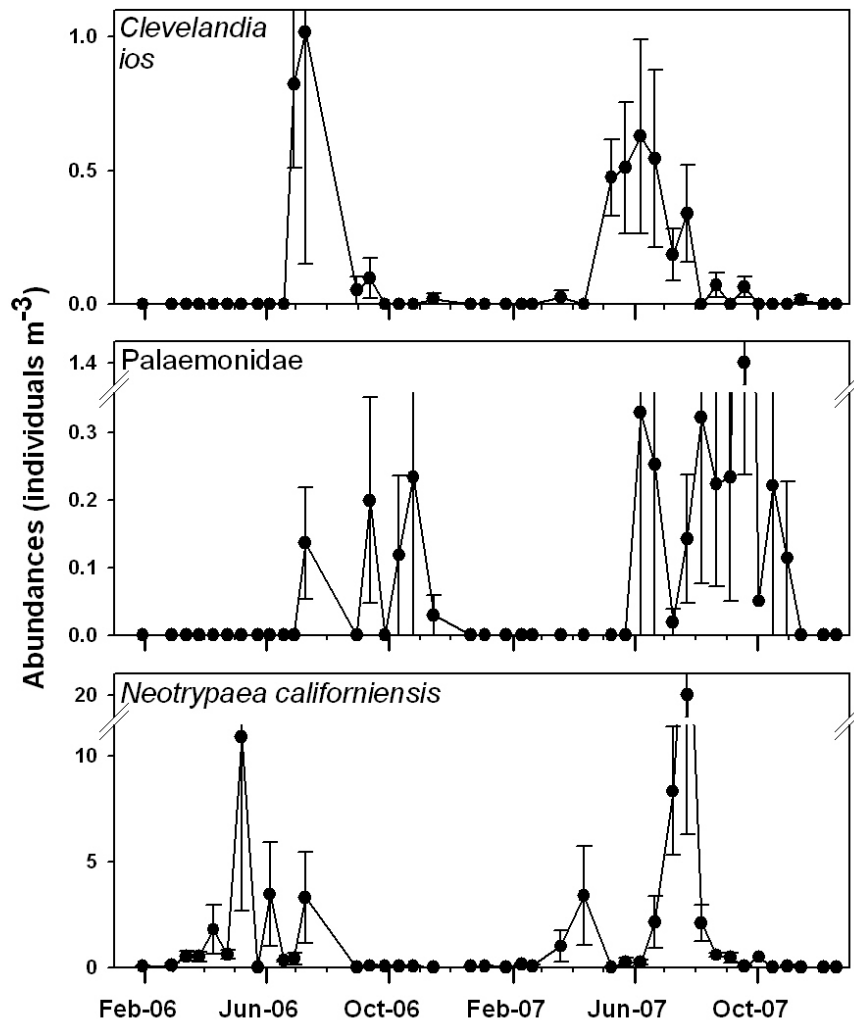


Figure 7. Bay-wide mean (\pm SE) abundances ($\# \text{ m}^{-3}$) of *C. ios*, Palaemonidae, and *N. californiensis* in Willapa Bay, 2006-2007.

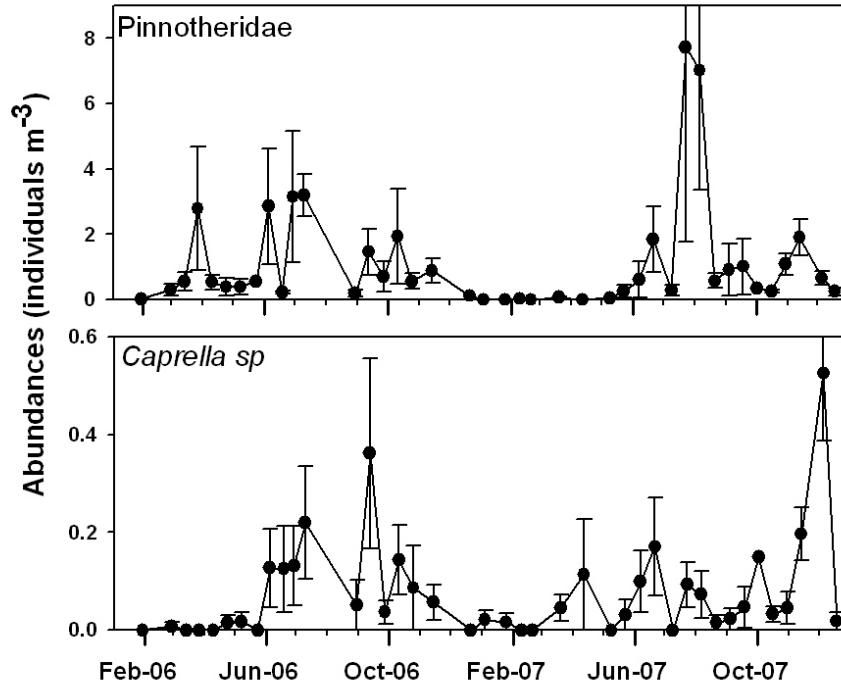


Figure 8. Bay-wide mean (\pm SE) abundances ($\# \text{ m}^{-3}$) of Pinnotheridae and *Caprella* sp. in Willapa Bay, 2006-2007.

CHAPTER 4

Discussion

Zooplankton, Chlorophyll a and Hydrography

Seasonal peaks in zooplankton are common in temperate estuaries as conditions become optimal; temperatures rise as light increases, generating more primary productivity, which supports larger populations of consumers (Hulsizer 1976). In our study, the peak in abundance was due to large increases in marine pelagic copepods, mainly *C. pacificus* and *C. abdominalis*. A similar marine influence was found in the Senegal River estuary, where peak macrozooplankton abundances were dominated by marine species (Champalbert et al. 2007). The range of total abundance observed in Willapa Bay (0-150 ind. m⁻³) was lower than other locations that sampled a similar size class (0-400 ind. m⁻³, Champalbert et al. 2007; 400-600 ind. m⁻³, Duggan et al. 2008), though no other study could be found that looked at exactly our size class (> 500 µm) in a temperate estuary.

Several zooplankton taxa had significantly higher abundances in 2007 than 2006 (*C. abdominalis*, Mysidae, *C. ios*, Palaemonidae) while only one had lower abundances in 2007 (Pinnotheridae). The differences in abundance might be explained by variation in the beginning of the upwelling season (Table 2). The timing of upwelling initiation has been linked to system productivity; earlier upwelling initiation generates greater productivity (Peterson et al. 2006). The range and pattern of temperature and salinity were similar to other temperate estuaries around the world (Frolander et al. 1973; Soetaert and Van Rijswijk 1993; Gewant and Bollens 2005). Although temperature did not vary between the years, 2006 had higher overall salinities than 2007. This could have been a result of higher river discharge in early 2007 (waterdata.usgs.gov).

The importance of coastal oceanography to phytoplankton biomass in the Pacific Northwest has been studied previously (Roegner et al. 2002; Hickey and Banas 2003; Banas et al. 2007). It is therefore not surprising that we found the coastal upwelling index to be an important environmental correlate to the community composition of macrozooplankton in Willapa Bay. While upwelling is generally associated with colder and more saline water conditions, Willapa Bay did not show this traditional relationship between temperature and upwelling values. Despite coastal upwelling, summer months had higher water temperatures due to solar heating (Hickey and Banas 2003). However, the waters of Willapa Bay were more saline during April-October when upwelling waters prevailed on the coast. This relationship was enhanced by the river discharge from the Willapa and Naselle rivers, which was large in winter months and close to zero during the summer months.

Willapa Bay is a long and narrow estuary with a small opening at one corner. Along the North-South axis there is nearly to a 20 km difference between the sampling station closest to the mouth of the bay and the one farthest upriver. It is therefore not surprising that hydrological and biological factors vary along the extent of the bay. Previous studies have shown the decreasing influence of the coastal ocean along the major axis of the bay (Roegner et al. 2002; Banas et al. 2004). Most of the variation observed by our study in salinity, chl-a and total macrozooplankton abundance occurred along this axis of the bay.

Although the variation of salinity and chl-a were more predominant than distance from the mouth of the bay, pair-wise comparisons did show statistically different zooplankton communities between several stations. These differences were expected, as they occur between the stations closest to and farthest from the mouth of the bay. With the demonstrated influence of the coastal ocean it follows that stations closest to this major source of water and organisms

would maintain different communities than the stations farthest from the input. In other regions, Siokou-Frangou et al. (1998) found seasonal zooplankton communities of the Saronikos Gulf and the adjacent Elefsis Bay (Greece), which slowly expanded in range as the currents transported the organisms throughout the study area.

Primary Source of Variation: Seasonality

Cluster analysis of community composition identified two primary seasons in which specific environmental variables played an important role: Cold and Warm. Season has been found to be an important indicator of community composition in other systems. Holt and Strawn (1983) defined two seasons in Trinity Bay, Texas, where the community composition switched from larval fish-dominated in the cold season to crustacean zoea-dominated during the warm season. In the San Francisco estuary, Gewant and Bollens (2005) described a two-season pattern of macrozooplankton and micronekton communities, defined by freshwater flows and temperature (e.g. dry and warm vs cold and wet months). Champalbert et al. (2007) also found two seasons defined by temperature and salinity, which were highly influenced by regulated freshwater flow and marine-water influence in the Senegal River estuary.

The cold season (October – April) was distinguished by cold water, negative upwelling values (downwelling conditions), a northward flowing coastal current, and high macrozooplankton abundances. The species found in these samples consisted predominantly of calanoid copepods, many of which have been found in coastal waters off Oregon and Washington (Frolander et al. 1973; Peterson and Miller 1977; Peterson and Keister 2003). However, the copepod species found co-occurring in Willapa Bay were members of different coastal regimes.

Two calanoid copepods (*C. pacificus*, *C. abdominalis*) were found in high abundances in Willapa Bay during winter and early spring months. *C. pacificus*, a warm-water species, has been found off the nearshore Oregon coast, primarily during late spring and fall months but in similar abundances (Peterson and Keister 2003), and in both on- and offshore environments in June and July (Morgan et al. 2003). Conversely, *C. abdominalis*, a cold-water neritic species, was found over the Oregon continental shelf during the strong upwelling season in the summer months (Morgan et al. 2003; Keister and Peterson 2003).

Mixing of taxa indicative of separately occurring communities has been observed in nearshore oceans. In a study of the seasonal cycle of zooplankton species composition off the central Oregon coast, Peterson and Miller (1977) found that summer communities were dominated by species with northern affinities while winter communities were a mix of northern and southern species. Southern species were present in these waters during the winter months because the Davidson Current flows northward and extends the ranges of the warm water species. Frolander et al. (1973) observed a similarly mixed winter zooplankton community in Yaquina Bay, an estuary on the coast of Oregon (USA).

The disparate temporal occurrence of certain taxa in the coastal ocean and Willapa Bay suggests the movement of organisms from the coast into the bay. One explanation could be biological. During the winter, upwelling is suppressed and the waters of the coastal oceans may be lacking nutrient resources, whereas increased river flow into the bay could bring elevated nutrient levels to the area and provide more resources than are available in the coastal ocean. Another reason these coastal taxa are found in the bay may be physical. Onshore winds, characteristic of the downwelling season, force surface water, and organisms within it, onshore and into Willapa Bay. A similar process of onshore transport was documented for phytoplankton

(Roegner et al. 2002), but ours is the first study to document this phenomenon in zooplankton in Willapa Bay. The influence of coastal zooplankton has been documented in other estuaries; the temporarily open-closed Kasouga estuary (South Africa) was dominated by marine species whenever the estuary was connected to the ocean (Froneman 2004).

Warm water temperatures, higher salinity and lower macrozooplankton abundance categorized the warm season. However, because of high variability and low abundances of zooplankton, only two taxa were commonly found in the warm season. The larval stage of the decapod family Palaemonidae was an indicator species of the primary warm season (Table 4), suggesting the use of the bay by juvenile decapods during periods of warm conditions and higher food availability (Holt and Strawn 1983). In the San Francisco estuary, Gewant and Bollens (2005) reported highest abundances of the estuarine resident *Palaemon macrodactylus* at the station farthest from the mouth of the estuary. We found Palaemonidae larvae displayed a spatial pattern suggesting estuarine dependency; larvae were positively correlated with distance from the mouth of the estuary, with the highest abundances found at stations farthest inland.

Another resident of the estuary is *C. ios*, a small goby that takes refuge in the burrows of other animals, including *N. californiensis* (MacGinitie 1934). These fish spawn during the spring and summer and spend 2-4 weeks as larvae in the water column. We found larval *C. ios* throughout the warm season, with peak abundances in June and July. In Dabob Bay, Washington, Bollens et al. (1992) found *C. ios* during the summer with maximum abundances at their shallower station. In Elkhorn Slough, California (USA), Yoklavich et al. (1992) recorded similarly sized peak abundances during late summer and early fall, and reported that larval and adult *C. ios* abundances increased with increasing distance from the entrance to the harbor.

Similarly, we found that abundances varied significantly across stations, with the highest abundances found in the upper estuary (Jensen and Naselle, Fig. 1).

As adults, *C. ios* are known to feed in the substrate, consuming crustaceans and other food particles in the mud. One report suggested *C. ios* prey on newly settled *N. californiensis* as the decapod transitions from its larval to its benthic stage (MacGinitie 1934). *N. californiensis* return to the estuary to settle between August and October and remain small through most of the first winter (Dumbauld et al. 1996). If newly settled crustaceans are a major food source for fish, it would be advantageous for them to spawn during periods of high decapod abundance, which in Willapa Bay appears to be during the summer months.

Secondary Sources of Variation: Chlorophyll a and Salinity

Varying levels of chl-a and salinity distinguished secondary communities within the cold and warm seasons. Offshore from Willapa Bay, phytoplankton blooms that arise due to active upwelling can be forced into the bay when the upwelling winds relax and water is forced onshore (Roegner et al. 2002). Presumably this occurs periodically throughout the upwelling season, suggesting that the peaks in chl-a captured between May and October may be of oceanic origin (Fig. 2). The inundation of the bay with food-rich waters may be timed with reproduction for taxa that breed within the bay. Changes in the salinity within the bay could indicate the fluctuating and competing influences from both the ocean and the rivers. While Willapa Bay is usually well-mixed, high salinity, and occasionally low oxygen, water from offshore can enter the bay and remain at depth (Bollens unpubl. data). However, the overall pattern of salinity within the bay fits the expected relationship of lower salinity during times of peak river outflow and higher salinity during the upwelling season, when saltier water is brought to the surface just

offshore (Hickey et al. 2002; Banas et al. 2004). A similar seasonal pattern of salinity was documented in Yaquina Bay (Frolander et al. 1973).

The presence of the Mysidae family in the community was the defining characteristic for the coldest secondary season (Fig. 3: Cold 1). In Willapa Bay, Mysidae was present in the water column a few months before and in larger abundances than those found in the San Francisco estuary (Gewant and Bollens 2005). Minimum Mysidae abundances have been found in conjunction with winter minimum salinities near 5 (Dean et al. 2005) and have been thought to potentially seek preferred conditions in the coastal ocean during low salinity events (Azeiteiro et al. 1999). In Willapa Bay, average salinities fell below 10 on only one date, suggesting that conditions in the bay are within Mysidae tolerance. Baldó et al. (2001) also observed low abundances in winter months and hypothesized a large rain event flushed the entire population out of the Guadalquivir estuary (Spain). This suggests the abundance patterns of Mysidae in Willapa Bay were the result of suboptimal conditions upriver and/or due to transport by increased river flow.

The other secondary cold group (Cold 2) was very similar to the primary cold season in hydrography and community composition. All indicator species for this group were also indicators for the primary cold season (Table 4) and were found in similar habitats both in and out of the estuary. Marine cladocerans, including *Podon* sp., are part of the nearshore community (Peterson and Keister 2002), similar to *C. abdominalis*. Likewise, *E. longipedata*, a nearshore coastal copepod, are commonly found in the coastal ocean during the summer (Peterson and Miller 1975).

Adult *N. californiensis* are residents of Willapa Bay that burrow into the sediments. These shrimp produce eggs that hatch between April and August. Larvae are present in the water

column as they move out of the estuary to develop in the nearshore coastal ocean. This development stage lasts 6-8 weeks, after which they return to settle in the bay (Dumbauld et al. 1996). Throughout our entire study we caught only stage I larvae, or those individuals presumably headed out of the estuary. *N. californiensis*, the strongest indicator species for Warm 1, was positively and most significantly correlated with chl-a.

In Willapa Bay, most of the primary production found within the bay is of oceanic origin (Roegner et al. 2002; Banas et al. 2007). This can create a gradient of decreasing chl-a with increasing distance to the mouth of the estuary. Our study observed this spatial variation for both chl-a and *N. californiensis*. The spatial gradient in larvae may be due to the proximity of the oyster beds, and therefore adult shrimp populations, to the mouth of the estuary. Additionally, Dumbauld et al. (1996) reported that females closer to the mouth of the estuary produced eggs before those farther upriver. This, combined with the correlation between larvae and chl-a, suggests that the transport of phytoplankton blooms from the coastal ocean into the bay may be an important cue and/or resource for *N. californiensis*.

We found multiple larval stages of several Pinnotheridae species throughout the year. Additionally, their abundances varied spatially within the bay, occurring in decreasing abundances with increasing distance from the mouth of the bay. This pattern may be related to salinity and/or chl-a (Table 5). The importance of this spatial component is unclear because it is unknown if the larvae require a coastal development period. Many studies have looked at larval behavior and it seems to vary with species. Breckenridge and Bollens (2008) found larval Pinnotheridae abundance in Willapa Bay varied with salinity. In Elkhorn Slough, California, relatively few larvae were caught outside the slough, with most of the larvae occurring within the

estuary, suggesting larval retention (Hsueh 1991). Because of this, the larvae of this family may be more reliant on production found within the estuary and therefore strongly correlated to chl-a.

Summary and Conclusions

Our study illustrates the importance of both internal and external estuarine processes on macrozooplankton communities. These insights are important to understanding the specific processes of the system and estuarine zooplankton dynamics in general. In Willapa Bay, the influence of the coastal ocean has been documented in terms of hydrography (Hickey et al. 2002; Banas et al. 2004), primary production (Roegner et al. 2002) and secondary production (Ruesink et al. 2003; Banas et al. 2007). Our study further explored the importance of coastal inputs into the bay and how it related to the macrozooplankton community. The findings here corroborate the previous findings that the coastal ocean is a major influence in Willapa Bay. This connectivity between the bay and the coastal systems accounts for only part of the seasonality within the bay. Estuarine processes and organisms play a large role in the status of the bay during summer months, when coastal input is lessened by offshore winds. Based on the similarity of Willapa Bay to other estuaries on the coasts of Oregon and Washington (Hickey and Banas 2003), processes observed here may also be occurring in these neighboring ecosystems.

This study produced the first comprehensive analysis of macrozooplankton in Willapa Bay. This provides important information regarding the quantity of resources available to higher trophic levels and adds to the knowledge of food web dynamics within Willapa Bay.

Additionally, this study documents the presence of stage I larvae of the ghost shrimp, *N. californiensis*, in the water column before they move into the coastal ocean for development.

In summary, we found much of the variation in the macrozooplankton community in Willapa Bay to be correlated with water temperature, chl-a and salinity. The seasonality in these variables was additionally influenced by the California Current System and the prevailing direction of upwelling winds. Cluster analysis revealed very different community compositions for two primary seasons distinguished by water temperature. Winter communities were predominantly comprised of marine species that are often found in the coastal oceans during other seasons, and summer communities were dominated by estuarine species, including larval stages of decapods and fish, which as adults are residents of the bay. Secondary variation over shorter time scales was related to changes in chl-a and salinity, and characterized by responses of individual taxa.

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