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Interannual patterns during spring and late summer of larvaceans and pteropods in the coastal Gulf of Alaska, and their relationship to pink salmon survival

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Larvacean (=appendicularian) and pteropod (*Limacina helicina*) composition and abundance were studied with physical variables each May and late summer across 11 years (2001–2011), along a transect that crosses the continental shelf of the sub-Arctic Gulf of Alaska (GoA) 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, being present at all stations. Late summer had highest abundances of *Oikopleura 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 GoA stations.

KEYWORDS: larvacean; appendicularian; pteropod; *Limacina*; *Oikopleura*; *Fritillaria*; time series; pink salmon; mesh size

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 (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.*, 2009) 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 more 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 zooplankton in sub-Arctic 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 $p\text{CO}_2$ 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.*, 2014).

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, 2003; Sato *et al.*, 2008; and references therein), with one study in the transitional water of the Kuroshio Current (Hidaka, 2008). In contrast,

only three long-term studies in the North Pacific have reported on thecosome pteropods, finding just two dominant species, *L. helicina* and *Clio pyramidata* (Tsurumi *et al.*, 2005; Ohman *et al.*, 2009; Mackas and Galbraith, 2012). Notably, interannual and seasonal variability was not described in these latter studies, as their focus was to establish if shoaling of aragonite saturation states is affecting these taxa (Ohman *et al.*, 2009).

In summary, the abundance and biomass of both larvaceans and pteropods remains poorly established for the sub-Arctic northern Gulf of Alaska (GoA). This paper 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 (PWS), 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 work also 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, both past and future.

The trophic importance of zooplankton groups is often defined by the importance to 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 GoA have now demonstrated the importance of both *L. helicina*, and the understudied larvaceans in their diet (Boldt and Haldorson, 2003; Armstrong *et al.*, 2005, 2008); however, prevalence in diet may not necessarily ensure enhanced pink salmon survival. The zooplankton community across the GoA and in PWS supports one of the largest releases of hatchery-raised, thermally marked pink salmon (~600 million smolt released each spring) (Vercesi, 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 GoA shelf will be positively correlated to pink salmon survival.

METHOD

Study area

Variability in meteorology, bottom bathymetry and surrounding mountainous terrain contribute to the GoA's extremely productive waters across its 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, 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 favorable 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 GoA Seward Line (Coyle and Pinchuk, 2003, 2005; Liu and Hopcroft, 2006a, b, 2007, 2008; Pinchuk and Hopcroft, 2006; Pinchuk *et al.*, 2008).

The GoA has experienced large regime shifts during the late 1970s, which caused a change from shrimp and capelin dominated fisheries to that of groundfish. Atmospheric 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. Interannual variability in zooplankton abundance and biomass, particularly for crustaceans, has been correlated with these indices (Mackas *et al.*, 2001) and sea-surface temperature anomalies. With detailed observations on the mucus-net feeders over an 11-year time line, their interannual abundances can be compared with these indices too.

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 PWS (Fig. 1). From 1998 to 2004, sampling occurred six to seven 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

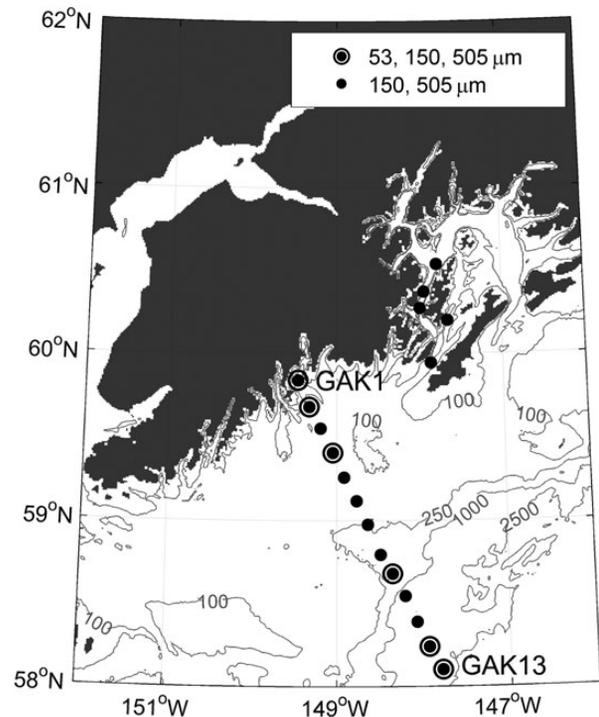


Fig. 1. The Seward Line across the northern Gulf of Alaska continental shelf from nearshore GAK 1 to offshore GAK 13. Different symbols represent analysis done with the different plankton net mesh sizes. The entire Seward Line and Prince William Sound (PWS) stations were analyzed for 150- and 505- μm samples, while the 53- μm samples were only analyzed at Stations 1, 2, 4, 9, 12 and 13. Samples within PWS were only considered for the 505- μm mesh.

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 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 ($\sim 0.5\text{ m s}^{-1}$) 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 were 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 $\sim 1\text{ m s}^{-1}$ during nighttime

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 time line (2001–2011) to observe spring, late summer 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 for 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 for both taxa were identified and measured than from the other mesh sizes. The 150- and 505- μm samples were processed at all 13 Seward Line stations, at three to five 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 ~ 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 I).

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. *L. helicina*. Pteropod size was determined by measuring shell diameter. Although the gymnosome *Clione limacina* was also present 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 non-parametric 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. 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*, *Oikopleura dioica* and *Fritillaria borealis*, collected in the 53- μm nets, including years 2001–2011, were log-transformed and compared with 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) based

Table I: Length–weight relationships used to determine the biomass of the dominant species

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

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).

on the location of the shelf break. 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- and 150- μm nets, which were sampled simultaneously always during daylight. 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 always 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 (CIs) 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 with 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 with the average winter index (November to April) and late summer cruises were compared with 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. Vercesi, 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 with winter and summer indices (above) and an annual average index (January to December) under the assumption that pre- and postrelease conditions are influential.

The availability of zooplankton prey is 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 the 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 with 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 ranged from ~ 4 to 7°C in the spring to ~ 7 to 11°C in the late

summer (Fig. 2). Temperatures during the spring cruise were generally consistent across the shelf, with slight interannual fluctuations from 0 to 100 m. Relatively warmer years in this paper are categorized with a May mean greater than the long-term mean over the observation period (5.6°C) and occurred in 2003, 2004, 2005, 2006 and 2010 while relatively colder years (mean $< 5^\circ\text{C}$) were during 2002, 2007, 2008, 2009 and 2011. Temperature during 2001 was at the long-term mean, 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 with colder waters at outer shelf stations.

Larvacean abundance, biomass and community analysis

A spring and late summer difference in relative species composition occurred (see below). Anomalously warm springs contributed to greater abundances of the temperate species *Fritillaria pellucida* at outer shelf stations in both

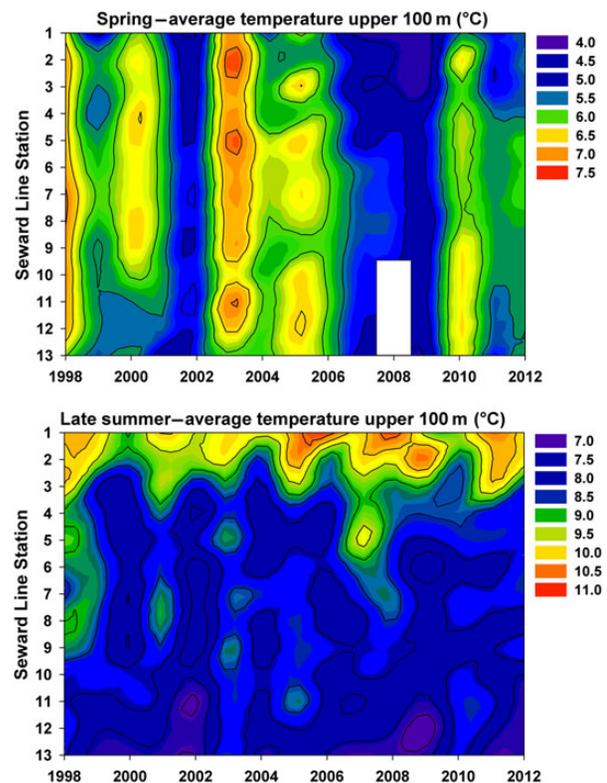


Fig. 2. Mean water temperatures integrated to 100 m for spring (top) and late summer (bottom) along the Seward Line, northern Gulf of Alaska.

spring and late summer (Figs 3 and 4), while spring temperature had no influence on abundance of *O. labradoriensis* or *F. borealis* (Figs 3 and 4). Species distributions were affected to different degrees by environmental variables (Table II). Across seasons, *O. labradoriensis* and *F. borealis* abundance were negatively related to temperature; they co-occurred during both seasons and in higher abundance during the spring (paired-samples Wilcoxon test: $P < 0.05$), with their abundances peaking at 1600 and 2600 ind m⁻³, respectively (Fig. 3). No significant correlations (Pearson correlation: $P > 0.05$) were found between total larvacean abundance or species abundance and the PDO, NPGO or MEI indices during spring or late summer.

The larvacean *O. dioica* occurred in highest abundance during late summer relative to spring (paired-samples Wilcoxon test: $P < 0.05$) (Figs 3 and 4). During this time, *O. dioica* abundance was positively related to temperature and chlorophyll-*a*, but negatively related to salinity (Table II), and had a maximum abundance at nearshore stations of up to 3900 ind m⁻³. *Fritillaria pellucida* was found in 9 samples during warm springs, and 2 samples during cold springs, as well as 18 samples during warm late summers and 4 samples during cold late summers (Figs 3 and 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

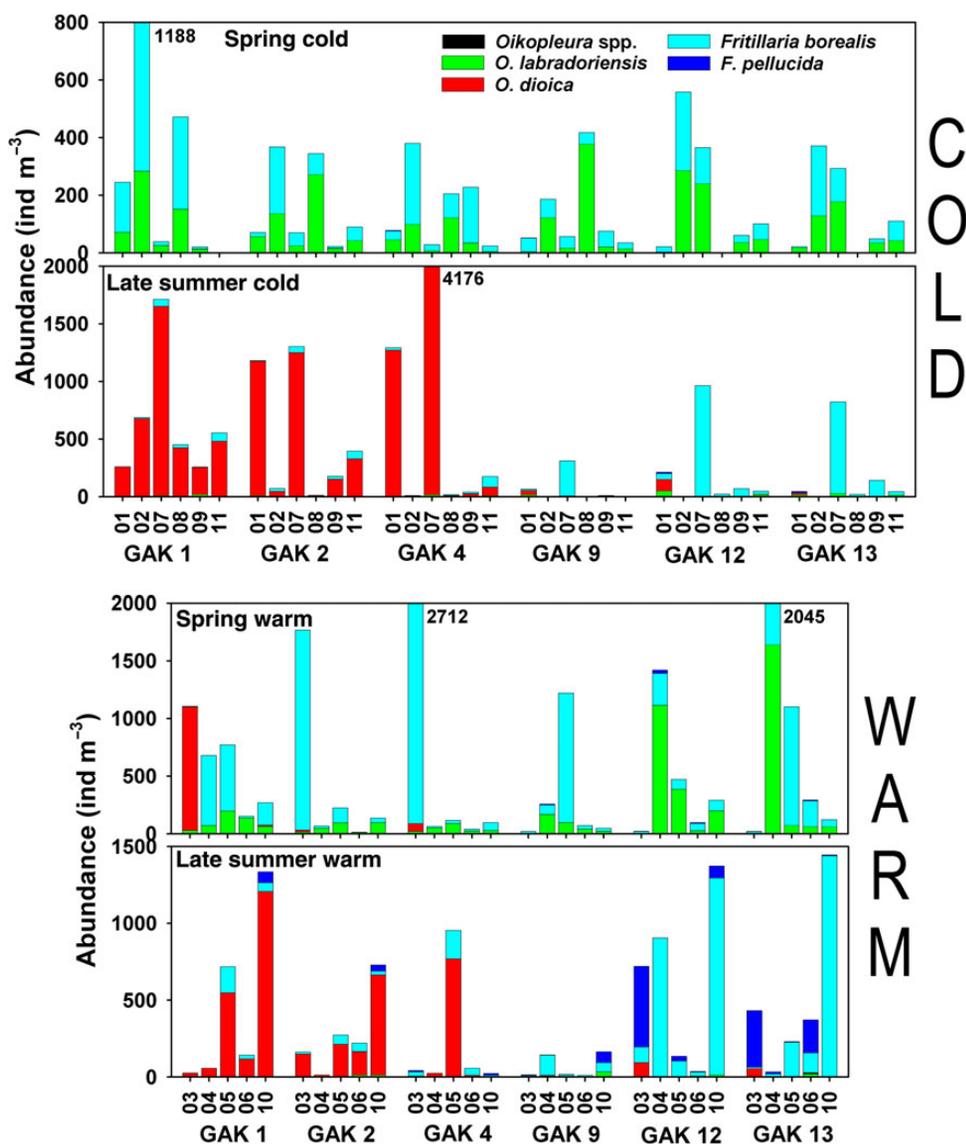


Fig. 3. Abundance (ind m⁻³) of the major larvacean species from the 53- μ m nets along the Seward Line, Gulf of Alaska. Panels are separated between spring and late summer, then further between cold and warm years.

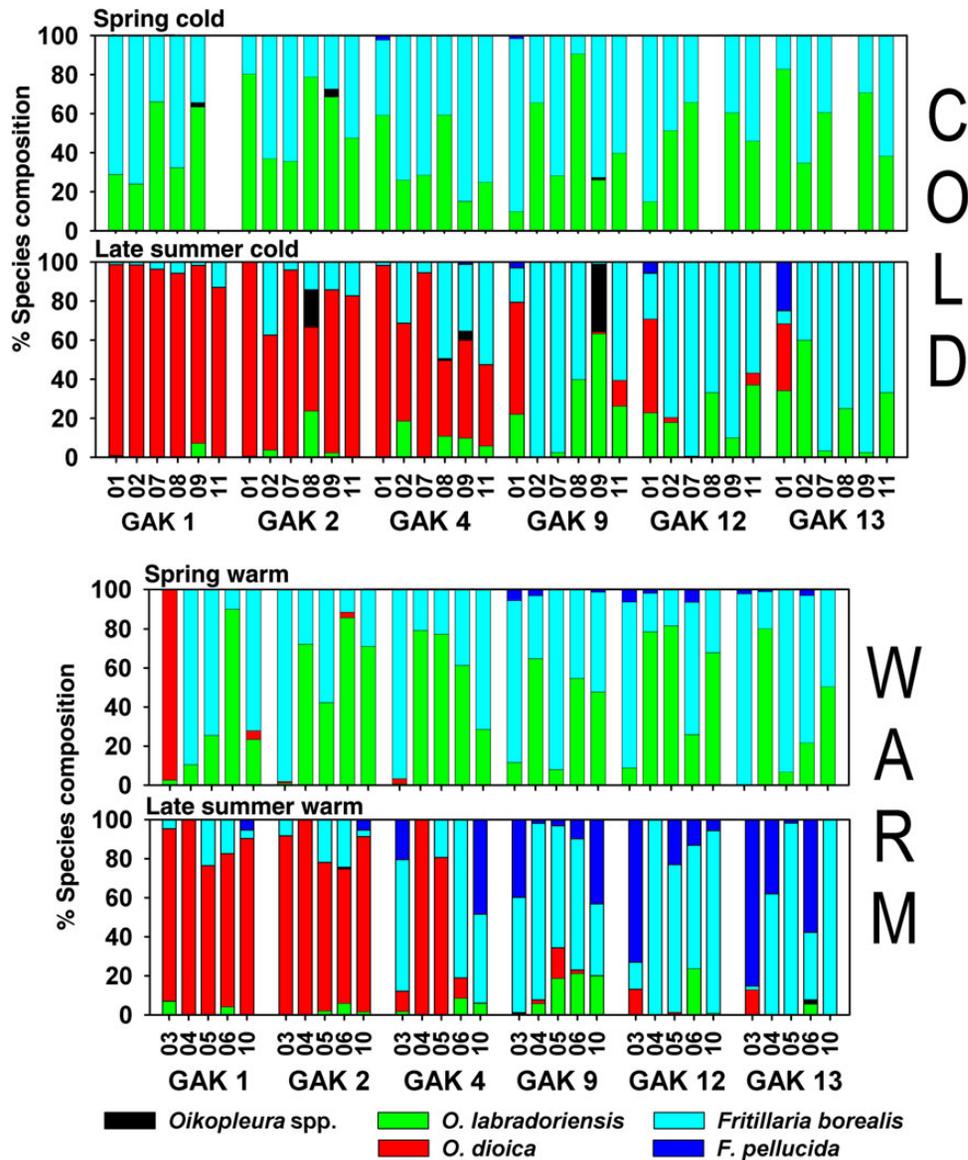


Fig. 4. The abundance as percent species composition of the major larvacean species from the 53- μm nets along the Seward Line, Gulf of Alaska. Panels are separated between spring and late summer, then further between cold and warm years.

outer shelf stations. Biomass estimates reflected the observed patterns of abundance: the larger *O. labradoriensis* dominated in the spring (Fig. 5) with a mean of $0.57 \pm 0.29 \text{ mg DW m}^{-3}$ (Table III). Late summer biomass was mostly *O. dioica* (Fig. 5), which had a mean of $0.20 \pm 0.11 \text{ mg DW m}^{-3}$ (Table III).

Seasonal differences were supported by general separation of clusters between spring and late summer sampling (Fig. 6A). The two-dimensional nMDS projection suggested relatively greater similarity among springs and more variable communities during late summers (Fig. 6B). The moderate to high 2D stress (0.14–0.17, dependent on the inclusion of unidentifiable *Oikopleura*) was

noticeably reduced (0.09–0.10) when a 3D projection was considered. The same emergent patterns, of relatively similar springs compared with late summer, occurred in the 3D nMDS projections. The BIO-ENV community-level analysis confirmed temperature to be the single most influential explanatory variable tested on abundance patterns, and had a rank correlation of $\rho = 0.36$; the addition of salinity and chlorophyll-*a* did not improve ρ . 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 in July instead of

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

Species	Temperature	Salinity	Chl a	Pooled season
<i>Oikopleura labradoriensis</i>	-0.63***	n/s	0.35***	Spring and late summer
<i>O. dioica</i>	0.65***	-0.71***	0.40**	Late summer
<i>Fritillaria borealis</i>	-0.22*	n/s	n/s	Spring and late summer

n/s, not significant.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

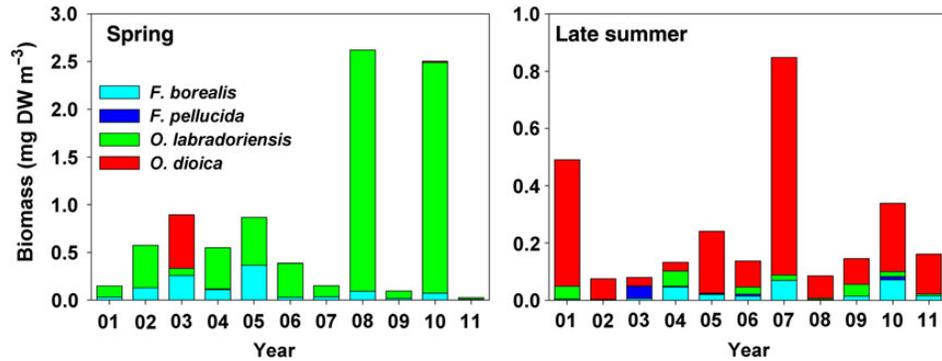


Fig. 5. Mean biomass (mg DW m^{-3}) of larvaceans during spring and late summer collected in the $53\text{-}\mu\text{m}$ nets along the Seward Line, Gulf of Alaska. Note the use of different biomass scales.

Table III: Abundance and biomass of larvacean and pteropod species along the Seward Line collected over the 11-year time period (2001–2011) by the $53\text{-}\mu\text{m}$ mesh nets

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

mean, arithmetic mean; CI, \pm 95% confidence interval. Dashes (–) signify biomass is < 0.01 .

August or September. Likewise, spring samples that clustered with late summer collections occurred during warm years, especially 2003, due to the high abundance of *O. dioica*.

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. 7). A three-way ANOVA revealed a significant interaction effect among year, season and station location ($P < 0.001$; $F = 8$) affecting

L. helicina abundance. Pteropod spring abundance did not vary within years between nearshore and offshore stations; however, it did vary among the warmer springs in 2004–2006, and the colder springs, 2001, 2002, 2007, 2008 and 2011 (Tukey test: $P < 0.05$) (Fig. 8). 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:

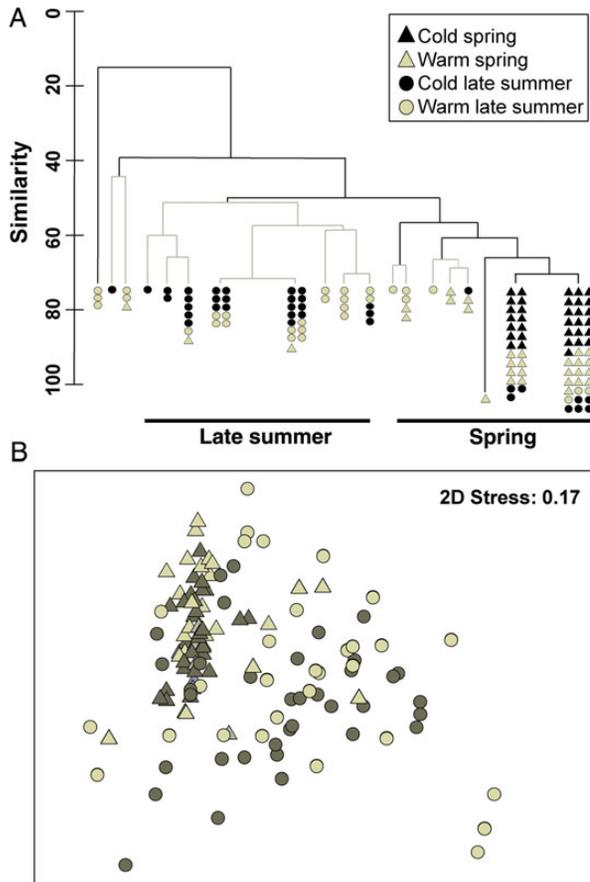


Fig. 6. Dendrogram (A) and nMDS (B) based on Bray Curtis similarity index of the larvacean community in the 53- μm nets along the Seward Line, Gulf of Alaska. Symbols represent stations. Warm years consist of 2003–2006 and 2010. Cold years are 2001, 2002, 2007–2009 and 2011. Black lines indicate significant difference between clusters, while gray lines are not significant (A). Clusters of greater than $\sim 74\%$ similarities are not shown (A). 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 (B).

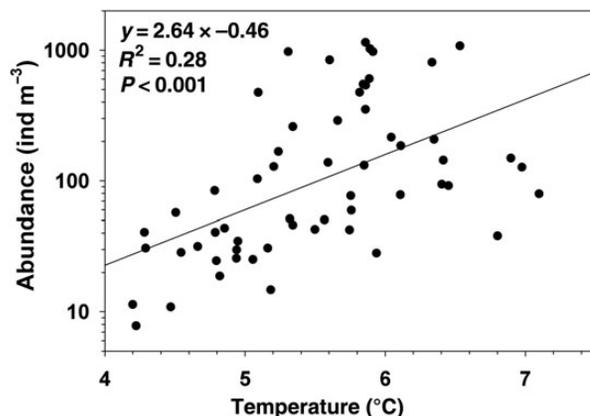


Fig. 7. Simple linear regression between the log abundance of *Limacina helicina* collected in the 53- μm nets along the Seward Line, Gulf of Alaska, in the spring and water temperature integrated to 100 m.

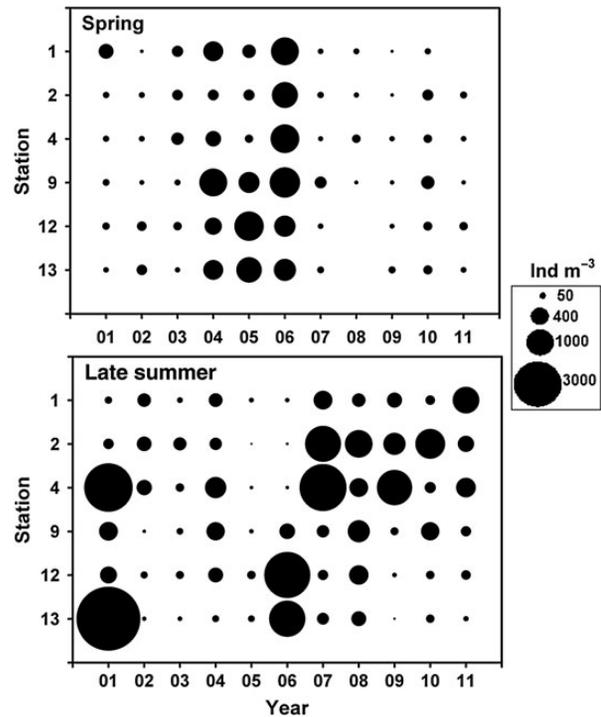


Fig. 8. Abundance of *Limacina helicina* during spring and late summer from the 53- μm nets at selected Seward Line stations, Gulf of Alaska. Due to weather, Spring 2008 stations 12 and 13 were not sampled. Also absent is Spring 2011 station 1.

217 ± 78 and 478 ± 215 ind m^{-3} , respectively (paired t -test: $P > 0.05$). *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 CIs overlapped (Fig. 9). There was a significant negative relationship between *L. helicina* spring abundance and NPGO winter anomalies (Pearson correlation: $P < 0.05$: $\rho = -0.70$) (Fig. 10). 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. 10). 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 between these indices and the abundance of pteropods in PWS during late summer (Pearson correlation: $P > 0.05$).

Net comparisons

A comparison among net mesh sizes used for collection confirmed that the finer mesh always collected higher abundances during both seasons for all groups (paired-samples Wilcoxon test: $P < 0.01$) (Fig. 11). When season and year were pooled, the 150- μm net collected 34% of

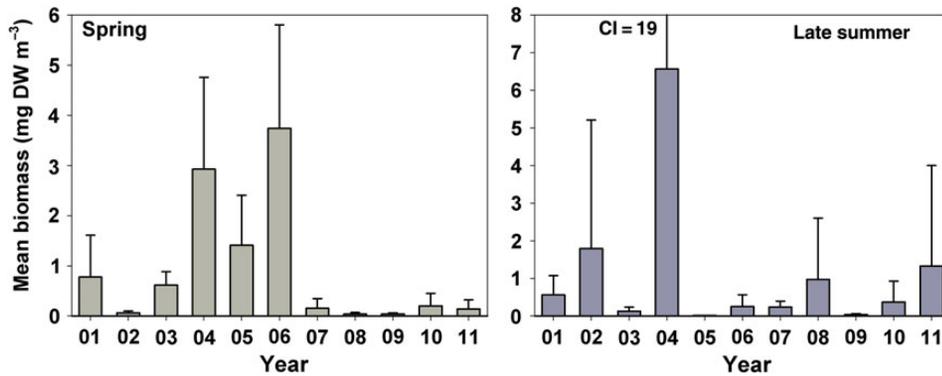


Fig. 9. Mean biomass with $\pm 95\%$ CI of *Limacina helicina* during spring and late summer collected in the 53- μm nets along the Seward Line, Gulf of Alaska. Note the different biomass scales.

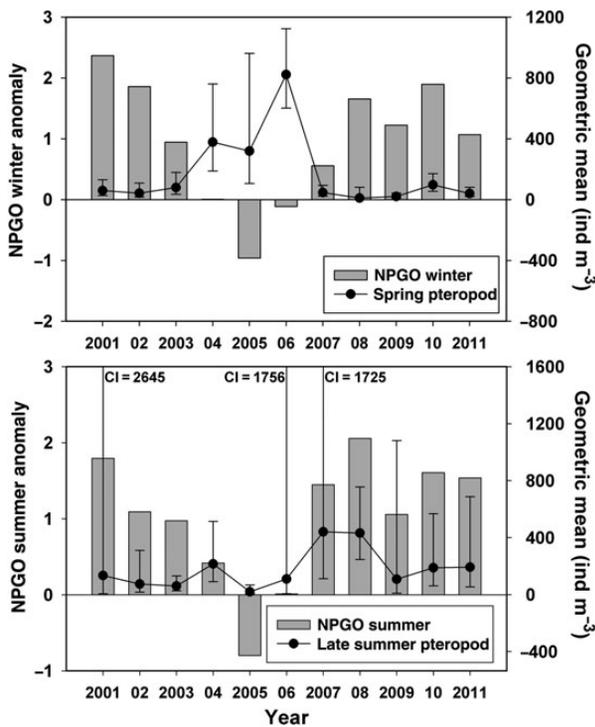


Fig. 10. The geometric mean abundance (ind m^{-3}) of *Limacina helicina* collected in the 505- μm nets along the Seward Line, Gulf of Alaska, separated between spring and late summer. Abundances are averaged for each GAK station among years 2001–2010 in the spring and 2001–2011 in the late summer. Note use of different abundance scales.

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*. If we assume, time-of-day has no impact on the distribution of either group (i.e. no diel vertical migrations), then the 505- μm net captures $<10\%$ of the 53- μm net.

There was no significant difference in *L. helicina* abundance between seasons (paired *t*-test: $P > 0.05$) in the

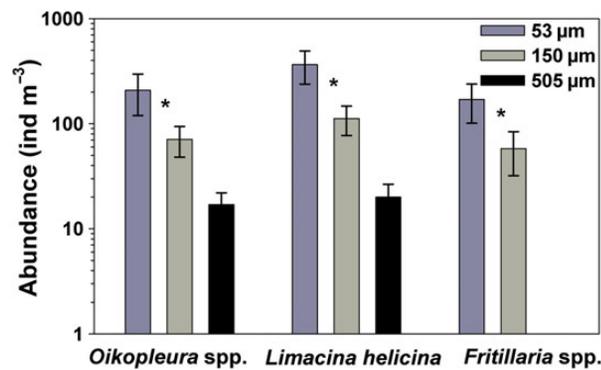


Fig. 11. A comparison of abundance with $\pm 95\%$ CI among the three different mesh sizes used on the Seward Line for each genus. Abundance is log-transformed and confidence intervals are used to determine differences among the 505- μm mesh and that of the 53 and 150 μm nets. The 53 and 150 μm can be statistically analyzed together; an asterisk indicates significant differences (paired-samples Wilcoxon test; $P < 0.01$) between these two mesh sizes.

505- μm net, the 150- μm net or the 53- μm net. 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: $P < 0.05$). *Fritillaria* spp. showed a significant difference between spring and late summer within the 53- μm net only (paired *t*-test: $P < 0.05$).

While the 505- μm nets only capture the largest individuals present, they nonetheless provide insights on vertical distribution at an increased number of stations. The 505- μm mesh nets indicate that *Oikopleura* spp. had highest abundance at the surface, and at single nearshore and offshore stations during spring, and the outer shelf during late summer. *Limacina helicina* also preferred surface waters, except at the most nearshore stations where they occurred deeper in both seasons, with peaks on the outer shelf during spring and offshore during late summer (Fig. 12).

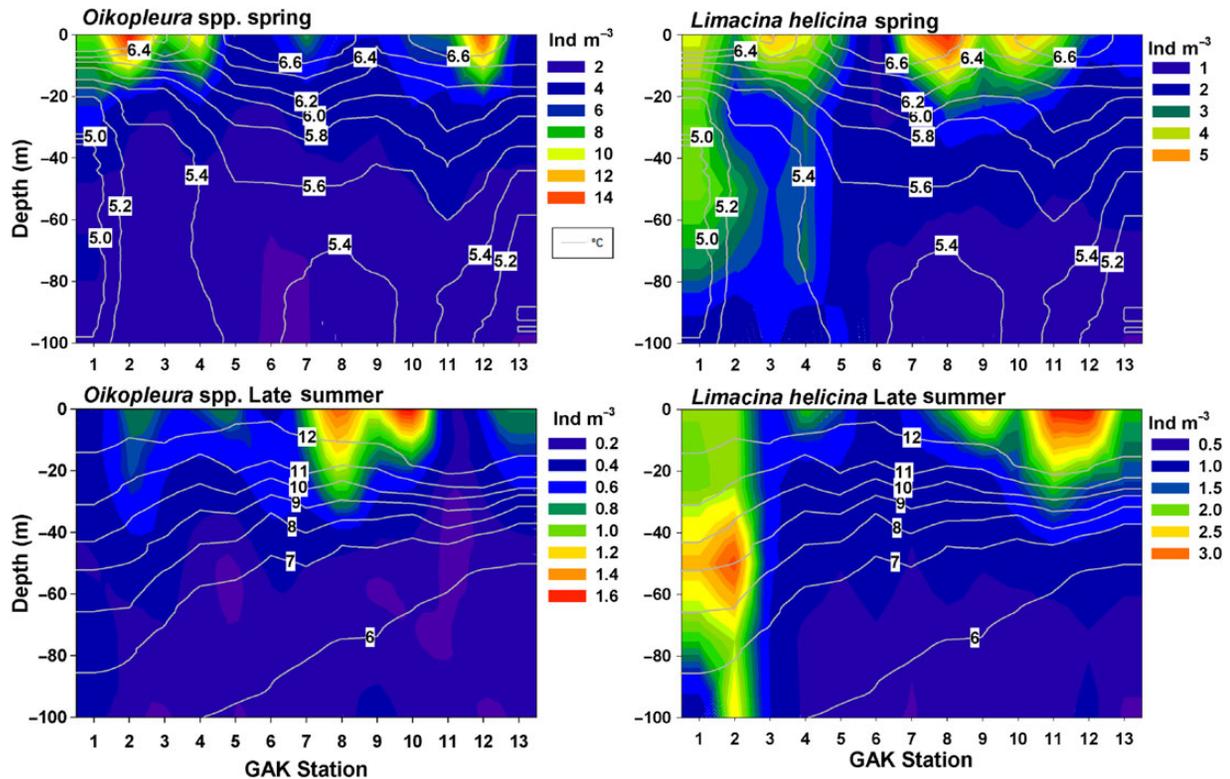


Fig. 12. The geometric mean abundance (Ind m^{-3}) of *Oikopleura* spp. and *Limacina helicina* collected in the 505- μm nets along the Seward Line, Gulf of Alaska, separated between spring and late summer. Abundances are averaged for each GAK station among years 2001–2010 in the spring and 2001–2011 in the late summer. Note use of different abundance scales.

Percent pink salmon survival

Significant relationships were not found ($P > 0.05$) with the taxa 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: $P < 0.05$; $\rho = 0.57$).

DISCUSSION

Larvaceans

We found that the larvacean community in the GoA was dominated by three species: *O. labradoriensis* that occurred primarily in spring, *O. dioica* 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 sub-Arctic. Samples taken in the mixing area between the sub-Arctic 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 sub-Arctic 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). Notably, *F. pellucida* was found in high abundance within the Kuroshio Current (Hidaka, 2008), where it might be transported into the GoA.

Low diversity is typical of colder waters, with only three dominant species observed 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). It is notable that while *F. borealis* is a cosmopolitan species with an affinity to mixed water columns (Lopez-Urrutia *et al.*, 2005), only forma *typica* is characteristic of colder waters. The GoA (five species) composition was more characteristic of the colder waters of sub-Arctic Conception Bay or Bering Sea, having less species than the northeastern Pacific around Japan, where even tropical species occurred sporadically.

A quantitative comparison of abundances with other studies in the North Pacific was hampered by differences in mesh sizes used for collection that extrude perhaps half to two thirds of the community numerically based on our net comparisons. However, looking at the seasonal cycles elsewhere is informative. For example in warmer habitats of both Toyoma Bay (Tomita *et al.*, 2003) and Volcano Bay (Shiga, 1985), *F. borealis* f. *typica* and *O. labradoriensis* were most abundant in winter months around Japan whereas, in colder Conception Bay, both *F. borealis* peaked in abundance during July and August, and *O. labradoriensis* peaked in abundance in October (Choe and Deibel, 2008), while *F. borealis* was also abundant within the Chukchi Sea during summer (Questel *et al.*, 2013). *Oikopleura labradoriensis* is the most abundant species in the Bering Sea and within the Alaska gyre (Shiga, 1982, 1993), but is replaced by *O. vanhoeffeni*, in Arctic waters (e.g. Deibel *et al.*, 2005; Questel *et al.*, 2013) including Conception Bay during summer. In contrast, *O. dioica* peaks in summer and fall (Tomita *et al.*, 2003; Shiga, 1985), with exceedingly high abundances (20 000–50 000 ind m⁻³) reported in Tokyo Bay and the Sea of Japan (Uye and Ichino, 1995; Sato *et al.*, 2008). It is notable that *O. dioica* is the most euryhaline member of this genus (i.e. Sato *et al.*, 2008), and prevails in coastal waters (Fenaux *et al.*, 1998).

In summary, the literature suggests larvacean distribution and seasonal prevalence are driven by temperature, and additionally in the case of *O. dioica*, by salinity. Minimum temperatures in the GoA (4–6°C) occur in the spring, when the entire shelf is roughly isothermal (Janout *et al.*, 2013). The spring larvacean community is dominated by species recognized as having an affinity for cold water (Bückmann and Kapp, 1975; Fenaux *et al.*, 1998). The large-bodied *O. labradoriensis* is at its highest abundance in spring, capitalizing on the productivity of large cells (Deibel and Lee, 1992). Seasonal warming, as well as snow melt entering the GoA intensify the ACC, creating an expanding niche for warm water, low salinertolerant neritic species, such as *O. dioica*. Warming and snow melt could then displace *O. labradoriensis* into deeper and more offshore waters within the GoA, as has been

documented in Volcano Bay (Shiga, 1985). *O. labradoriensis* populations in the Bering Sea may have several generations, but are presumed to overwinter as premature 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 with the smaller *O. dioica* in late summer.

Pteropods

The pteropod community in the GoA was dominated by the single species *L. helicina* that showed sometimes large spring, late summer 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. 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 versus 53 µm, respectively. In colder Arctic water, the time of peak abundance was similar to that in the sub-Arctic 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 waters 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).

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).

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 of 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).

Relevance to higher trophic levels

Mucus-net feeders have been recognized as an important trophic link, which shortcuts 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 essential 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* have heterogeneity of fatty acid composition, presumably reflective of the particulates and phytoplankton they consume (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

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 study coincides 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 influences 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. However, a relationship did occur with 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 agrees with the significant relationship found between *L. helicina* within our PWS dataset. However, we cannot exclude 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 all planktonic prey species in relation to pink salmon returns.

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