SEASONAL AND INTERANNUAL PATTERNS OF LARVACEANS AND

PTEROPODS IN THE COASTAL GULF OF ALASKA, AND THEIR

RELATIONSHIP TO PINK SALMON SURVIVAL


By

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PTEROPODS IN THE COASTAL GULF OF ALASKA, AND THEIR

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A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

December 2013

**Abstract**

Larvacean (=appendicularians) and pteropod (*Limacina helicina)* composition and abundance were studied with physical variables each May and late summer across 11 years (2001 to 2011), along one transect that crosses the continental shelf of the subarctic Gulf of Alaska and five stations within Prince William Sound (PWS). Collection with 53-µm plankton nets allowed the identification of larvaceans to species: five occurred in the study area. Temperature was the driving variable in determining larvacean community composition, yielding pronounced differences between spring and late summer, while individual species were also affected differentially by salinity and chlorophyll-*a* concentration. During the spring *Oikopleura labradoriensis* and *Fritillaria borealis* were most abundant and present at all stations. Late summer had highest abundances of *O. dioica* at nearshore stations, while *F. borealis* dominated numerically at outer stations. The 53-µm plankton nets collected higher abundances of *Oikopleura* spp., *Fritillaria* spp., and *L. helicina* than coarser 150 and 505-µm plankton nets. *Limacina helicina* abundance had a significant interaction effect among years, seasons and station location. *Limacina helicina* abundance in nearby PWS explained 30% of the variability in pink salmon survival; however, no significant correlations existed with larvacean or *L. helicina* abundances from the Gulf of Alaska stations.

**Table of Contents**

**List of Figures**

## List of Tables

## Acknowledgments

**Seasonal and Interannual Patterns of Larvaceans and Pteropods in the Coastal Gulf of Alaska, and their Relationship to Pink Salmon Survival**

**Introduction**

Mesozooplankton communities are typically dominated by crustaceans, but there has been increasing interest in other suspension-feeding mesozooplankton species that feed using mucus nets (Lalli and Gilmer, 1989; Bone, 1998). Their ability to collect and utilize small particles allows relatively direct transfer of energy from bacterioplankton or picoplankton to higher trophic levels, thus bypassing the microbial loop (Flood and Deibel, 1998). Recent studies suggest these neglected groups may even be surprisingly important prey items for upper trophic levels (Purcell *et al.*, 2005; Zavolokin, 2009).

Larvaceans (a.k.a.=appendicularians) are well known for their elaborate "houses" of mucopolysaccharides (Alldredge, 1977; Flood and Deibel, 1998; Thompson *et al.*, 2001) that consist of multiple filters used to collect, concentrate and consume food particles. The ability to culture larvaceans in a laboratory has produced data on house production rates (Sato *et al.*, 2001), respiration rates (Gorsky *et al.*, 1987; Lombard *et al.*, 2005), ecophysiology (Lombard *et al.*, 2009b), and genetic expression (Spada *et al.*, 2001; Danks *et al.*, 2013). However, there remains patchy geographic information on species distribution and abundance. This is not surprising considering damages inflicted on these fragile organisms when sampled with standard mesh-sized nets (Hopcroft, 2005).

Other than distribution, less is known about another common mucus-filter feeding group, the thecosome pteropods (van der Spoel, 1967). Aside from providing the pteropod with neutral buoyancy, these mucus webs collect small particles that are ingested (Gilmer and Harbison, 1986). Within the thecosomes, *Limacina helicina* is a common and often prominent zooplankter in subarctic and arctic waters (Gilmer and Harbison, 1991; Mackas and Galbraith, 2012; Questel *et al.*, 2013). Although the aragonitic shell of *L. helicina* has been studied in detail due to its susceptibility to elevated $p$CO$_2$ levels (Orr *et al.*, 2005; Fabry *et al.*, 2008; Lischka *et al.*, 2011), basic

knowledge of their life cycle is still lacking. An absence of information on spawning, development time, and growth rate is partly due to the challenge of keeping pteropods alive under laboratory conditions (Howes *et al.*, unpublished data).

There is a scarcity of information regarding the seasonality of the occurrence of pteropods and larvaceans in much of the North Pacific. Larvacean distribution has been documented for this region (Tokioka, 1960), but the majority of larvacean studies in the North Pacific have been in the temperate to tropical waters around Japan (Shiga, 1985; Tomita *et al.*, 1999; Tomita *et al.*, 2003; Sato *et al.*, 2008; and references therein), with one study done in the transitional water of the Kuroshio Current (Hidaka, 2008). *Oikopleura dioica* was most abundant in neritic waters (Hidaka, 2008) and peaked in abundance during early summer in a eutrophic inlet (Uye and Ichino, 1995) and during February and October in Tokyo Bay (Sato *et al.*, 2008). *Fritillaria borealis* f. *typica* and *O. labradoriensis* were the most abundant during the spring in Volcano Bay, Japan (Shiga, 1985). *Oikopleura longicauda*, a warm water species, dominated during early spring in Kuroshio water (Hidaka, 2008) and peaked in abundance during the late spring in the Japan Sea (Tomita *et al.*, 1999; Tomita *et al.*, 2003). High-nutrient Anadyr water, present in part of the northern-most Bering Sea's St. Lawrence Island Polynya, had a higher abundance and biomass of larvaceans than two other high-arctic polynyas (Deibel *et al.*, 2005). Together, these studies suggest both larvacean abundance and composition are dependent upon geographic locations, which are thereafter influenced by different oceanographic conditions. In contrast, only three long-term studies in the North Pacific have reported on thecosome pteropods, finding just two dominant species, *Limacina helicina* and *Clio pyramidata* (Tsurumi *et al.*, 2005; Ohman *et al.*, 2009; Mackas and Galbraith, 2012). Interannual and seasonal variability was not described in all studies, as their focus was to establish if shoaling of aragonite saturation states is affecting these taxa (Ohman *et al.*, 2009).

In summary, the seasonal abundance and biomass of both larvaceans and pteropods remains poorly established for the subarctic northern Gulf of Alaska (GoA). This thesis documents the abundance, biomass and species composition on the Seward

Line transect, located on the shelf south of the Kenai Peninsula and within Prince William Sound, of mucus net feeders relative to season, temperature, salinity, chlorophyll-*a*, and oceanographic indices. Like most zooplankton groups, interpretation of abundance and biomass data can be biased by gear selectivity (Bé and Gilmer, 1977). Consequently, this thesis aimed to establish the extent to which mesh size may underestimate the contribution of larvaceans and pteropods to the zooplankton community to facilitate comparisons among other studies.

The trophic importance of zooplankton groups is often defined by the importance of their predators, generally a challenging task. Until recently, our knowledge of who eats these mucus net feeders was limited (see reviews in Lalli and Gilmer, 1989; Gorsky and Fenaux, 1998). Pink salmon diet studies in the Gulf of Alaska have now demonstrated the importance of both *L. helicina*, and the under-studied larvaceans in their diet (Boldt and Haldorson, 2003; Armstrong *et al*., 2005; Armstrong *et al*., 2008); however, prevalence in diet may not necessarily ensure enhanced pink salmon survival. The zooplankton community across the GoA and in Prince William Sound (PWS) supports one of the largest releases of hatchery-raised, thermally-marked pink salmon (about 600 million smolt released each spring) (Vercessi, 2013). The ability to determine survival rates from thermal marking provides a unique opportunity to explore if pink salmon success is related to variability in mucus-net prey. It is hypothesized that a greater abundance of mucus net feeders collected along the Seward Line on the northern Gulf of Alaska shelf will be positively correlated to pink salmon survival.

**Methods**

**Study area**

Variability in meteorology, bottom bathymetry, and surrounding mountainous terrain contribute to the GoA's extremely productive waters across the continental shelf and slope, in comparison to the adjoining high-nutrient low-chlorophyll oceanic domain. Aleutian lows during the winter bring strong easterly winds over the shelf, deepening the mixed layer and distributing nutrients vertically, while a weak reversal of the winds during summer, when the high pressure system dominates, creates southward transport

offshore (Royer, 1975). These forces cause downwelling during winter months and weak upwelling during summer (Royer, 1975; Royer, 2005). Large eddies that propagate along the shelf-break (Ladd *et al.*, 2007) further contribute to this complexity (Mackas and Coyle, 2005). In May, the inner coastal surface waters of the Alaska Coastal Current (ACC) freshen due to spring melt, contributing to stratification (Weingartner *et al.*, 2005) and creating a unique environment for species with lower salinity tolerances. This physical environment stimulates a productive spring and a less productive summer season (Strom *et al.*, 2007). These unique atmospheric and oceanographic conditions support a well-studied zooplankton community across the Gulf of Alaska Seward Line (Coyle and Pinchuk, 2003, 2005; Liu and Hopcroft, 2006a,b, 2007, 2008; Pinchuk and Hopcroft, 2006; Pinchuk *et al.*, 2008).

The Gulf of Alaska has experienced large regime shifts during the late 1970s, which caused a change from shrimp and capelin dominated fisheries to that of groundfish. Pressure oscillations such as the Pacific Decadal Oscillation (PDO) (Hare and Mantua, 2000), the Multivariate Enso Index (MEI) (Wolter and Timlin, 1993) and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo *et al.*, 2008) were influential in varying degrees to abiotic conditions and biotic communities. Interannual variability in zooplankton abundance and biomass has been correlated with these indices (Mackas *et al.*, 2001) and their impact on sea-surface temperature anomalies. By observing these mucus net feeders over an 11-year timeline, interannual and seasonal abundances can be compared to these indices.

**Sampling**

Sampling was initiated during the Global Ocean Ecosystem Dynamics (GLOBEC) program, which sampled 13 fixed stations across the shelf (~18 km apart) labeled GAK 1 to GAK 13 and 5 stations in Prince William Sound (PWS) (Fig. 1).
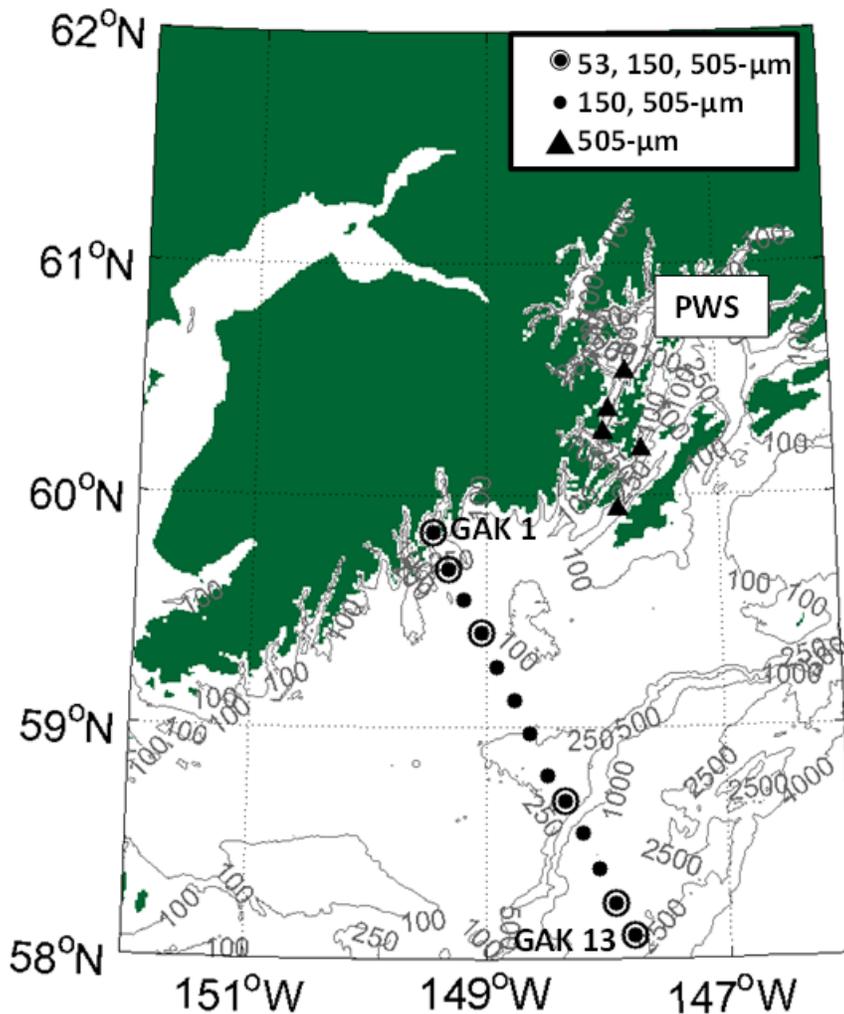
**Figure 1:** The Seward Line across the northern Gulf of Alaska continental shelf from nearshore GAK 1 to offshore GAK 13. Different symbols represent analysis done with the different plankton net mesh sizes. The entire Seward Line and Prince William Sound (PWS) stations were analyzed for 150 and 505-μm samples, while the 53-μm samples were only analyzed at stations 1, 2, 4, 9, 12 and 13. Samples within PWS were only analyzed with the 505-μm mesh.

From 1998-2004, sampling occurred 6-7 times annually, including routine collections during May and August, except in 2004 where summer observations were only available

during July. After 2004, samples were only collected in early May and early September. On each cruise, a Seabird 9/11+ CTD profiled the water column along with a rosette of 12 5-L Niskin bottles. CTD profiles were processed from the downcasts (Weingartner *et al*., 2002), while water samples were collected during the upcast at each station. Water for chlorophyll-*a* was collected from each Niskin bottle every 10 m, from 50 m to the surface, filtered under low pressure onto Whatman 47-mm GF/F filters, and frozen at -20 °C until analyzed fluorometrically post-cruise (Parsons *et al*., 1984).

Smaller zooplankton were sampled during daylight, initially using a Calvet pair of 150-µm nets, then from 2001 onward with a Quadnet consisting of two 150-µm mesh nets and two 53-µm mesh nets, each net having a 25 cm diameter and a long aspect ratio (10:1). Both systems were hauled vertically (~0.5 m s$^{-1}$) from 100 m to the surface. Each pair of nets with the same mesh size was combined after collection. General Oceanics flowmeters were positioned in the mouth of each net to calculate the volume of water filtered, and were prevented from spinning during net descent. Larger zooplankton was collected at night with a 1 m$^2$ MOCNESS (Wiebe *et al*., 1976) fitted with 505-µm mesh nets from 1998 to 2004, and during May of 2005 and 2006. A Hydrobios Midi Multinet (0.25 m$^2$) with 505-µm mesh nets replaced the MOCNESS in late summer of 2005 and 2006, and for all sampling from 2007 to 2011. These nets were towed obliquely at ~1 m s$^{-1}$ during night-time darkness from 100 m to the surface, and triggered every 20 m. All zooplankton samples were preserved in 10% formalin and seawater. This creates a unique 11-year timeline (2001 to 2011) to observe seasonal and interannual patterns of mucus-net feeders based on the fine 53-µm mesh net, and a longer timeline (to 1998) to observe abundances collected from larger mesh sizes from PWS.

**Processing**

Data were generated from all three mesh sizes; however, taxonomic identification of specimens from coarse mesh nets was compromised by damage to the specimens, especially with fragile groups like the larvaceans (Hansen *et al*., 1996). For the 150-µm and 505-µm nets, all samples were analyzed at all stations as part of a general GLOBEC-Seward Line community analysis, but without emphasis on the larvaceans or pteropods

(e.g. Coyle and Pinchuk, 2003, 2005). For the 53-µm mesh samples, a greater number of specimens in both taxa were identified and measured than in the other mesh sizes. The 150 and 505-µm samples were processed at all 13 Seward Line stations, at 3-5 stations in PWS, and the 53-µm mesh samples were only analyzed from Seward Line stations 1, 2, 4, 9, 12, and 13 (Fig. 1). Subsamples were obtained using a Folsom splitter until there were approximately 100 specimens of a target species present, and increasingly larger fractions were examined to fill in data on other species. Animals in the 53-µm nets were examined in a Bogorov sorting tray under a Leica MZ12.5 microscope, and measured using the ZoopBiom digitizing system (Roff and Hopcroft, 1986), with species-specific dry-weights (DW) predicted from size (Table 1).

**Table 1**: Length-weight relationships used to determine the biomass of the dominant species. Dry weight regression for *Fritillaria pellucida* was used for *F. borealis*. DW=dry weight (mg); TL=trunk length (µm); AFDW=ash-free dry weight (mg); D=diameter (µm).

| Taxa | Regression | Reference |
|---|---|---|
| *Oikopleura labradoriensis* | log DW=2.51 log (TL-6.54) | Gorsky *et al*., 1987 |
| *O. dioica* | log DW=2.60 log (TL-6.66) | Paffenhöfer, 1976 |
| *Fritillaria borealis* | log AFDW=3.21 log (TL-9.11) | Fenaux, 1976 |
| *F. pellucida* | log AFDW=3.21 log (TL-9.11) | Fenaux, 1976 |
| *Limacina helicina* | AFDW=0.039 D$^{(3.5032)}$ | Mumm, 1991 |

Larvaceans in the 53-µm nets were identified to species level (i.e. Bückmann and Kapp, 1975) and trunk length was measured, starting from the lower lip and ending at the posterior point of the trunk (ovary or testis). Larval pteropods were distinguished from other larval gastropods by the sinistral spiral of the shell, and were presumed to be the only species present at larger sizes, i.e., *Limacina helicina*. Pteropod size was determined

by measuring shell diameter. Although the gymnosome *Clione limacina* also existed in the samples, its numbers were too low to allow interpretation of temporal or spatial patterns; a *Clio* species also occurred sporadically in offshore samples, but for the rest of this paper, "pteropod" will refer exclusively to *L. helicina*.

Data from the MOCNESS and Multinet were analyzed to determine larvacean and pteropod depth distribution. For these nets, larvaceans were identified only to genus (Coyle and Pinchuk, 2003, 2005) due to the destruction of taxonomic features by the 505-µm mesh.

**Data analysis**

Larvacean community level analysis was performed with the software package Primer v6 (Clarke and Gorley, 2006) using a Bray Curtis similarity index on fourth-root transformed abundances from the 53-µm nets. Lower stress-levels in the ordination reflect more accurate nonparametric Multidimensional Scaling (nMDS). Further community analysis with environmental variables was completed using a BIO-ENV BEST model (Clarke and Ainsworth, 1993). This method selects different combinations of the environmental variables to determine an 'optimal match' between the biotic and abiotic ordinations. The rank correlation ($\rho$) between the biotic and abiotic matrices was calculated several times using variables temperature, salinity, and chlorophyll-*a*, integrated to the sampled depth of 100 m and to shallower depths. From these different combinations a maximum $\rho$ was attained; this included the best combination of abiotic variables that described the biotic variables. Differences did not occur when environmental variables were averaged over shallower depths than the depth sampled (100 m). From these analyses, it became clear that differences occur among those years with above average (i.e. "warm" years) and below average (i.e. "cold" years) temperatures, so results have been structured to help highlight these differences. Individual species abundance of the dominant larvaceans, *Oikopleura labradoriensis*, *O. dioica* and *Fritillaria borealis*, collected in the 53-µm nets, including years 2001-2011, were log-transformed and compared to environmental variables using a Pearson correlation test. *Oikopleura labradoriensis* and *F. borealis* occurred in spring and late

summer, but *O. dioica* occurred during late summer only. Thus, only *O. dioica* abundance from late summer was used in Pearson correlation tests.

Based on residuals, a linear model was used to look for significant correlations among environmental variables (temperature, salinity, and chlorophyll-*a*) averaged to the depth sampled of 100 m, and *L. helicina* abundance. Differences did not occur when environmental variables were averaged over shallower depths. A three-way factorial ANOVA was performed including year, season, and station location using data from 53-μm nets of *L. helicina* log-transformed abundance. Samples were grouped by station location on the shelf between nearshore (GAK station 1, 2, 4) and offshore (GAK station 9, 12, 13). A post-hoc Tukey Multiple Comparisons test was done to explore the interaction effect of year, season, and station. A paired samples Wilcoxon test was used to look for differences in abundance between the 53-μm and 150-μm nets, which were sampled simultaneously. This comparison in net size was done when season and year were pooled. The 505-μm net could not be included in this analysis because it was sampled at night and thus violated the assumption of independent random sampling. For a comparison of the 505-μm net with the smaller sized nets, 95 % confidence intervals are shown (Stefano, 2004).

Larvacean and pteropod log-transformed abundance of the 53-μm net collected at Seward Line stations, and pteropod log abundance from PWS, was compared to indices of the PDO (Hare and Mantua, 2000) and the NPGO (Di Lorenzo *et al.*, 2008), as well as the MEI (Wolter and Timlin, 1993), using Pearson correlation. May cruises were compared to the average winter index (November to April) and late summer cruises were compared to the average summer index (May to October). Percent pink salmon survival was calculated using data supplied by the Alaska Department of Fish and Game (L. Vercessi, ADFG, personal communication). Percent pink salmon survival was $arcsin(sqrt(x/100))$ transformed over the timeline of data (1998-2011). The year of release was compared to winter and summer indices (above) and an annual average index (January to December) under the assumption that pre and post release conditions are influential.

The availability of zooplankton prey are believed to be most important energetically within smolt and juvenile diets during late summer and autumn, the time when these stages of fish enter the coastal GoA from sheltered PWS (Cross *et al*., 2005); thus, we correlated prey abundance to survival during year of release using a linear regression. The samples from the nearshore shelf station group were used in the linear regression analysis because juvenile pink salmon are found primarily on the inner shelf from their emigration out of PWS (Willette, 1996; Armstrong *et al*., 2005). Pteropod abundance from the 505-μm mesh collected in PWS (1998-2011) was also compared to pink salmon survival, due to the importance of prey availability when juveniles first enter oceanic water (Cross *et al.*, 2005).

**Results**

**Temperature**

Integrated temperature across the Seward Line in the Gulf of Alaska ranged from ~4 to 7 °C in the spring to ~7 to 11 °C in the late summer (Fig. 2).
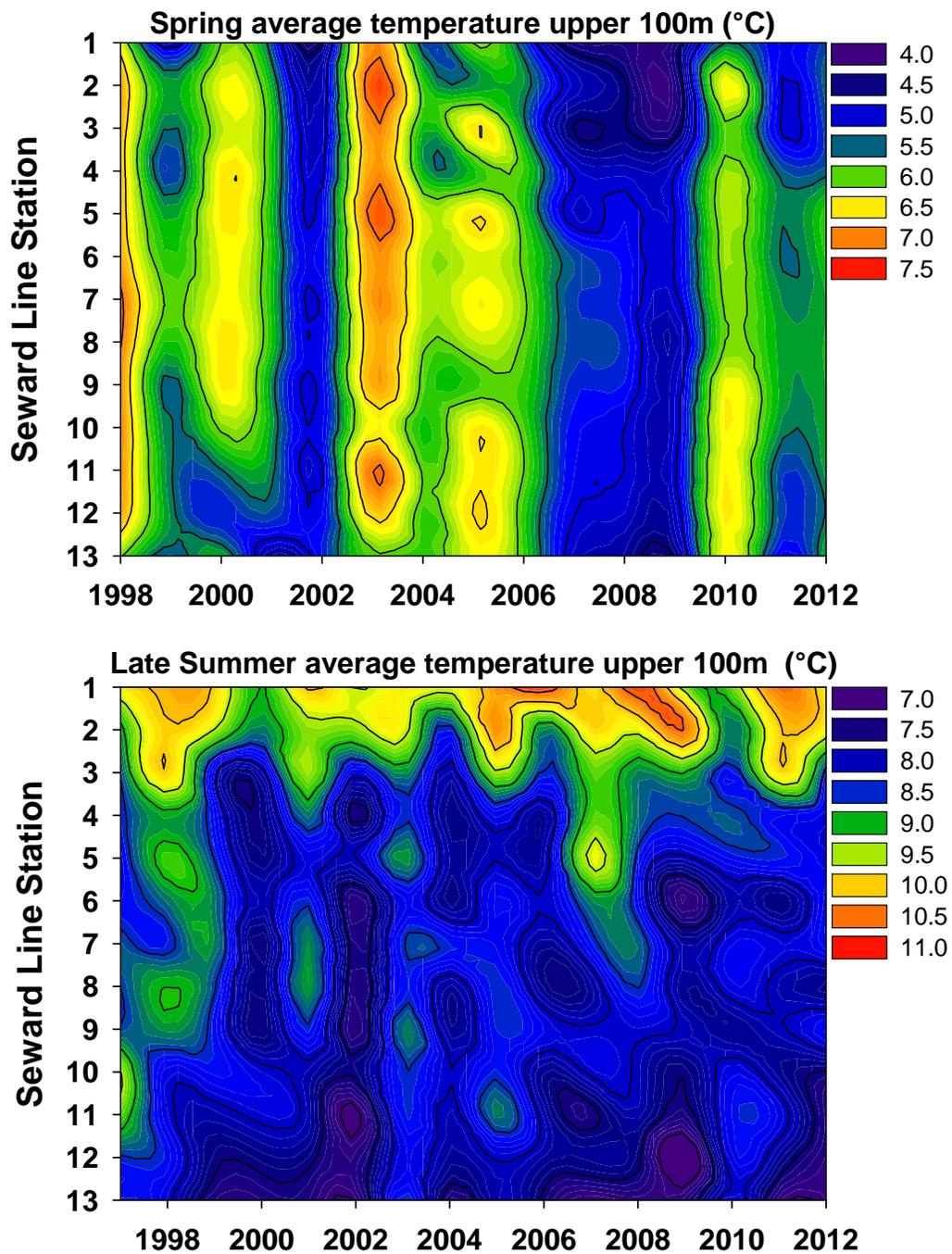
**Figure 2:** Mean water temperatures integrated to 100 m for spring (top) and late summer (bottom) along the Seward Line, northern Gulf of Alaska.

Temperatures during the spring cruise were generally consistent across the shelf, with slight interannual fluctuations from 0-100 m. Relatively warmer years in this paper are categorized with a mean >5 °C and occurred in 2003, 2004, 2005, 2006 and 2010 while relatively colder years (mean <5 °C) were during 2002, 2007, 2008, 2009 and 2011. Temperature during 2001 was neutral but community characteristics were similar to cold years and thus accordingly grouped. An anomalously warm spring occurred in 2003 and anomalously colder springs in 2002, 2007 and 2008 (Janout *et al*., 2010). During late summer, a nearshore and offshore temperature pattern existed partly due to the inner ACC, where there was a mean difference of 1 °C in warmer, fresher waters closer to the coast compared to colder waters at outer shelf stations.

**Larvacean abundance, biomass and community analysis**

A seasonal difference in relative species composition occurred (see below). Anomalously warm springs contributed to greater abundances of the temperate species *F. pellucida* at outer shelf stations (Fig. 3,4) while colder springs favored *O. labradoriensis* (Fig. 3,4).
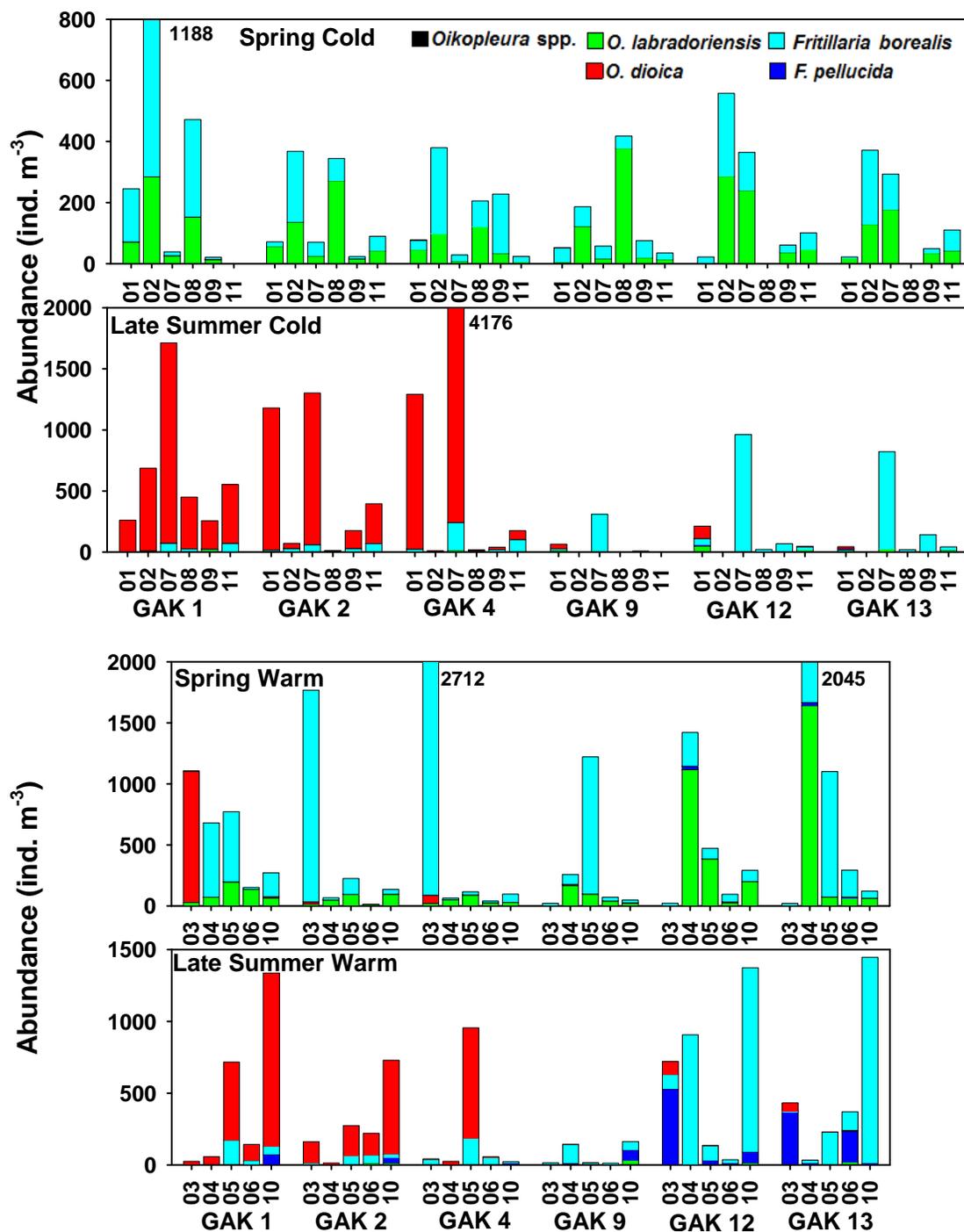
**Figure 3:** Abundance (ind. m$^{-3}$) of the major larvacean species from the 53-µm nets along the Seward Line, Gulf of Alaska. Graphs are separated between spring and late summer and between cold and warm years.

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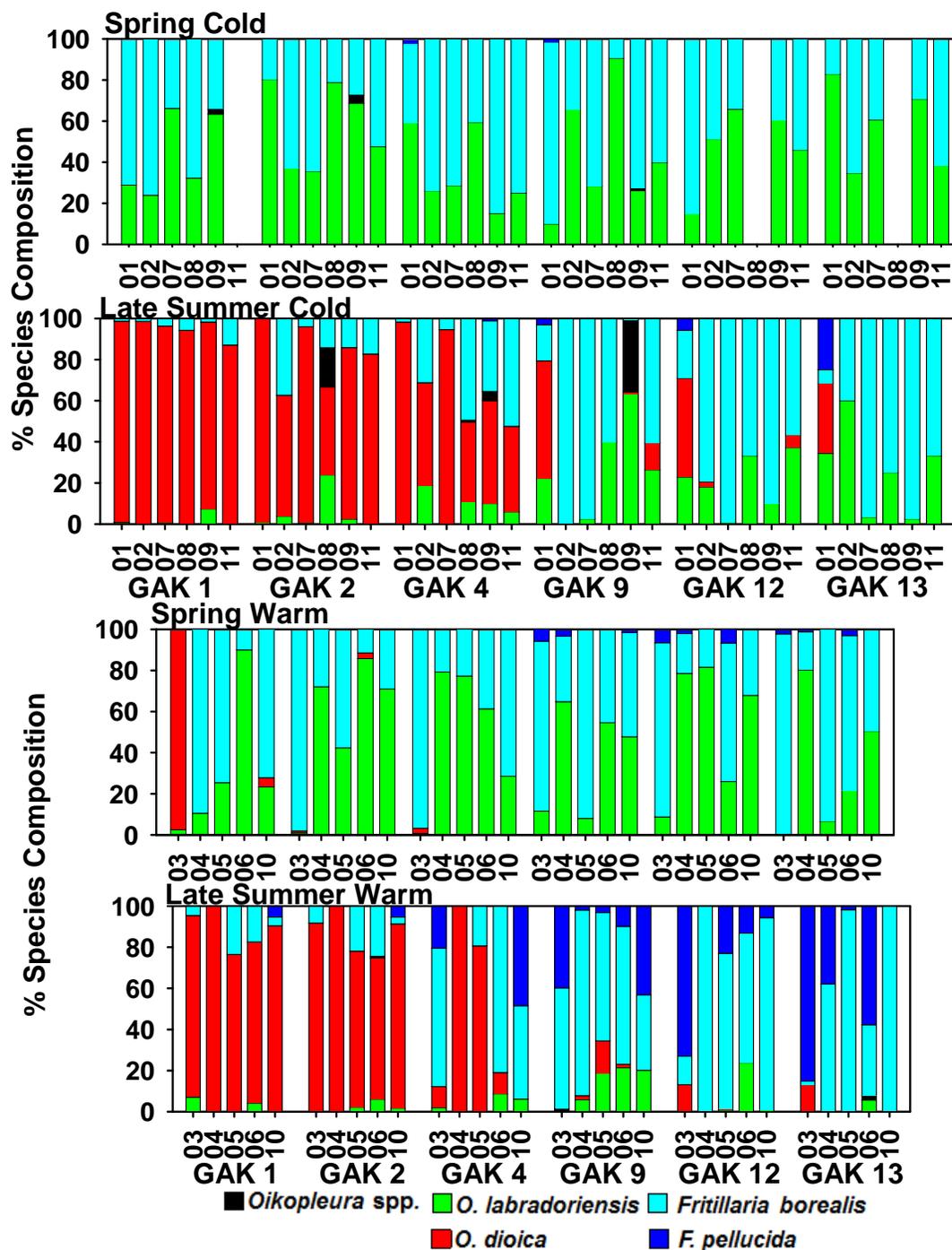


**Figure 4:** The abundance as percent species composition of the major larvacean species from the 53-μm nets along the Seward Line, Gulf of Alaska. Graphs are separated between spring and late summer and further between cold and warm years.

However, no correlations (Pearson correlation: p>0.05) were found to total larvacean abundance or species abundance and the PDO, NPGO or MEI indices during spring or late summer. Species distributions were affected to different degrees by environmental variables (Table 2).

**Table 2**: Relationship among larvacean species abundance (log ind. m$^{-3}$) and environmental variables along the Seward Line using Pearson correlation.

| Species | Temperature | Salinity | Chl *a* | Pooled season |
|---|---|---|---|---|
| *Oikopleura labradoriensis* | -0.63*** | n/s | 0.35*** | spring & late summer |
| *O. dioica* | 0.65*** | -0.71*** | 0.40** | late summer |
| *Fritillaria borealis* | -0.22* | n/s | n/s | spring & late summer |

n/s represents not significant. p<0.05* p<0.01** p<0.001***

*Oikopleura labradoriensis* and *F. borealis* abundance were negatively related to temperature; they co-occurred seasonally and in higher abundance during the spring (paired samples Wilcoxon test: p<0.05) when waters were colder with their abundances peaking at 1600 ind. m$^{-3}$ and 2600 ind. m$^{-3}$, respectively (Fig. 3).

The larvacean *O. dioica* occurred in highest abundance during late summer relative to spring (paired samples Wilcoxon test: p<0.05) (Fig. 3,4). During this time, *O. dioica* abundance was positively related to temperature and chlorophyll-*a,* but negatively related to salinity (Table 2), and had a maximum abundance at nearshore stations of up to 3900 ind. m$^{-3}$. *Fritillaria pellucida* was found in nine samples during warm springs, and two samples during cold springs (Fig. 3,4). *Fritillaria pellucida'*s maximum abundance of 530 ind. m$^{-3}$ occurred during the anomalously warm year of 2003. The larvacean *Appendicularia sicula* was present in seven samples during warmer temperatures at outer shelf stations. Biomass reflected the observed patterns of abundance: the larger *O.*

*labradoriensis* dominated in the spring (Fig. 5) with a mean of $0.57 \pm 0.29$ mg DW m$^{-3}$ (Table 3).
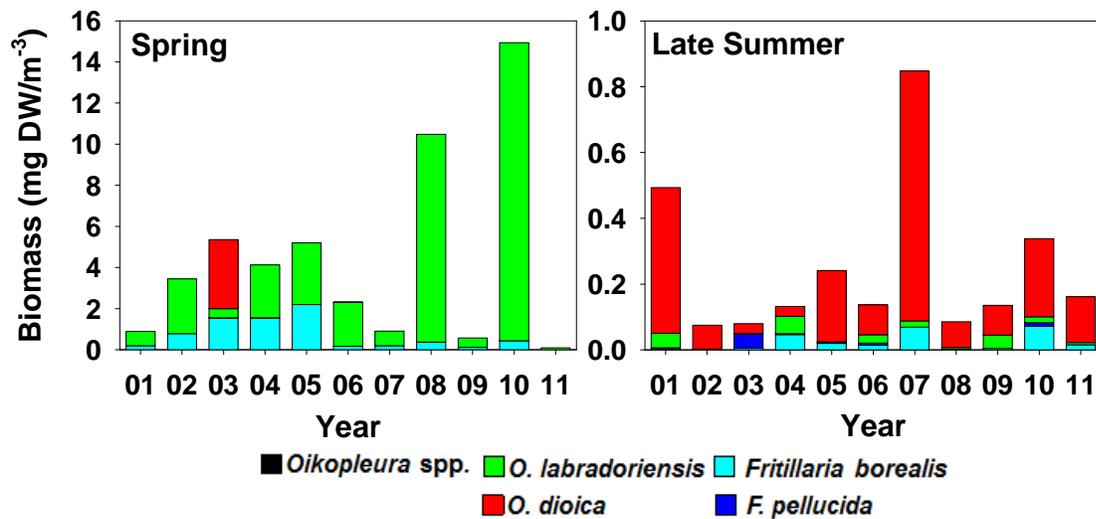


**Figure 5:** Mean biomass (mg DW/m$^{-3}$) of larvaceans during spring and late summer collected in the 53-μm nets along the Seward Line, Gulf of Alaska. Note the use of different scales for each season.

**Table 3**: Abundance and biomass of larvacean and pteropod species along the Seward Line collected over the 11 year time period (2001-2011) by the 53-µm mesh nets. Mean=arithmetic mean; CI= ± 95% confidence interval. Dashes (--) signify biomass is < 0.01.

| | Spring | | | | Late Summer | | | |
|---|---|---|---|---|---|---|---|---|
| | Abundance (ind. m$^{-3}$) | | Biomass (mg DW m$^{-3}$) | | Abundance (ind. m$^{-3}$) | | Biomass (mg DW m$^{-3}$) | |
| species | mean | ±CI | mean | ±CI | mean | ±CI | mean | ±CI |
| *Oikopleura labradoriensis* | 124 | 63.0 | 0.57 | 0.29 | 6.37 | 2.13 | 0.02 | 0.01 |
| *O. dioica* | 18.6 | 34.1 | 0.05 | 0.10 | 245 | 145 | 0.20 | 0.11 |
| *Fritillaria borealis* | 210 | 110 | 0.10 | 0.05 | 125 | 70.9 | 0.02 | 0.01 |
| *F. pellucida* | 1.36 | 1.28 | -- | -- | 22.5 | 20.3 | -- | -- |
| *Appendicularia sicula* | 0.11 | 0.19 | -- | -- | 0.12 | 0.12 | -- | -- |
| **Larvacean total** | **353** | **134** | **0.72** | **0.31** | **390** | **160** | **0.25** | **0.11** |
| *Limacina helicina* | 217 | 77.5 | 0.83 | 0.22 | 478 | 215 | 1.11 | 0.32 |

Late summer biomass was mostly *O. dioica* (Fig. 5), which had a mean of 0.20 ± 0.11 mg DW m$^{-3}$ (Table 3).

Seasonal differences were supported by general separation of clusters between spring and late summer sampling (Fig. 6,7).
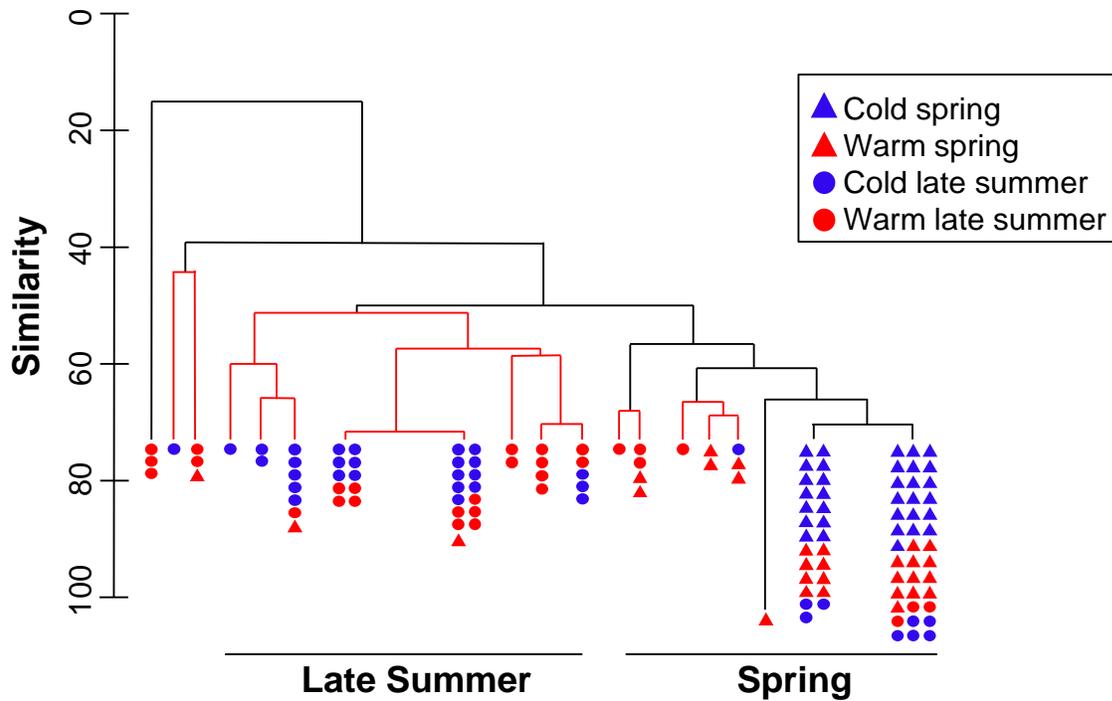
**Figure 6:** Dendrogram based on Bray Curtis similarity index of the larvacean community in the 53-µm nets along the Seward Line, Gulf of Alaska, as 4$^{th}$ root transformed abundance (ind. m$^{-3}$). Symbols represent stations. Warm years consist of 2003 to 2006 and 2010. Cold years are 2001, 2002, 2007 to 2009 and 2011. Black lines indicate significant difference between clusters, while red lines are not significant. Clusters of greater than ~ 74% similarities are not shown.
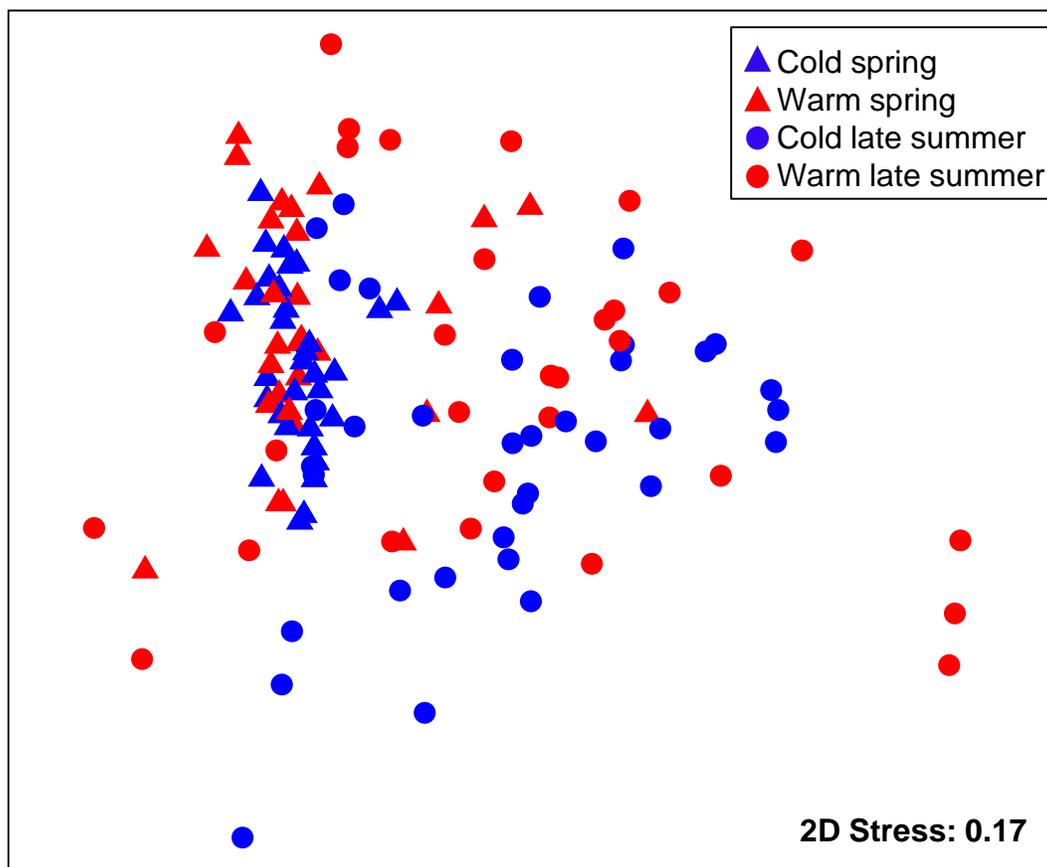
**Figure 7:** Bray Curtis similarity index as an nMDS plot of the larvacean community in the 53-µm nets along the Seward Line, Gulf of Alaska, using 4$^{th}$ root transformed abundance (ind. m$^{-3}$). Symbols represent stations. Warm years consist of 2003 to 2006 and 2010. Cold years are 2001, 2002, 2007 to 2009 and 2011. Groups used in analysis are *Oikopleura* spp., *O. labradoriensis, O. dioica, Fritillaria borealis, F. pellucida* and *Appendicularia sicula*. When *Oikopleura* spp. is excluded stress is reduced to 0.14.

The BIO-ENV community level analysis confirmed temperature to be the single most influential explanatory variable tested of abundance patterns, and had a rank correlation of $\rho=0.36$; the addition of salinity and chlorophyll-*a* did not improve $\rho$. Collections during late summer that cluster with spring data were driven by *O. labradoriensis* longer residence during colder years. Samples collected during late summer 2004 contributed to

spatial separation of stations, probably because sampling was done in July instead of August or September. Likewise, spring samples that clustered with late summer collections arose during warm years, especially 2003, due to high abundance of *O. dioica*. Vertical distribution collected from the 505-µm mesh nets demonstrated that *Oikopleura* spp. had highest abundances at the surface, and in pockets nearshore and offshore during the spring (Fig. 8).
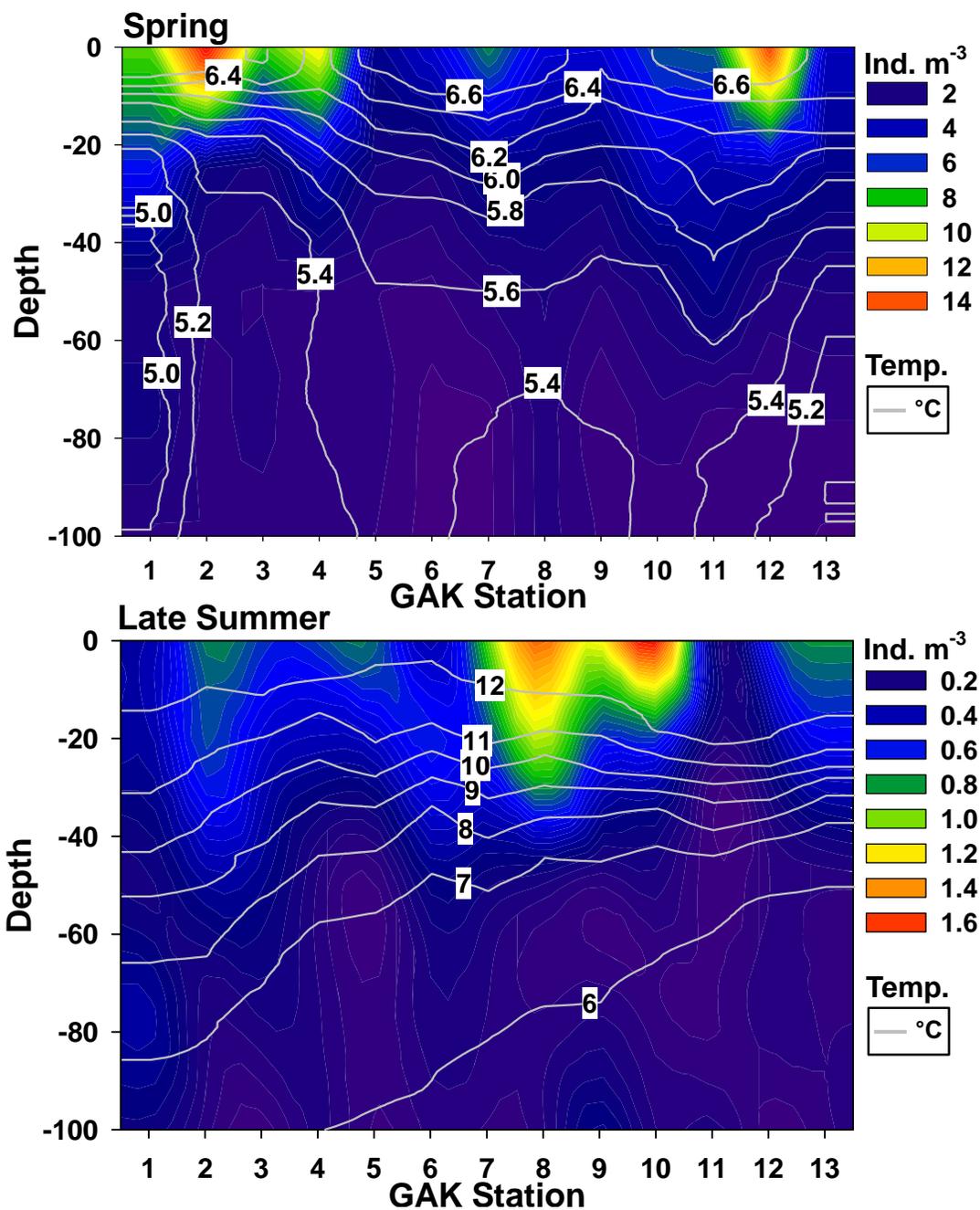
**Figure 8:** The geometric mean abundance (ind. m$^{-3}$) of *Oikopleura* spp. collected in the 505-μm nets along the Seward Line, Gulf of Alaska, separated between spring and late summer. Abundances are averaged for each GAK station among years 2001-2010 in the spring and 2001-2011 in the late summer. Note use of different scales for each graph.

**Pteropod abundance and biomass**

*Limacina helicina* abundance in the spring was driven by its relationship to temperature, which explained 28% of the variability in abundance (Fig. 9). A significant interaction effect revealed differences among year, season, and station location (Table 4).
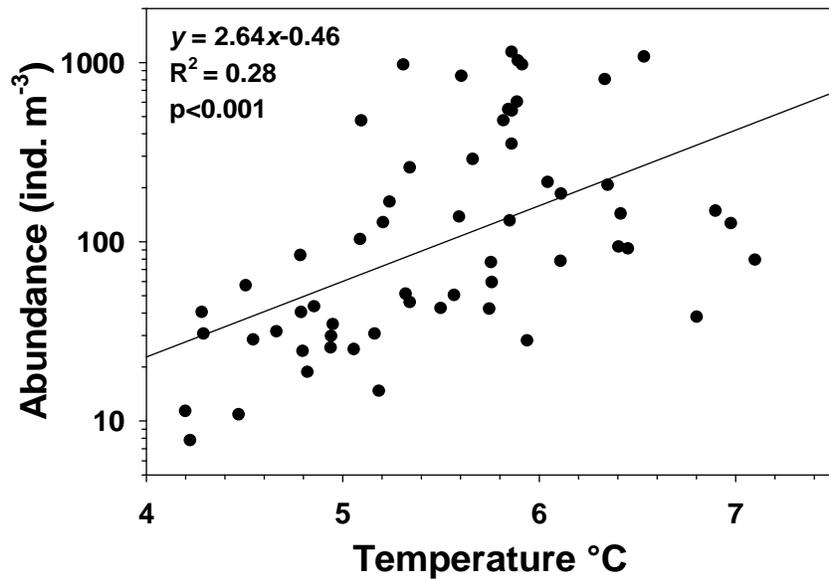


**Figure 9:** Simple linear regression between the log abundance of *Limacina helicina* collected in the 53-μm nets along the Seward Line, Gulf of Alaska, in the spring and water temperature integrated to 100 m.

**Table 4:** Influence of year, season, and station location on *Limacina helicina* abundance (log ind. m$^{-3}$) along the Seward Line, analyzed with a three-way ANOVA.

| | Year | | Season | | Location | |
|---|---|---|---|---|---|---|
| | F | P | F | P | F | P |
| **Year** | 6.8 | <0.001 | -- | -- | -- | -- |
| **Season** | 13 | <0.001 | 9.8 | 0.002 | -- | -- |
| **Location** | 5.6 | <0.001 | 4.7 | 0.032 | 0.3 | 0.57 |

Pteropod spring abundance did not vary within years between nearshore and offshore stations; however, it did vary among the warmer springs in 2004 to 2006, and the colder springs, 2001, 2002, 2007, 2008, and 2011 (Tukey test: p<0.05) (Fig. 10).
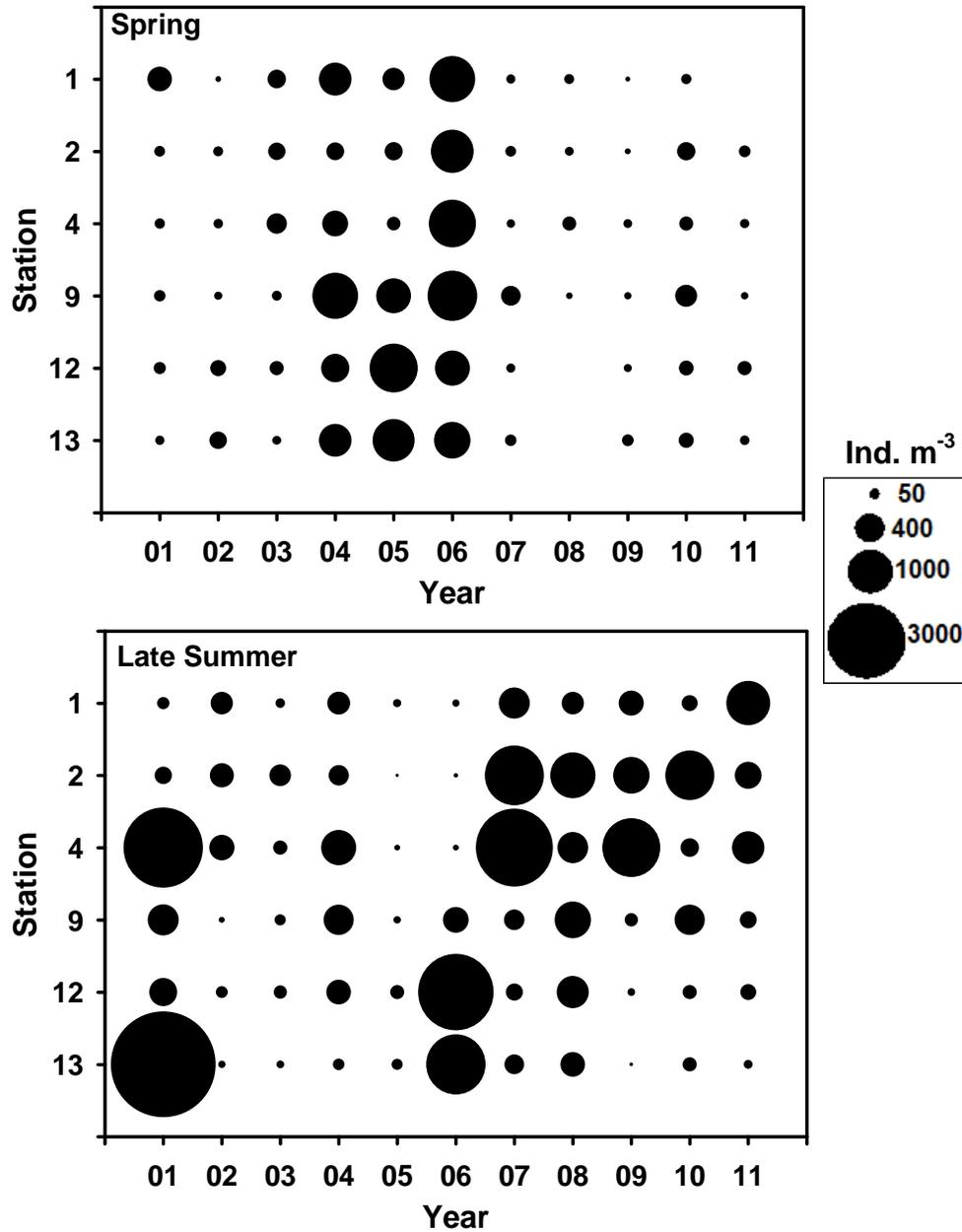
**Figure 10:** Abundance of *Limacina helicina* during spring and late summer from the 53-µm nets at selected Seward Line stations, Gulf of Alaska.[1]

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[1] Due to weather inclination spring 2008 station 12 and 13 were not sampled. Also absent is spring 2011 station 1.

Late summer displayed a different pattern, with significantly different abundances within 2006 between nearshore and offshore stations (Tukey test: p<0.05), and also differences among years due to the low abundances of 2005 and 2003 (Tukey test: p<0.05). When all data were pooled by year and season, spring abundance was not significantly greater than late summer abundance: $217 \pm 78$ ind. $m^{-3}$ and $478 \pm 215$ ind. $m^{-3}$, respectively (paired t-test: p>0.05); similarly, yearly average abundance confidence intervals overlapped (Fig. 11).
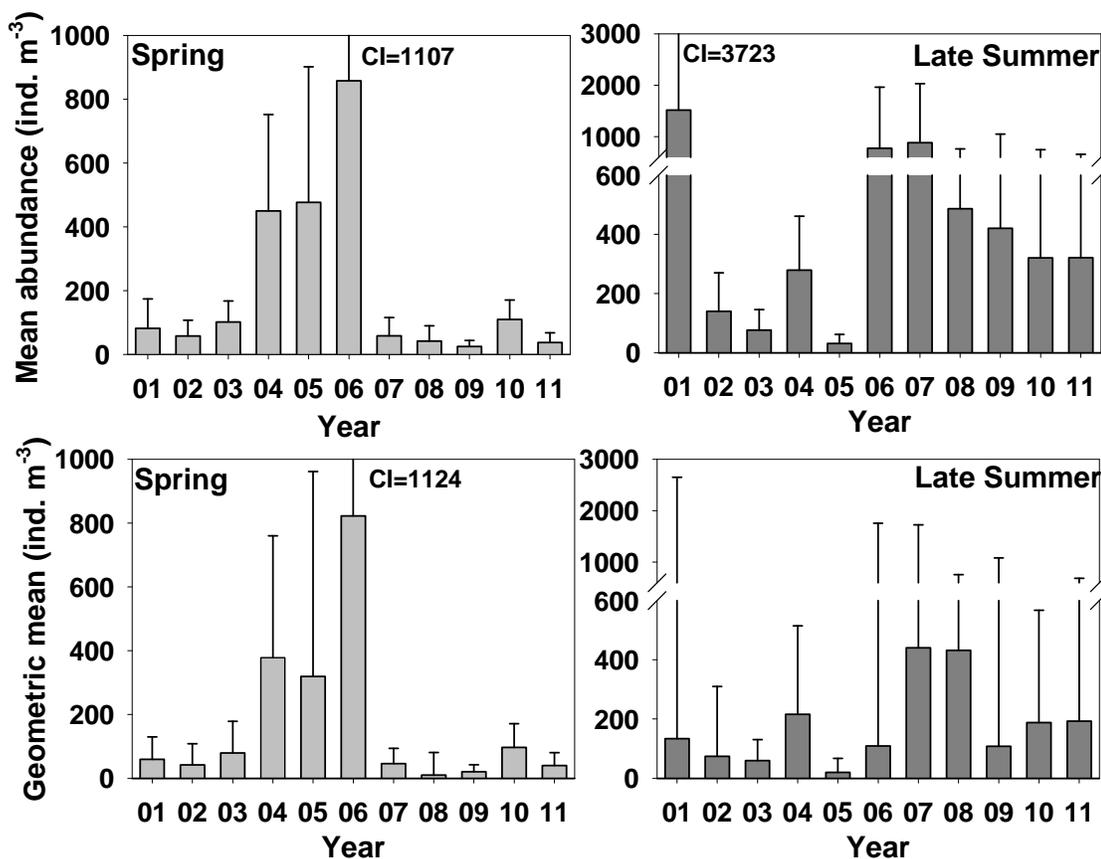


**Figure 11:** Mean *Limacina helicina* abundance (top) and geometric mean *L. helicina* abundance (bottom) along the Seward Line, Gulf of Alaska, both with + 95% confidence intervals during spring (left) and late summer (right) from the 53-μm nets. Note the different axis scales between graphs.

*Limacina helicina* biomass in the spring (0.83 ± 0.22 mg DW m$^{-3}$) was not significantly different than in the late summer (1.11 ± 0.32 mg DW m$^{-3}$) (paired t-test: p<0.05) and yearly average abundance confidence intervals overlapped (Fig. 12).
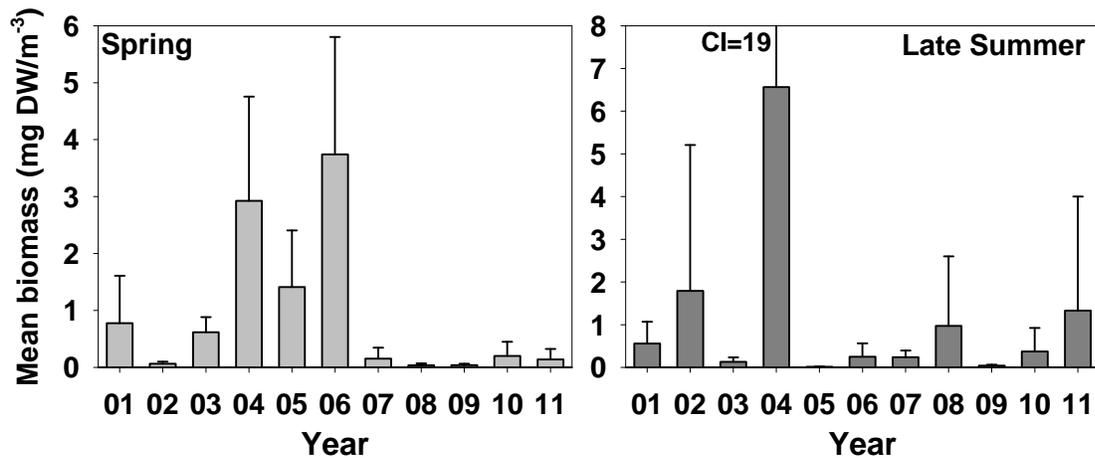


**Figure 12:** Mean biomass with + 95% CI of *Limacina helicina* during spring and late summer collected in the 53-µm nets along the Seward Line, Gulf of Alaska. Note the different axis scales between graphs.

There was a significant negative relationship between *L. helicina* spring abundance and NPGO winter anomalies (Pearson correlation: p<0.05: ρ=-0.70) (Fig. 13).
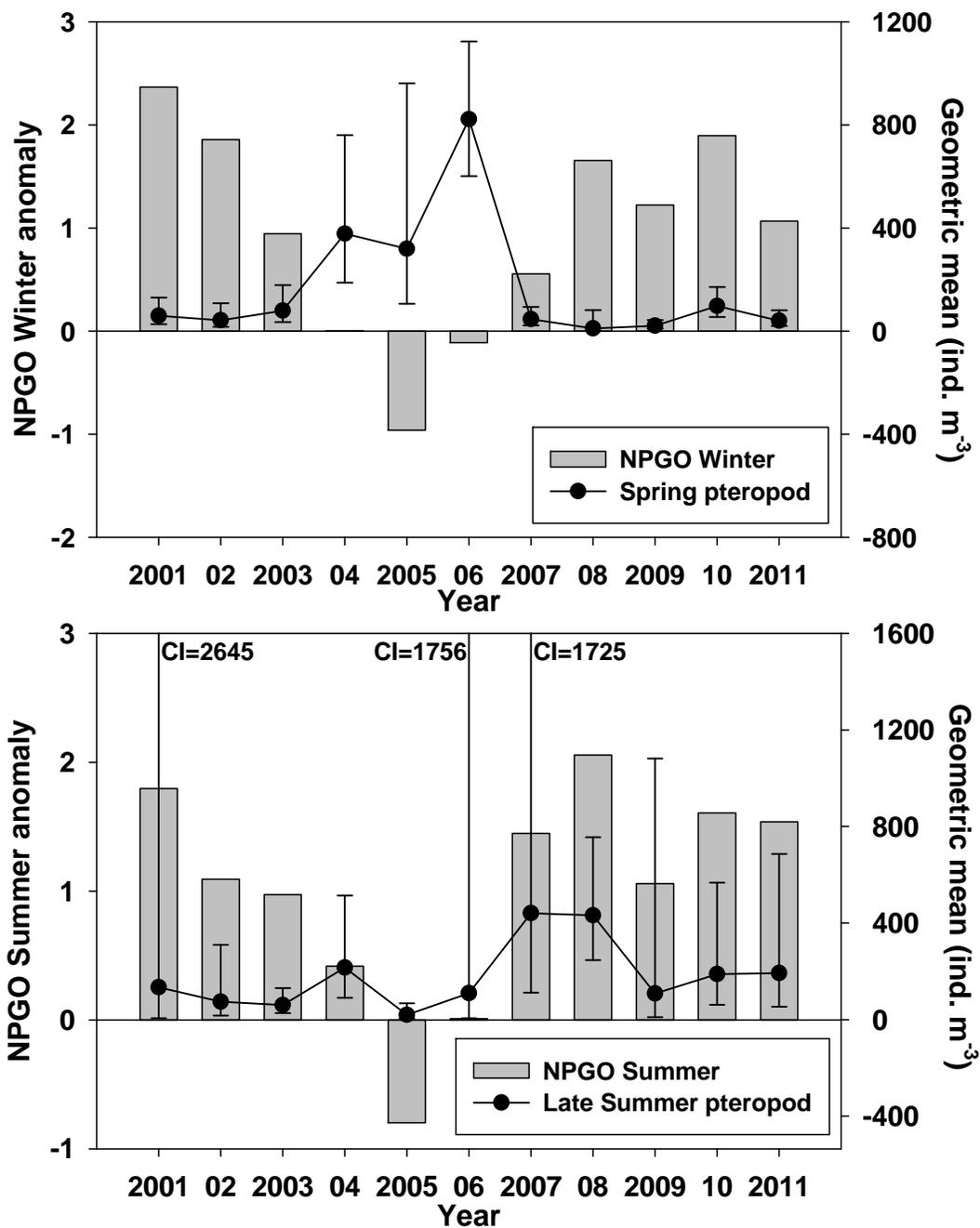
**Figure 13:** The geometric mean abundance with ± 95% CI of *Limacina helicina* during the spring along the Seward Line, Gulf of Alaska compared to the average winter NPGO (November to April), top. The geometric mean abundance with ± 95% CI of *L. helicina* during late summer compared to the average summer NPGO (May to October), bottom.

There was a significant positive relationship between *L. helicina* late summer abundance and summer NPGO anomalies (Pearson correlation: $p<0.01$: $\rho=0.78$) (Fig. 13). The PDO summer index was negatively correlated to pteropods during late summer (Pearson correlation: $p<0.05$: $\rho=-0.62$). However, no correlation was found to these indices and the abundance of pteropods in PWS during late summer (Pearson correlation: $p>0.05$). The vertical distribution of *L. helicina* collected in the 505-µm nets illustrated this species' preference for nearshore and surface locations in the GoA, with similar patterns between seasons (Fig. 14).
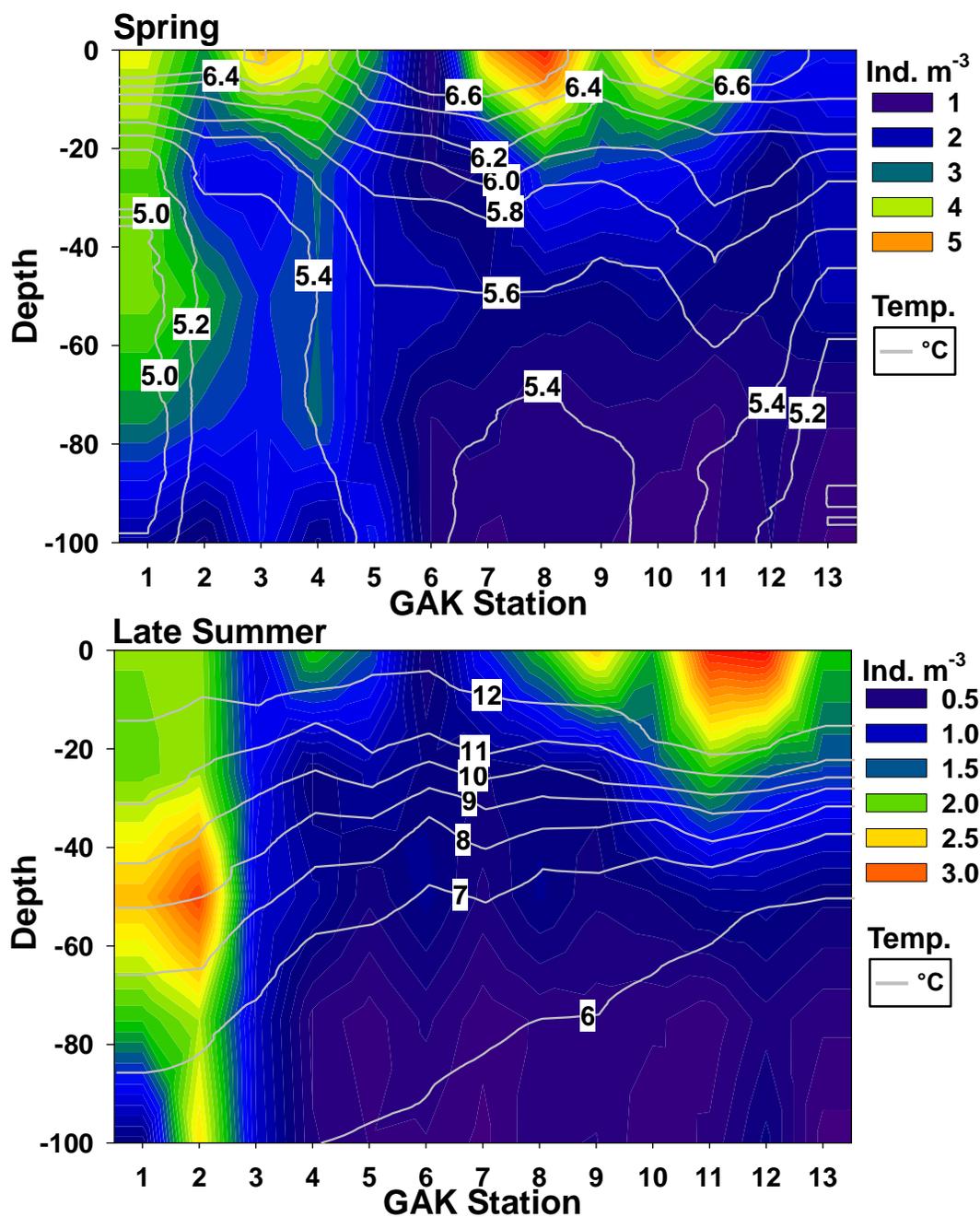
**Figure 14:** The geometric mean abundance (ind. m$^{-3}$) of *Limacina helicina* collected in the 505-μm nets along the Seward Line, Gulf of Alaska, separated between spring and late summer. Abundances are averaged for each GAK station among years 2001-2010 in the spring and 2001-2011 in the late summer. Note use of different scales for each graph.

**Net comparisons**

A comparison among net mesh sizes used for collection showed the finer mesh always collected higher abundances during both seasons for all groups (paired samples Wilcoxon test: p<0.01) (Fig. 15).
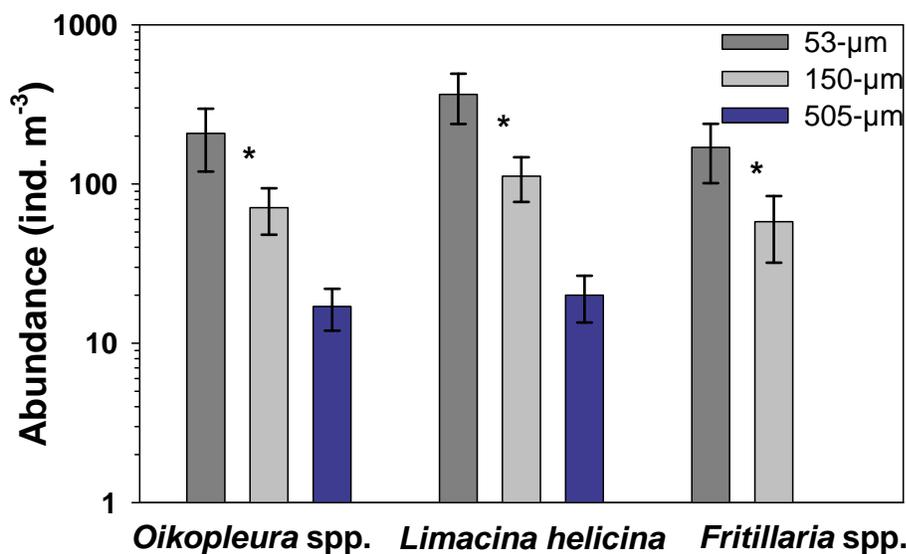


**Figure 15:** A comparison of abundance with ± 95% CI among the three different mesh sizes used on the Seward Line for each genus. Abundance is log transformed and confidence intervals are used to determine differences among the 505-μm mesh and that of the 53 and 150-μm nets. The 53-μm and 150-μm can be statistically analyzed together; an asterisk (*) indicates significant differences (paired samples Wilcoxon test; p<0.01) between these two mesh sizes.

The 505-μm net abundances could not be compared statistically with the other two nets due to differences in the time of sampling; however, they were compared using confidence intervals (Stefano, 2004) (Fig. 15). When season and year were pooled, the 150-μm net collected 34% of the abundance that the 53-μm net collected for *Oikopleura*

spp., 34% of the abundance for *Fritillaria* spp. and 30% of the abundance for *L. helicina*. In general, similar interannual trends in abundance occurred for each net size (Fig. 16).
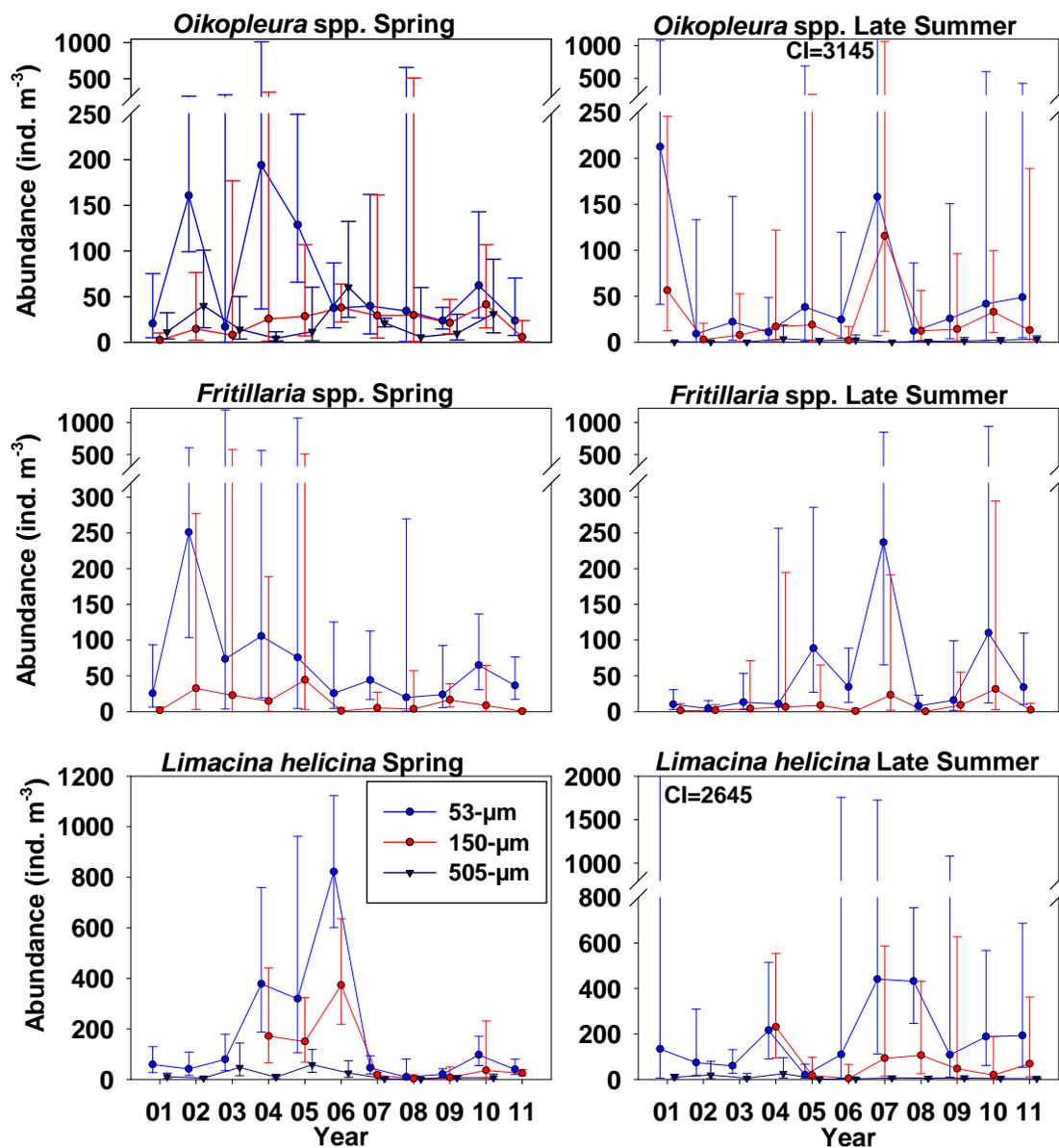
**Figure 16:** Geometric means of abundance (ind. m$^{-3}$) and ± 95% confidence intervals (back transformed values) collected in the three different sized nets of stations 1, 2, 4, 9, 12 and 13 along the Seward Line, Gulf of Alaska. Graphs are separated between spring (left) and late summer (right).[2]

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[2] Abundances are unreliable in 150-μm mesh during years 2001-2003 for *L. helicina* (Fig. 16).

When nets were pooled by year and averaged by season, the late summer *Oikopleura* spp. had over two orders of magnitude greater abundance in the 53-µm net than the 505-µm net (Table 5).

**Table 5:** Mean abundance (ind. m$^{-3}$) and ±95% confidence interval (±CI) for data along the Seward Line pooled by year of species collected with the three different mesh sizes (n/a=not available). An asterisk (*) indicates significant difference between seasons for that mesh size.

| Species | net (µm) | Spring | | Late summer | |
|---|---|---|---|---|---|
| | | mean | ±CI | mean | ±CI |
| *Oikopleura* spp. | 53 | 143 | 70 | 252 | 145 |
| | 150 | 61 | 25 | 73 | 35 |
| | *505 | 32 | 8.7 | 2.5 | 1.2 |
| *Fritillaria* spp. | *53 | 194 | 106 | 125 | 71 |
| | 150 | 65 | 39 | 41 | 27 |
| | 505 | n/a | n/a | n/a | n/a |
| *Limacina helicina* | 53 | 217 | 77 | 478 | 215 |
| | 150 | 125 | 49 | 170 | 70 |
| | 505 | 25 | 11 | 14 | 6.4 |

*Limacina helicina* mean abundance nearly doubled in the 53-µm net, progressing from spring to late summer, with an opposite pattern in the 505-µm net. There was no significant difference in *L. helicina* abundance between seasons (paired t-test: p>0.05) in the 505-µm net, 150-µm net or the 53-µm net (Table 5). Notably, there was an increase of *L. helicina* abundance from spring to late summer in the smaller nets, when data were not pooled by year (ANOVA: p<0.05) (Table 4). *Fritillaria* spp. showed a significant difference between spring and late summer within the 53-µm net only (paired t-test: p<0.05) (Table 5).

**Percent pink salmon survival**

Significant relationships were not found (p>0.05) with the groups collected in the 53-µm nets and percent pink salmon survival, and relationships were not improved with larger mesh sizes utilized on the Seward Line. However, the *L. helicina* abundance from the 505-µm net during late summer within PWS stations, where the salmon smolts are released, explained 30% of the variability in percent pink salmon survival (p<0.05: $R^2$=0.30: F=5.2). The annual or seasonal indices, PDO and NPGO, did not affect the percent pink salmon survival (Pearson correlation: p>0.05); however, the MEI summer average was correlated (Pearson correlation: p<0.05: ρ=0.57).

**Discussion**

**Larvaceans**

We found that the larvacean community in the Gulf of Alaska was dominated by three species: *O. labradoriensis* that occurred primarily in spring, *O. dioca* that occurred during late summer, and *F. borealis* that occurred throughout both seasons but more so in spring. *Fritillaria pellucida* and *A. sicula* occurred irregularly in warmer summers. In an extensive review of the North Pacific (Tokioka, 1960), only two species, *O. labradoriensis* and *F. borealis* f. *typica*, occurred in samples collected in the subarctic. Samples taken in the mixing area between the subarctic and warm water contained six species, predominantly *O. longicauda* (in warmer areas) and *O. labradoriensis*. Collections within the Japan Sea found *F. borealis* f. *typica* and *O. labradoriensis* to be abundant during the spring (Shiga, 1985). The subarctic larvacean *O. labradoriensis* distribution was associated with colder water, often residing at depth, whereas the warmer water larvaceans *O. longicauda*, *O. fusiformis*, and *O. dioica* often occurred in the warmer upper layers during late autumn (Shiga, 1985). Seven species were identified in Volcano Bay, Japan (Shiga, 1985), 21 species in Toyama Bay, Japan Sea (Tomita *et al*., 2003), and 21 species in the Kuroshio Current (Hidaka, 2008), while only three dominant species occurred in Conception Bay, Newfoundland (Choe and Deibel, 2008), and two dominant species in the Chukchi Sea (Questel *et al*., 2013). In the Arctic, there were three prominent cold water species: *O. labradoriensis*, *O. vanhoeffeni*, and *F.*

*borealis* f. *typica*, with observations of *F. polaris* (Fenaux *et al.*, 1998). The GoA (five species) composition was more characteristic of the colder waters of sub-arctic Conception Bay, having less species than the northeastern Pacific-around Japan, where even tropical species occurred sporadically. A comparison of abundance with other studies in the North Pacific was hampered by differences in mesh sizes used for collection; with most studies being done with 100-μm mesh nets (Shiga, 1985; Tomita *et al.*, 2003; Sato *et al.*, 2008) that extrude perhaps half to two-thirds of the community numerically based on my net comparisons.

   *Fritillaria borealis* f. *typica* was most abundant in winter months around Japan, with a maximum abundance of 201 ind. m$^{-3}$ in February in Toyoma Bay (Tomita *et al.*, 2003), and a maximum of 1177 ind. m$^{-3}$ in March in Volcano Bay (Shiga, 1985), whereas the GoA maxima was 2625 ind. m$^{-3}$ in May. In Conception Bay, *F. borealis* peaked in abundance during July with 526 ind. m$^{-3}$ in the surface layer (0-30 m) and 639 ind. m$^{-3}$ in August from 30-100 m. Within the Chukchi Sea (sampled with 150-μm mesh), *F. borealis* average interannual abundance from 2008 to 2010 was 898 ind. m$^{-3}$, 3809 ind. m$^{-3}$ and 1425 ind. m$^{-3}$, respectively (Questel *et al.*, 2013). *Fritillaria pellucida* was found in high abundance within the Kuroshio Current (Hidaka, 2008), where it might be transported into the GoA. *Fritillaria* species in general are present during mixed water column conditions (López-Urrutia *et al.*, 2005).

   Maximum abundance of *O. dioica* occurred in June with 50 ind. m$^{-3}$ in Toyoma Bay (Tomita *et al.*, 2003), and in September to December in Volcano Bay, which had a maxima of 243 ind. m$^{-3}$ (Shiga, 1985). In the GoA, *O. dioica* reached 3934 ind. m$^{-3}$ during September. There were exceedingly high abundances in Tokyo Bay of *O. dioica*, 20,000 ind. m$^{-3}$ (Sato *et al.*, 2008) and within the Sea of Japan, 53,200 ind. m$^{-3}$ (Uye and Ichino, 1995). It is notable that *O. dioica* is the most euryhaline member of this genus (i.e. Sato *et al.*, 2008), and prevailed in coastal waters (Fenaux *et al.*, 1998), consistent with our observations of its preference for the inner GoA shelf, where the ACC dominated during summer.

*Oikopleura labradoriensis* did not contribute significantly to abundance within Toyoma Bay (Tomita *et al*., 2003). Within Volcano Bay, *O. labradoriensis* was largely confined to winter months, with highest abundances (216 ind. m$^{-3}$ ) during March (Shiga, 1985). *Oikopleura labradoriensis* was the most abundant species in the Bering Sea and reached 328 ind. m$^{-3}$ within the Alaska gyre collections (Shiga, 1982). *Oikopleura labradoriensis* abundance peaked in May in the GoA (1640 ind. m$^{-3}$), followed by a near absence during late summer. In Conception Bay, *O. labradoriensis* peaked in abundance in October with ~900 ind. m$^{-3}$ from 0-30 m and ~450 ind. m$^{-3}$ from 30-100 m, but none were collected in the surface layer during summer, May to August (Choe and Deibel, 2008). *Oikopleura vanhoeffeni*, another cold water species, replaced *O. labradoriensis* in Conception Bay (Choe and Deibel, 2008) and in Arctic waters (Questel *et al*., 2013). Lower abundances of *O. labradoriensis* during late summer in the GoA may be due to their residence at depths below collection or displacement to outer oceanic waters, both locations of colder temperature. Another possibility is the completion of their spawning season. *Oikopleura vanhoeffeni* in Bering shelf water had a different vertical distribution during late summer, with juveniles near the surface and adults at deeper layers (Shiga, 1993).

Minimum temperatures in the GoA (5 to 6 °C) occurred in the spring, when the shelf had a constant temperature distribution (Janout *et al*., 2013). The spring larvacean community was dominated by species recognized by having an affinity for cold-water (Bückmann and Kapp, 1975; Fenaux *et al*., 1998). The large-bodied *O. labradoriensis* was at its highest abundance in spring, capitalizing on the productivity of large cells (Deibel and Lee, 1992). Seasonal warming, as well as snow melt that entered the GoA and intensified the ACC, created a niche for warm water, low saline-tolerant neritic species, such as *O. dioica*. Warming and snow melt could possibly displace *O. labradoriensis* into deeper and more offshore waters within the GoA, as has been documented in Volcano Bay (Shiga, 1985). Populations in the Bering Sea are presumed to overwinter as pre-mature stages and spawn as adults in the following spring to summer (Shiga, 1982). In Conception Bay, Newfoundland, there was a succession from larger

sized larvaceans that occurred in the spring to smaller sized species later in the year (Choe and Deibel, 2008), similar to results in the GoA, where larger *O. labradoriensis* occurred in the spring compared to the smaller *O. dioica* in late summer. *Fritillaria borealis* is a cosmopolitan species, although forma *typica* is characteristic of colder waters. Consistent with our observations in the GoA, it occurred in higher abundances during the spring and mainly in cooler outer shelf waters during late summer. Similarly, in north-western Pacific waters around Japan, there were peaks in *F. borealis* abundance during the winter/spring, but some animals also occurred throughout all months from January to December (Shiga, 1985).

Community succession can also be related to food size preference (Choe and Deibel, 2008; Lombard *et al.*, 2009a). Under productive bloom conditions the GoA is dominated by >8 µm cells comprising diatoms, ciliates, and dinoflagellates (Strom *et al.*, 2001). Larger *Oikopleura* species are capable of digesting larger particles, including 48-µm in diameter *Distephanus speculum* and diatom chains >40-µm long (Deibel and Turner, 1985). The concentration of *Oikopleura* spp. near the surface in late summer may be reflective of an area of high food concentration since chlorophyll-*a* maxima are associated with the pycnocline during this time (Strom *et al.*, 2006). *Oikopleura dioica* was adapted to late summer conditions when particles were smaller and at lower concentrations (Troedsson *et al.*, 2007). Interestingly, *O. labradoriensis* and *F. borealis* co-occurred in the GoA during the spring time, yet there was a clear separation in distance (nearshore versus offshore) between *O. dioica and F. borealis* during the late summer. Considering that *F. borealis* and *O. dioica* feed on similar sized particles (Fernández *et al.*, 2004), there could be competition for food between the two species, in addition to their different thermal preferences.

Oceanographic variability can concentrate or disperse plankton. The zooplankton community in the Northern California Current (NCC) contained warm water species from years 2004 to 2006 (Keister *et al.*, 2011) similar to the years *F. pellucida* and *A. sicula* were present in the GoA (2003 to 2006). The Davidson Current travels in the opposite direction to the NCC during winter months (Reid and Schwartzlose, 1962) and could

transport these warm-water species to the north and into the GoA. Warm-water species can also be advected into the subarctic by the equatorial Pacific water traveling northward, especially when the bifurcation between the Alaska Current and the NCC occurs most northerly (Batten and Freeland, 2007; Cummins and Freeland, 2007).

**Pteropods**

The pteropod community in the Gulf of Alaska was dominated by the single species *Limacina helicina* that showed sometimes large seasonal and interannual variability. Sampling in the northeast Pacific for pteropods north and south of Vancouver Island and out to Ocean Station Papa located within the Alaska gyre showed high abundances of *L. helicina* during all months of the year, where outer oceanic waters had greater abundances than inner stations, and seasonal maximum of both abundance and biomass during spring (Mackas and Galbraith, 2012). In the GoA, maxima occurred in the late summer (September), with an average density of 478 ind. $m^{-3}$, but this seeming disparity may arise from differences in mesh sizes, 230-µm verses 53-µm, respectively. In colder Arctic water, the time of peak abundance was similar to that in the subarctic GoA in the Chukchi (July to October) with 525 ind. $m^{-3}$ collected with 150-µm mesh net (Questel *et al.*, 2013) and to the northeast of Svalbard (August) with 114 ind. $m^{-3}$ sampled with 180-µm mesh net (Blachowiak-Samolyk *et al.*, 2008). The presence of *L. helicina* in Arctic water during winter (March) was demonstrated when sampled in the Barents Sea, 5 m below the ice underside, where abundance reached 179 ind. $m^{-3}$ collected with 50-µm mesh gauze (Werner, 2005). Previous work in the upper 50 m of PWS demonstrated the relative importance of *L. helicina* to the plankton community. There, juveniles were the most abundant behind *Pseudocalanus* species during June and remained in the top 10 taxonomic groups in July, September, and December (Cooney *et al.*, 2001b). Samples off southern California and off central California contained more species (e.g. *Limacina* spp., *Clio pyramidata*, *Clio* spp., *Cavolina* spp., *Desmopterus pacificus*, *Corolla spectabilis*, *Cymbulia peroni*) than found in the Seward Line. Heteropods were also found off California, but were less abundant and not discussed (Ohman *et al.*, 2009). Warmer

waters typically contain a higher number of pteropod species, yet colder waters contain higher numbers of individual species (Lalli and Gilmer, 1989).

Pteropod abundance varied among and within years, seasons, and nearshore versus offshore stations. This group was generally influenced during the spring by temperatures, but influenced by more complex oceanographic parameters during late summer that caused stronger dissimilarities between nearshore and offshore stations. The uncoupling between spring and late summer further illustrates the dynamic oceanography present across the shelf. This difference in physical forcing is consistent with relationships observed between pteropod abundance and the NPGO index (see below).

Temperature was significantly correlated to *L. helicina* abundance during the spring. Years with higher GoA temperatures (2003-2006, 2010) typically had higher abundances of pteropods. This is consistent with observations at Ocean Station Papa located within the Alaska gyre, where greater pteropod abundances were found in sediment traps following El Niño winters (Tsurumi *et al*., 2005). Additionally, *L. helicina* biomass was positively correlated with warm water anomalies in the northeast Pacific (Mackas and Galbraith, 2012). Higher water column temperatures during warm years should increase rates of development and accelerate spawning, as has been shown for copepods (Hirst and Bunker, 2003; Bonnet *et al*., 2009), and thereby produce more veligers earlier in the year. Veligers produced from *L. retroversa* during the spring and summer have faster growth and show sexual development at smaller sizes than those spawned in the fall, which must survive through the winter months (Lalli and Gilmer, 1989).

The pteropod *L. helicina* was negatively correlated to the NPGO in the winter, but positively correlated during summer. This index is associated with basin wind-driven upwelling and horizontal advection (Di Lorenzo *et al*., 2008). The NPGO correlation to pteropod abundance was stronger than the PDO, possibly because the limited period of data collection, and the NPGO had greater amplitude than the PDO during the last decade (Cummins and Freeland, 2007; Di Lorenzo *et al*., 2008). When the NPGO is positive there is an increase in transport within the Alaska Current and the GoA gyre. Within the

GoA, the NPGO was positively related to near bottom temperature at GAK 1 (200-250 m) (Danielson *et al.*, 2011).

During the spring there was a higher pteropod abundance during a negative NPGO and a lower abundance during a positive NPGO. Conversely, late summer pteropod abundance was positively related to NPGO anomalies. The opposite correlation between seasons is due to the difference in pteropod abundance and not to the signal of the NPGO, which is similar during both seasons for the years analyzed. *Limacina helicina* across-shelf similarity in abundance during the spring is likely more representative of the GoA due to the coherence of the weather patterns, which occur during the winter to instigate the timing of the phytoplankton bloom. Late summer is more variable due to advection and differences in wind patterns, occasionally causing intermittent upwelling. Other North Pacific time series have found *L. helicina* biomass negatively related to the annual NPGO (Mackas and Galbraith, 2012).

In our study, typically the peak abundance of pteropods occurred during late summer (August and September), likely as a consequence of spring spawning. Egg release occurs once hermaphroditic females have developed and are typically larger (Lalli and Gilmer, 1989), with female *L. helicina* in the Arctic becoming sexually mature at 800-µm (Kobayashi, 1974). Larger pteropods were more prominent in the 505-µm mesh early in the spring within the GoA, and larger animals likely had much higher per capita egg production than smaller animals (Lalli and Gilmer, 1989). *Limacina helicina* abundance from the 505-µm mesh were elevated and vertically dispersed in nearshore waters beneath the ACC, but centered in surface waters near the shelf break, possibly reflecting food availability since summer diatom blooms can occur within the ACC (Strom *et al.*, 2006). From May to early autumn, there is also an onshore movement of saline slope waters at ~50 m or greater (Royer, 1975; Weingartner *et al.*, 2005); both events may have influenced distribution. In the Arctic, *L. helicina* may have a 1 to 2 year life cycle (Kobayashi, 1974; Gannefors *et al.*, 2005; Lischka and Riebesell, 2012). Allowing for a typical $Q_{10}$ of ~2-3 on growth rate (e.g. Liu and Hopcroft, 2006a,b), warmer temperatures in the GoA should produce multiple generations per year. At Ocean

Station P, highest abundances in sediment traps were also typically recorded during late summer and autumn (Tsurumi *et al*., 2005).

**Relevance to higher trophic levels**

Mucus net feeders were recognized as an important trophic link, which shortcut the food web, transferring energy from small phytoplankton to larvaceans/pteropods and then to fish larvae in the NW Atlantic (Mousseau *et al*., 1998). Larvaceans have nutritional qualities reflective of the phytoplankton, which they feed upon and often contain high amounts of critical fatty acids (Troedsson *et al*., 2005). These fatty acids are important for larval fish development, and are present in commercial species such as pink salmon (Huynh and Kitts, 2009) and Pacific coho salmon (Daly *et al*., 2010). Similarly, *L. helicina* in Svalbard waters had heterogeneity of fatty acid composition, presumably reflective of the particulates and phytoplankton that they consumed (Falk-Petersen *et al*., 2001).

In the North Pacific, pink salmon are a large contributor to fisheries production, and understanding their success has been an ongoing research topic (Parker, 1968; Willette *et al*., 2001; Miller *et al*., 2012). They are considered opportunistic feeders, but are also selective feeders with prey preferences (Auburn and Ignell, 2000). Larvaceans made up 49.8% of juvenile pink salmon stomach volume in the GoA during July, but only 12% in September (Armstrong *et al*., 2005). The high abundance of small pteropods found during late summer in this research coincide with diet studies that reported gut contents in August and September dominated by smaller pteropods (Boldt and Haldorson, 2003; Armstrong *et al*., 2005). Veligers and juveniles of *L. helicina* sampled during the summer in Kongsfjorden, Spitsbergen, had the highest lipid content relative to body size, and females showed consistently low lipid content (Gannefors *et al*., 2005) giving the smaller specimens relatively high nutritional value.

Major fluctuations in North Pacific salmon production between Washington and Alaska stocks have been related to atmospheric indices (Hare *et al*., 1999). Catch estimates for the five species of commercial salmon back to 1950 and Alaskan Pacific salmon stocks were positively correlated to the Aleutian low, ENSO, and the PDO (with

the latter being most influential), but negatively correlated with the West Coast Pacific salmon stocks (Hare *et al.*, 1999). On these longer time scales, atmospheric variability influence the stocks (Mantua *et al.*, 1997); however, the coastal GoA seems to function on shorter time scales rather than basin-scale atmospheric circulation anomalies (Stabeno *et al.*, 2004). The zooplankton community on the GoA shelf was not extremely influenced by the strong ENSO during 1997-1998 (Coyle and Pinchuk, 2003), nor was copepod abundance in Icy Strait, southeastern AK (Park *et al.*, 2004). Over the time period of our observations, pink salmon were not significantly correlated to the PDO or NPGO (although a significant correlation does occur to the MEI index), suggesting their abundance had responded to that of pteropod abundance within PWS rather than both tracking the same atmospheric signal.

The hypothesis that the abundance of these mucus net feeders across the Seward Line would explain some of the variability in the percent pink salmon survival was not supported, although a relationship did occur to pteropods within nearby PWS. Pink salmon spend their first month after ocean entry primarily within the nearshore PWS habitat (Cooney, 1993) because it provides a protective nursery in which juveniles can gain weight rapidly if the appropriate prey is present. These larger juveniles have a higher chance of surviving their first winter (Beamish *et al.*, 2004). This idea is in agreement with the significant relationship found between *L. helicina* in PWS in our data set.

The springtime zooplankton stocks within PWS were positively correlated to the Bakun Upwelling Index (BUI) also known as the Lake River Hypothesis (Cooney and Coyle, 1996). This index is associated with low zooplankton abundance during strong downwelling events outside the sound, which flushes the community out due to the ACC intrusion (Niebauer *et al.*, 1994). The opposite phase (positive BUI) was related to higher zooplankton abundance due to their continued residence within the sound. Prey availability on the shelf may be important during a negative BUI when zooplankton within PWS is low. Separate studies have documented the seasonal prevalence of pteropods and larvaceans within PWS (Cooney *et al.*, 2001b). Furthermore, we cannot preclude that salmon success is influenced by a combination of other food sources, for

example *Neocalanus* spp. (Cooney *et al*., 2001a), which are a leading biomass contributor to the GoA in the spring before they descend to diapause at depth (Coyle and Pinchuk, 2003, 2005). The availability of other food sources in PWS and the GoA, as well as predation from fish, including returning pink salmon themselves, should continue to be monitored to better establish the relative influence of these species to pink salmon returns.

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