Exxon Valdez Oil Spill
Long-Term Monitoring Program (Gulf Watch Alaska) Final Report

The Seward Line: Marine Ecosystem monitoring in the Northern Gulf of Alaska

Exxon Valdez Oil Spill Trustee Council Project 16120114-J
Final Report

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Study History: Begun in fall 1997 as part of the joint National Oceanic and Atmospheric Administration and National Science Foundation's Global Ocean Ecosystems Dynamics program, the Seward Line has become the most comprehensive long-term multidisciplinary sampling program in the coastal Gulf of Alaska, monitoring changes in the oceanography of a region that is critical to Alaska's commercial and subsistence fisheries, and tourism economies. From 1998 to 2004, conditions along the Seward Line were sampled on 6-7 cruises per year spanning from March to December. When field studies ended in December 2004, the North Pacific Research Board continued to fund the program, reducing its scope to a cruise each May and September, with a focus along the Seward Line and the main passageways in western Prince William Sound. In 2010, the Alaska Ocean Observing System began to also provide financial support for the Seward Line observations. During 2011-2013, the Seward Line was embedded within the North Pacific Research Board's Gulf of Alaska Integrated Ecosystem Research Program which added determination of microzooplankton analysis to many cruises. With the addition of *Exxon Valdez* Oil Spill Trustee Council support through Gulf Watch Alaska in 2012, additional sampling stations were added in eastern Prince William Sound passageways. Finally, elevation of the Seward Line to a Long-Term Monitoring program by NPRB during the summer of 2014 has allowed the permanent addition of microzooplankton, seabird and marine mammal observations to cruise activities.

Abstract: The ocean undergoes year-to-year variability in the physical environment, superimposed on longer-term cycles and potential long-term trends. These variations influence ocean chemistry and propagate through the lower trophic levels, ultimately influencing fish, seabirds and marine mammals. The Seward Line program monitors these changes in physics, chemistry and lower trophic levels (i.e., plankton) to describe the current state and natural variability inherent in an ecosystem at risk of significant anthropogenic impact. These observations are the basis for critical indices of ecosystems status that help us understand key aspects of stability or change in upper ecosystem components over both the short and longer-term. During the 2012-2016 study years, the ecosystem has been affected by three consecutive years of warm-water anomalies; these have altered phytoplankton community structure and increased the co-occurrence of warm-water zooplankton species with the historic subarctic assemblage typical of the region. Overall, the anomalous phytoplankton and zooplankton compositions have resulted in displacement of zooplankton community structure and alteration of energy flow pathways.

Key words: biological, chemical, Gulf of Alaska, marine mammals, nutrients, oceanography, physical, phytoplankton, Prince William Sound, seabirds, zooplankton

Project Data: Data exist in three major groups: ocean physics, nutrients and chlorophyll, and species-resolved zooplankton catches.

There are no limitations on the use of the data, however, it is requested that the authors be cited for any subsequent publications that reference this dataset. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate data set limitations or intended use.

Data Location - all data reside online in the publically available AOOS data portal (https://portal.aoos.org/gulf-of-alaska.php#metadata/e25fe1f2-1c98-44f6-856f-5d61c87c0384/project).

Data Contact – Carol Janzen, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703, janzen@aoos.org, http://portal.aoos.org/gulf-of-alaska.php.

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EXECUTIVE SUMMARY

The Seward Line program has sampled the physical, chemical and biological properties along a 150 mile-long transect from the mouth of Resurrection Bay, Alaska to offshore waters using ships for nearly 20 years. It's principle tools are electronic packages that profile the physical properties of the water column (e.g., temperature and salinity), bottles that sample discrete depths for measuring water chemistry (e.g., nutrients) and single-celled organisms (i.e., phytoplankton and microzooplankton), nets that sample the multicellular meso- and macro-zooplankton, and observers that census seabirds and marine mammals. Its major objectives are to monitor the state of these ecosystem components, describe their variability, and understand the relationships between them to thereby improve our understanding and management of this highly productive habitat.

Long time-series are required before meaningful patterns or trends begin to emerge in oceanographic studies. Multi-decadal observations have shown large interannual variability impacted by climatological forcing, but until recently there has been limited systematic change in the ecosystem. The warm-water anomaly of 2014-2016, however, has resulted in a smaller and delayed spring bloom and a decrease in phytoplankton mean size. Spring zooplankton communities appeared largely unaffected, but changes in late-summer zooplankton communities were apparently driven by an increased contribution of advected warm-water and smaller-sized taxa. Seabird communities also showed a response to the recent anomaly, with birds concentrated inshore during warm years, where they often showed signs of nutritional stress. These changes foreshadow a future of reduced production regimes that would be expected if the frequency and/or intensity of such warm events were to increase, with negative consequences to existing fisheries.

INTRODUCTION

Long time-series are required for scientists to tease out secular change (and infer cause) in the face of substantial year-to-year variability. Like other regions, the Northern Pacific undergoes significant interannual variability, driven partially by variations in basin- or global-scale climate (e.g., El Niño, the Pacific Decadal Oscillation). Longer-term variations referred to as "regime shifts" have occurred in the past, and will likely occur again. These are expressed as fundamental shifts in ecosystem structure and function, such as the 1976 regime shift that resulted in a switch within the Gulf of Alaska (GOA) from a shrimp-dominated fishery to one dominated by pollock, salmon, and halibut. Long-term observations are also critical to describe the current state, and natural variability inherent in an ecosystem at risk of significant anthropogenic impact such as occurred during the *Exxon Valdez* oil spill. Given the potential for such profound impacts, the Seward Line Long-term Observation Program (http://www.sfos.uaf.edu/sewardline/) provides these critical observations on the current state of the northern GOA ecosystem.

Inherent in the concept of any long-term observation program is the ability to assess effects of climate variation. Beyond this long-term aspect, the sampling program is designed to capture the major gradients in lower tropic level production as estimated from broad-scale analyses of satellite ocean color imagery (assumed to represent phytoplankton production gradients). This design allows us to investigate the mechanisms by which variations in physical and chemical conditions translate into changes in the composition and abundance of organisms in the planktonic food web, and how apex predators, such as seabirds, integrate and reflect these changes. The first-order driver of production variability is the intense seasonality of the system (Brickley and Thomas 2004, Waite and Mueter 2013). Our cruises capture the major spring-late summer gradient in this seasonality, while retaining a focus on important periods for the life cycles of various zooplankton species. The early May period was selected to capture the peak productivity associated with the spring bloom. The consistent timing of the May cruise has allowed us to look at phenology shifts (e.g., Mackas et al. 2012) in the large *Neocalanus* spp. copepods that dominate the spring zooplankton biomass (Hopcroft and Coyle, in prep). The September cruise captures the end of the low productivity oceanographic summer, when smaller phyto- and zooplankton dominate, and precedes the stormy fall overturn. Changes in the microzooplankton community are likely to accompany this seasonal gradient, as hinted at in earlier work showing, for example, higher abundances of dinoflagellates in summer compared to spring (Strom et al. 2007, Strom and Fredrickson 2008).

Dominant spatial gradients in the coastal GOA are the east-west contrast (recently explored by the North Pacific Research Board (NPRB) Gulf of Alaska-Integrated Ecosystem Research Project (GOA-IERP) program) and the cross-shelf zonation (Brickley and Thomas 2004, Waite and Mueter 2013). The Seward Line station layout is explicitly designed to capture the important cross-shelf divisions (described above), as well as incorporating Prince William Sound (PWS) as a largely enclosed, estuarine "end member" of this coastal continuum. Mating biological observations (e.g., plankton community composition) directly to physical and chemical sampling allows us to define these zones according to their oceanographic properties rather than fixed geographic coordinates (Coyle and Pinchuk, 2003, 2005). This is crucial in a region where variations in cross-shelf transport, down- or upwelling intensity, and mesoscale eddy activity can shift frontal boundaries rapidly (Stabeno et al. 2004). It is likely that multi-decadal observation of the coastal GOA is required for broad-scale atmospheric indices to emerge, although it has been proposed that some such as the El Niño Southern Oscillation may have little impact on the region's shelf seas (Stabeno et al. 2004). Most recently, a warm-water anomaly referred to as "the Blob" (Bond et al. 2015) has had far ranging impacts in the GOA. Ultimately, the Seward Line observations will help us understand how environmental effects (i.e., oceanographic conditions and their variability) relate to higher-order ecological properties such as spatial and temporal coherence of communities, resilience and diversity (Beaugrand et al. 2010, Wiltshire et al. 2008).

OBJECTIVES

The scientific purpose of this project is to develop an understanding of the marine ecosystem response to climate variability, and provide baselines against which to assess anthropogenic influences on the GOA ecosystem. Toward this end, the Seward Line cruises on the GOA shelf determine the physical-chemical structure, phytoplankton biomass and size composition, and the distribution and abundance of zooplankton, along with their seasonal and interannual variations. Some of the data are compared with historical data sets whereas other data sets are a more recent product of our continuing sampling effort.

Specifically, the objectives for cruises each May and September are:

1. Determine thermohaline, velocity, and nutrient structure of the Seward Line across the GOA shelf, and at stations throughout PWS (Fig. 1).
2. Determine phytoplankton (chlorophyll) biomass and size distribution.
3. Determine the distribution and abundance of meta-zooplankton.
4. Determine the distribution and abundance of microzooplankton (starting in 2014).
5. Opportunistically, determine rates of growth and egg production of selected key zooplankton species.
6. Support determination of carbonate chemistry (i.e., ocean acidification).
7. Determine distribution and composition of seabirds (and marine mammals) along the Seward Line, PWS and Kenai coastline.
8. Provide at-sea experience for graduate and undergraduate students.

Objectives 4-8 are primarily supported through other consortium funding, as were proposed rates of primary production, although this distinction was not made clear in the original proposal. Consequently, this report focuses on Objectives 1, 2, and 3, which were primarily supported by *Exxon Valdez* Oil Spill Trustee Council (EVOSTC) funds, while other objects may be covered in lesser detail.

METHODS

Project Design and Conceptual Approach

Core program: The Seward Line Program consists of 13 primary and 9 secondary stations along the Seward Line, and 12 stations in PWS (eastern PWS stations were added in 2012) sampled in May and early September from the U. S. Fish and Wildlife Service (USFWS) vessel *R/V Tiglax* (Fig. 1). Beginning in 2014, we added an additional two stations to the offshore end of the line to ensure coverage of the oceanic 'end member' of this coastal ecosystem.

Oceanographic sampling methodology has remained stable since sampling began in the fall of 1997 (Weingartner et al. 2002), although the logistics of vessel availability (*R/V Tiglax*) has pushed summer sampling from mid-August to early/mid-September. All hydrographic and bottle-based sampling is conducted during the day, as well as collection of the smaller zooplankton species that do not migrate vertically, and do not avoid nets. Seabird and mammal observations are made during station transits. At night, sampling is conducted for the larger and more mobile zooplankton, many of which can only be sampled efficiently during their daily migration toward the surface under the cover of darkness. Although this protocol results in some backtracking along the transect line, it ensures that all data can be employed in analysis without biases arising from diel cycles. At present, there are no

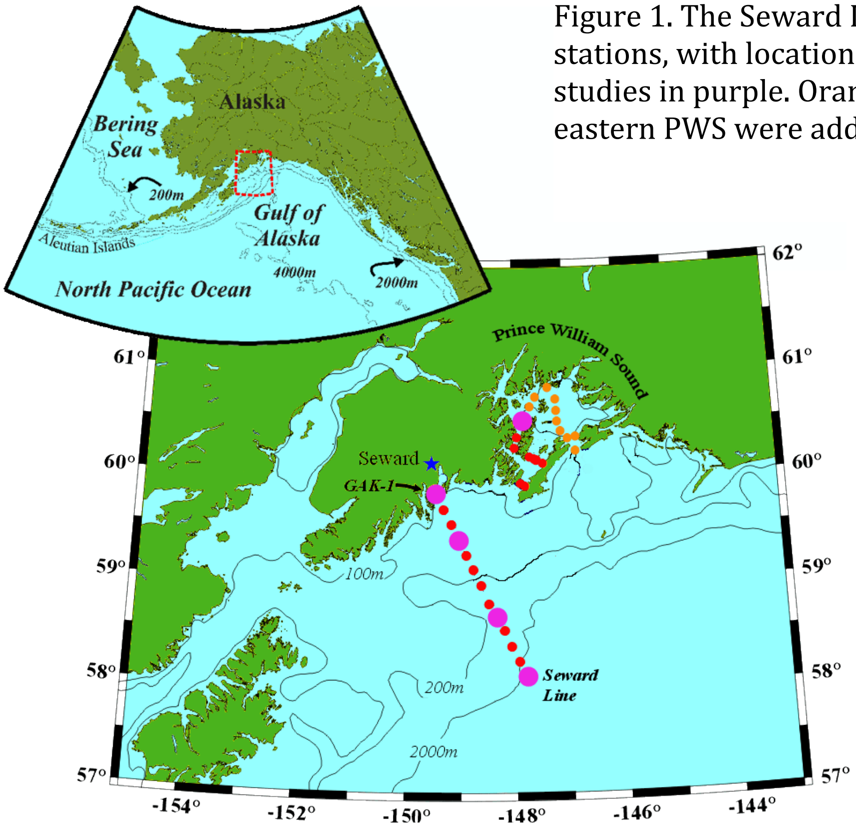

Figure 1. The Seward Line's primary stations, with locations of process studies in purple. Orange stations in eastern PWS were added in 2012.

autonomous or remote sensing technologies that allow sufficient sampling of the biological components of this program – they can only be adequately assessed by vessel-based observations. Nonetheless, the Seward Line program provides the opportunity for testing and validating any such technologies as they become available.

Hydrography and nutrients

Each station includes high-resolution vertical profiling of water properties (including temperature, salinity, chlorophyll fluorescence, photosynthetically active radiation (PAR), oxygen) to within 4 m of the bottom using a Seabird 911Plus conductivity-temperature-depth (CTD) with dual temperature, conductivity and oxygen sensors. Dissolved inorganic nutrients (phosphate, silicic acid, nitrate, nitrite, ammonium) and carbonate chemistry (a.k.a., "Ocean Acidification" parameters) are collected from rosette (Niskin) bottles that sample at 10 m depth intervals in the upper 50 m, and at irregularly spaced but consistent depths to the bottom. Water samples are analyzed for dissolved inorganic carbon (DIC) and total alkalinity (TA) from which the partial pressure of carbon dioxide (pCO2), pH, and calcium carbonate saturation states (Ω) are calculated. Oxygen samples are collected from rosette bottles for calibration of high-resolution sensors. Nutrient samples are collected, filtered (0.4 μm), frozen, and transported to laboratories at the University of Alaska Fairbanks (prior to 2013) or at the National Oceanic and Atmospheric Administration (NOAA) Pacific Marine Environmental Laboratory (PMEL) in Seattle (after 2012) for analysis. Nutrients and oxygen are measured according to specifications set forth by the World Ocean Circulation Experiment (WOCE; Gordon et al. 1993). The autoanalyzers used at PMEL are continuous flow analyzers with segmented flow and colorimetric detection, and have been successfully used to collect high-precision nutrient data for World Ocean Circulation Experiment, Climate Variability and Predictability, Global Ocean Ecosystem Dynamics, and Fisheries Oceanography Coordinated Investigations programs.

The physical and chemical data are used to quantify the seasonal, interannual, and along- and cross-shelf distributions of water masses and their variability. Interdecadal time scales are also addressed through use of ship-based sea surface temperatures, upwelling indices, the Pacific Decadal Oscillation (and other atmospheric indices), oceanographic buoy data, and the EVOSTC-supported continuous measurements at GAK 1 (EVOSTC project 16120114-P). Although limited to surface observations, satellite sensor data is used to place our shipboard data in broader spatial and temporal contexts (Appendix 1). These data, combined with atmospheric and oceanographic model reanalysis hindcasts, can help characterize aspects of the system that we do not directly measure. This holistic approach to interpreting the physical environment is critical to a physics-to-birds-and-mammals understanding of the GOA ecosystem.

Chlorophyll

Chlorophyll *a* is the most widely used index of phytoplankton, and one of the few biological parameters that can be sensed in situ or remotely by satellites. Chlorophyll *a* concentrations are determined at all stations as a measure of phytoplankton biomass and as a means to calibrate in vivo fluorescence sensors on the CTD package. We coordinate sampling depths with water column chemistry measurements (i.e., at 10 m intervals in the upper 50 m). Samples are collected with the rosette on up-casts and filtered at low vacuum onto glass fiber (0.7 µm effective pore size) filters. At most stations particles are size-fractionated through 20 µm pore-size polycarbonate filters to estimate phytoplankton biomass partitioning into ≥20 and <20 µm size classes. Previous work has shown that these two size classes respond to different sets of environmental conditions and have different fates in the coastal GOA food web (Strom et al. 2007, 2010). In the past, chlorophyll samples were stored frozen for post-cruise fluorometric analysis (Parsons et al. 1984). Recent concerns about degradation of pigments by this approach (Wasmund and Topp 2006) have resulted in the extraction process commencing immediately after filtration and fluorometry conducted on shipboard.

Phytoplankton and Microzooplankton

Determination of phyto- and microzooplankton composition and biomass provides information on the functioning of the ecosystem, and responses to environmental forcing. Knowledge of phytoplankton composition allows us to relate physical processes (mixing, light availability) and nutrient supplies to the nature of the production response. Large chain diatoms may be particularly important in connecting pelagic production with the benthos. Large heterotrophic dinoflagellates can respond strongly to diatom blooms; their biomass indicates potential grazing impact of microzooplankton on diatom blooms, a major trophic transfer pathway in coastal GOA waters sampled so far (Strom et al. 2001, 2006, 2007). Large microzooplankters are also important prey for the crustacean zooplankton (Liu et al. 2005, 2008). In general, knowledge of phyto- and microzooplankton composition and biomass is essential for evaluating the food web structure and potential trophic transfer efficiency of the region.

Phytoplankton community composition (primarily diatom and dinoflagellate identification) is assessed using inverted light microscopy of formalin-fixed samples. Acid Lugol's fixation and inverted light microscopy (Sherr and Sherr 1993) are used to identify, count and size all microzooplankton ≥15 µm in size (using a semi-automated digitizing system, Roff and Hopcroft 1986). Biomass is estimated from microzooplankton cell volumes using published conversion factors (Strom et al. 2006, 2007). The ≥15 µm size class of microzooplankton can be directly consumed by mesozooplankton. All phytoplankton and microzooplankton sampling was confined to the same surface mixed layer (50 m and above) as employed for chlorophyll determination.

Primary Production

Intermittent point measurement of primary production using both stable and radio-isotopes over the past 2 decades have highlighted that the intense day-to-day (and within day) variability in solar irradiance due to cloud cover obfuscates attempts to estimate the magnitude or underlying patterns in productivity (Strom et al. 2010). At best simple shipboard approaches using ambient light establish the upper and lower limits of potential production. More useful insights into primary production are gained through short term incubations that establish photosynthetic–irradiance curves (e.g., Strom et al 2016), however such determinations are only possible using radio-isotope approaches that cannot be licensed on the vessel routinely employed by this program.

Ocean color as observed by satellites offers more appropriate times frame over which to estimate relative productivity. Through appropriate interpolation and averaging of pixels, it is possible to construct weekly, monthly or seasonal values of chlorophyll which over these longer periods tend to correlate with the magnitude of primary production. Here we generated 8-day mean chlorophyll concentrations from MODIS Aqua for a 100 km wide swath center along the Seward Line. These data were further averaged to yield a "spring" (April-May) and summer (June-August) value, for which anomalies were calculated over the life of this satellite (2003-present).

Metazooplankton

Metazoan zooplankton represent the key linkage between production by single-celled organisms, and larger organisms such as fish, seabirds and marine mammals. Although typically considered as a single unit, the term encompasses a wide array and vast size range of species for which no one piece of sampling equipment can suffice. To address this challenge, our sampling uses three different types of plankton nets. During daytime, mesozooplankton samples are collected with a Quad net consisting of 25 cm diameter nets of 2.6 m length equipped with General Oceanics flowmeters. A pair of these nets is constructed of 150 µm mesh and samples small, primarily early copepodid stages of calanoids (e.g., Coyle and Pinchuk 2003, 2005), while nauplii and the smallest copepodid stages of neritic species are sampled with a pair of nets equipped with 50 µm mesh (not generally processed). Quad net tows are made from 100 m to the surface at the 13 primary stations along the Seward Line, and at all PWS stations. During night-time, a 0.25-m^2 Hydrobios Multinet system with 0.5 mm mesh nets is fished to assess larger meso/macrozooplankton and micronekton, such as euphausiids that are important components in the diet of many fish, sea-birds and marine mammals. The Multinet is equipped with one drogue net plus five nets that can be programmed to open and close at specific depths, or opened and closed electronically from the deck if a conducting cable is available. Depth, flow meter counts, and volume filtered are recorded at 1 second intervals. The Multinet is fished at each of the 13 primary Seward Line stations (Fig. 1), plus the 10-12 stations within PWS. At each station, 5 samples are collected at 20 m depth intervals from 100 m depth to the surface. As time permits, additional Multinet collections are made to 600 m at GAK13 and PWS2 to assess over-wintering populations of *Neocalanus* spp. in 5 layers: 600-400 m, 400-300 m, 300-200 m, 200-100 m, and 100-0 m. All zooplankton samples are preserved in 5-10% formalin and stained with Rose Bengal for later analysis to the lowest taxonomic category possible.

During traditional taxonomic processing, all larger organisms (primarily shrimp and jelly fish) are removed and enumerated, and the sample is repeatedly split using a Folsom splitter until the smallest subsample contains about 100 specimens of the most abundant taxa. The most abundant taxa are identified, copepodites staged, measured, enumerated and weighed, with each larger subsample examined for the larger, less abundant taxa. Blotted wet weights of all specimens of each taxa and stage are taken on each sample with ±1 µg Cahn Electrobalance until weights stabilize, after which point the wet weight biomass is estimated using mean wet weight. Wet weights on euphausiids, shrimp and other larger taxa are always measured and recorded individually for each sample. Typically at least 400-600 organisms are recorded per net-sample. The data are uploaded to a Microsoft Access database for sorting and analysis. Long-term patterns and trends are typically performed on power-transformed data (typically power 0.15). Analysis to date indicates the Multinet collections are consistent with those obtained using a 1.0 m^2 MOCNESS during the GLOBEC years (1998-2004).

Multivariate analyses employ non-parametric multidimensional scaling (nMDS) of Bray-Curtis similarity index between samples (Clarke et al. 2014) using the Primer (V7) software package. Abundances are fourth-root transformed, and only taxa contributing at least 3% to transformed values are retained for analyses.

Seabirds and Mammals

The Seward Line design (spring and fall seasons, cross-shelf) provides an opportunity to examine seabird and marine mammal responses to seasonal changes and the cross-shelf gradient of physical and biological parameters. The spring survey occurs just prior to or at the beginning of the breeding period and the fall survey occurs when birds must prepare for harsh winter conditions or long migrations. Seabird distribution patterns vary among species. However, we might expect inshore shifts in distribution of 'offshore' seabirds during storms or upwelling events, while years with strong stratification inshore might drive 'inshore' seabird species toward the shelf break, where upwelling is more consistent and prey may be more available. Similarly, many marine mammals have seasonal migrations, while others are resident, sometimes with seasonal differences in habitat utilization.

Marine bird and mammal surveys use standard strip-transect methodology and USFWS protocols (USFWS 2008), with one observer stationed on the flying bridge, entering data into a GPS-integrated laptop computer. While bird data is considered relatively quantitative because it surveys an area in relative proximity to the ship, mammal data is more qualitative owing to species-specific differences in detection and assigning an animal's distance from the ship both of which are greatly influenced by sea-state and atmospheric visibility. Marine bird data are processed by subdividing continuous survey transects into 3-km segments and calculating the density (birds • km^{-2}) of each seabird taxon within each segment. Marine mammal data is simply plotted as occurrence. To examine distribution across the shelf, the study area is divided into four regions, using data collected on any transects within 80 km of the Seward Line and within PWS. The PWS region is separated from the inner shelf region at the ocean entrances. Because the Alaska Coastal Current front is typically within 50 km from shore near the Seward Line, a 50 km shoreline buffer is used to separate the inner shelf from the middle shelf. The oceanic region extends from the shelf-break at the 1000 m isobath to past the last Seward Line station.

For seabirds, we calculate the mean density of each taxon for each cruise and region and compare cross-shelf distributional patterns of marine birds during 'cold' vs 'warm' years. The temperature regimes are defined by the springtime average water temperature in the upper 100 m. We combined data from years 2007-2009, 2013 for cold years, and data from 2010, 2014, 2015 for warm years (2011 and 2012 were removed; they were near average or had no seabird survey). We focused on 10 seabird taxa that regularly occurred in both spring and fall. For mapping, density values of 3-km transects were averaged using 20-km hexagonal grid cells.

RESULTS

Each Seward Line cruise collects a wealth of information, but we do not believe this report is well-served by presenting all such details. We will primarily summarize the larger scale patterns observed during the study period, and in particular by placing them in the context of the prior 15 years of sampling. Observations made within PWS have generally not been presented, for efficiency, and because their shorter duration provides more limited context.

Physics

Using the average temperature within the upper 100m of the ocean as a heat index, it is clear that May temperatures along the Seward Line were well above average during 2015 and 2016 (Fig. 2). This anomaly was due to the sequential occurrence of a feature referred to as "the Blob" that began in early 2014 followed by an El Niño during 2015/16. It is notable that the other two warm May months in the time series, 1998 and 2003, were also El Niño-related. September temperatures and their anomalies appear less clearly influenced by El Niño events; however, 2014-2016 appears consistently warm. A unique aspect of the 2014-2016 warm period was the large depth range over which this extra heat was distributed, with anomalously warm temperatures occurring down to 300 m (Fig. 3). The apparent negative anomalies at 30-50m during the falls of 2014-2016 are a manifestation of the thermocline being shallower and more abrupt than normal.

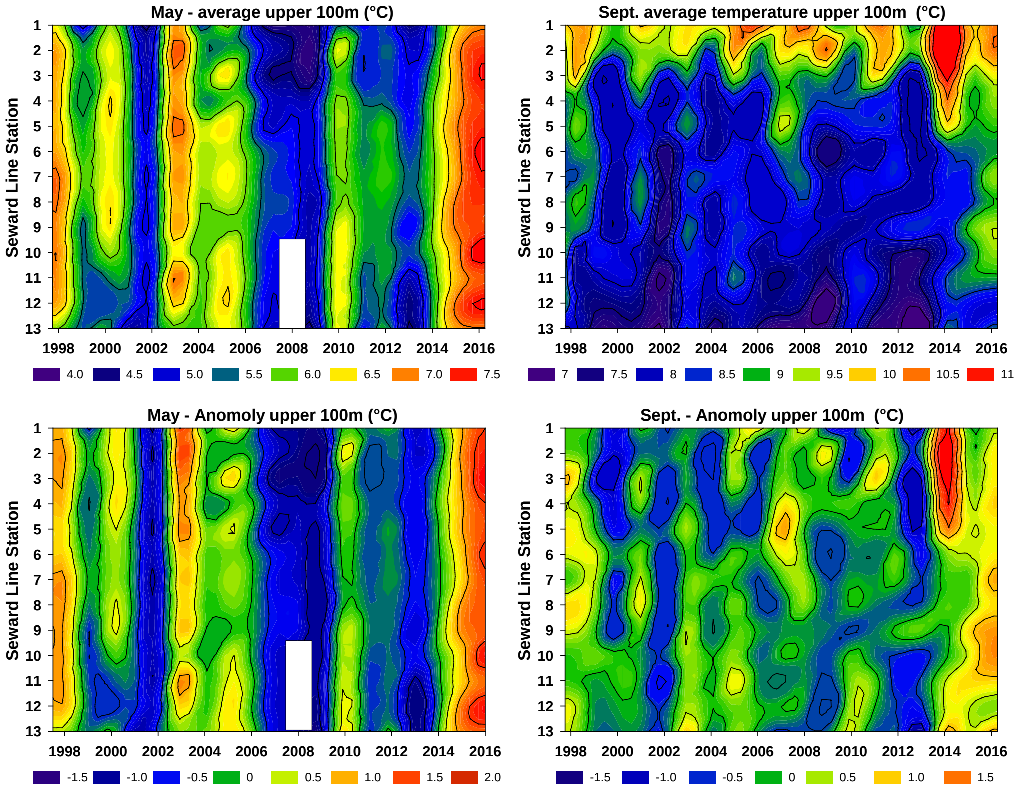

Figure 2. Average water temperatures in the upper 100 m along the Seward Line during May and September (upper), and the station-specific temperature anomalies (lower).

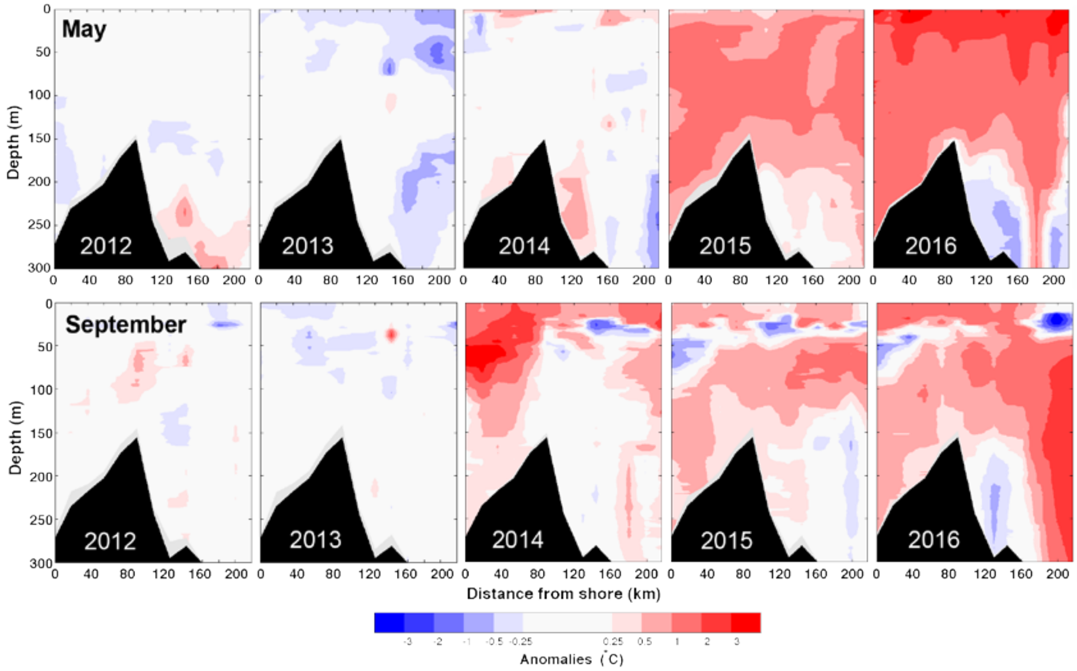

Figure 3. Water temperature anomalies (color bar) along the Seward Line during May and September for the 5-year study period.

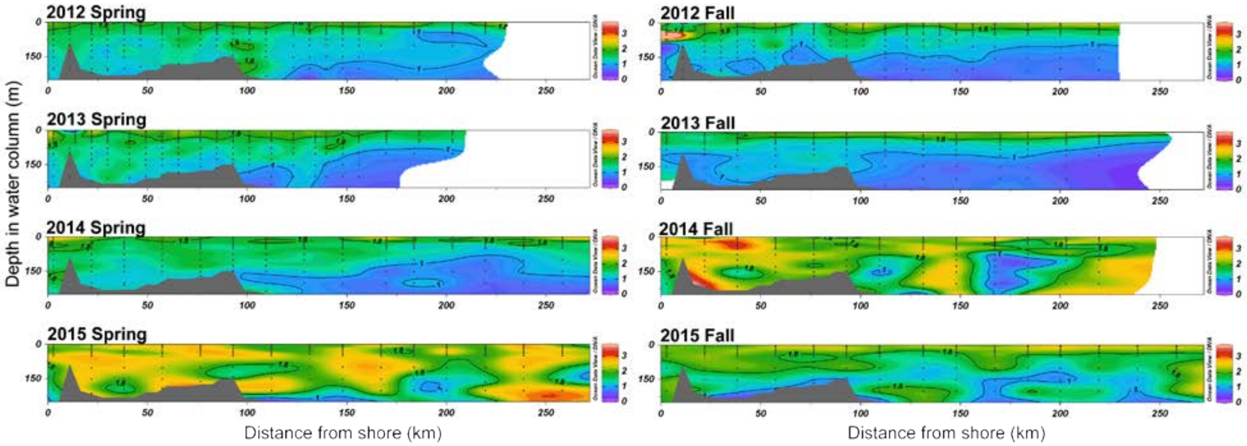

Figure 4. Aragonite saturation state (Ω) along the Seward Line 2012-2015. J. Mathis, preliminary data.

Carbonate system

Although offshore data was limited during May 2012 and 2013, prior to the warm water anomaly, we observe under-saturation of aragonite (i.e., Ω<1) in the deeper and more offshore waters during May, with more acute under-saturation observed during September (Fig. 4). Arrival of the anomaly in September 2014 corresponded to more consistently saturated system during spring and fall, patterns that are being more fully described elsewhere (Evans et al. 2013, Siedlecki et al. 2017, Mathis et al. in prep).

Macronutrients

Macronutrient concentrations in surface waters during May reflect the extent to which the nutrients recharged into surface waters during winter have been utilized by the spring phytoplankton community. High concentrations observed at most stations during 2014 suggest pre-bloom conditions. Moderate concentrations observed during 2012 and 2015 suggest the cruise occurred during the pre-bloom or early bloom periods (except the inner station where nutrients were already depleted), while the moderate to low concentrations during 2013 and 2016 suggest the bloom was well underway or had already occurred (Fig. 5). These interpretations are supported by comparison to concurrent measurement of chlorophyll (see below). It is notable that GAK1, and sometimes GAK2, are generally depleted in nutrients by the May cruise. Nutrients remain depleted in surface water through early fall when wind mixing of the water column commences, as is apparent in several years. During September of 2015-2016 nitrate remained below 1 µM at all stations and was only slightly higher during 2014.

The ratios of macronutrients during May 2013 and (on most of the shelf) during 2014, shows the silicate:nitrate drawdown ratio in surface waters was 1.8 (Fig. 6). In the recent warm years, and especially during 2016, silicic acid drawdown associated with spring production is more modest, with an overall silicate:nitrate drawdown ratio of 1.1, suggestive of a lower silica demand by diatoms.

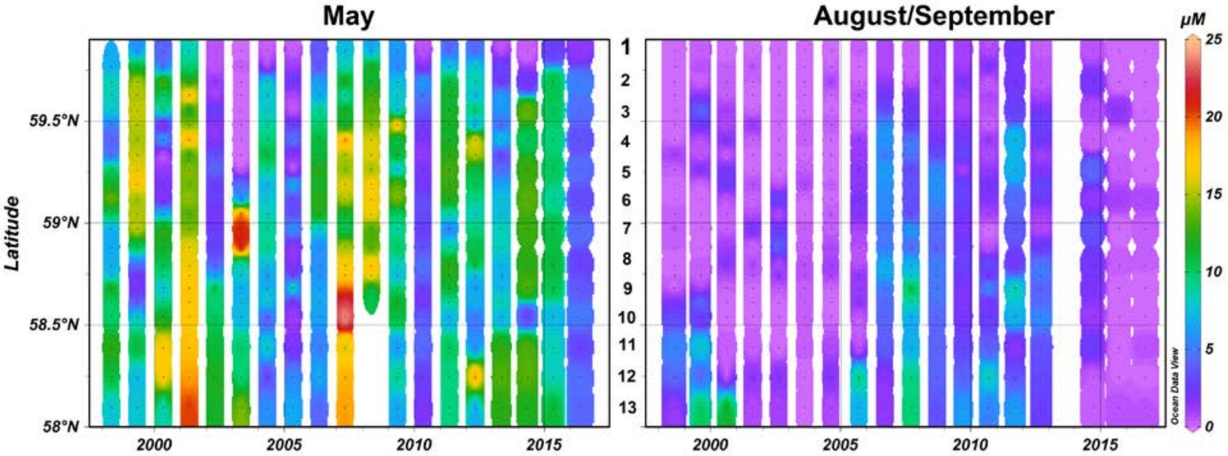

Figure 5. Nitrate concentration in near-surface (<10m) waters of the Seward Line during May (left) and September (right).

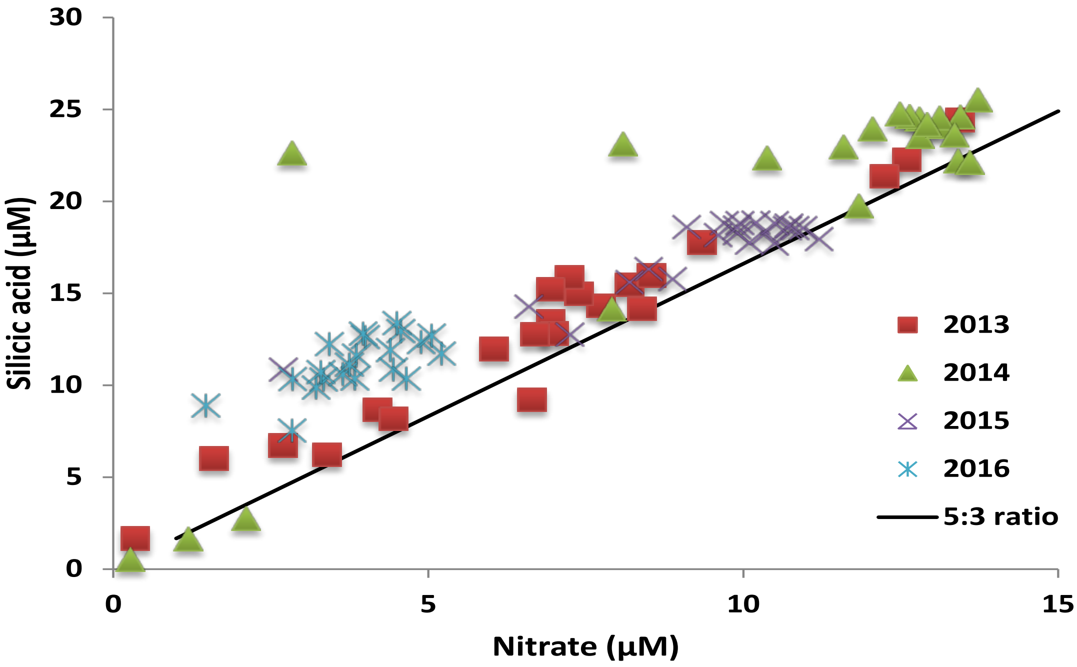

Figure 6. Relationship between nitrate and silicate during May along the Seward Line.

Phytoplankton (Chlorophyll)

Phytoplankton measurements during May target the month of typically highest chlorophyll concentration over the shelf in the satellite record when rapid phytoplankton growth outpaces grazing pressure. Nonetheless, in the past two decades we have rarely sampled a fully developed bloom coherent across the entire Seward Line, either because we have missed it, or because it was not manifested in a given year (e.g., 2011 and possibly some of the ”Blob” years). In general, satellites reveal that PWS and the innermost shelf bloom

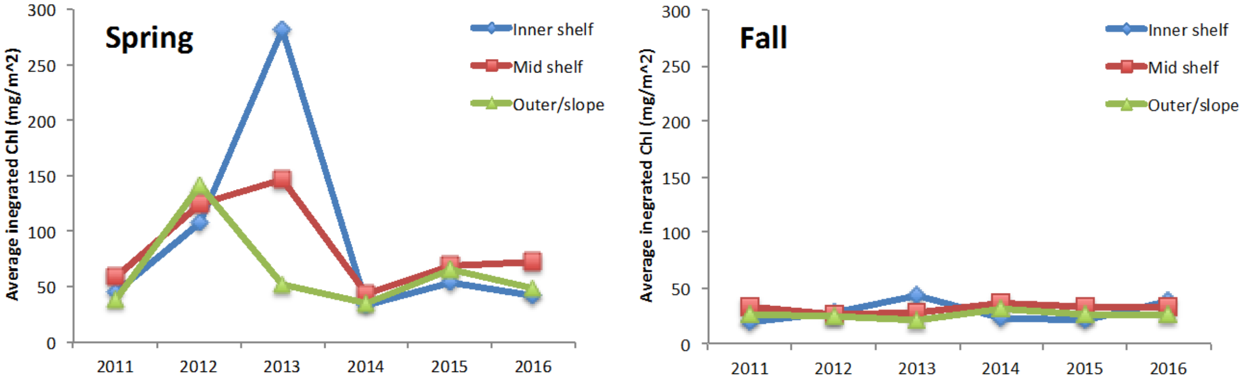

Figure 7. Average integrated May chlorophyll by shelf zone (inner = GAK 1-4; mid = GAK 5-9; outer = GAK 10-13).

earliest, often several weeks before the remainder of the shelf, due to stratification induced by their fresher surface waters. The highest chlorophyll concentrations during the last 5 years were observed during May 2013, but they were not coherent across the shelf suggesting different cross-shelf domains were at different stages in bloom progression (Fig. 7). In contrast, the early bloom period observed during 2012 shows high coherence across the shelf. Chlorophyll concentrations observed during September were typically lower than observed during May, but also relatively variable across shelf domains.

The spring phytoplankton bloom normally is driven by a shift toward predominance of large cells (Fig. 8). The warm-water anomaly in 2014-2016 resulted in reduced chlorophyll (<45 mg m^{-2}) during May when the spring bloom normally occurs (i.e., maxima in the 40-100 mg m^{-2} range). In addition, elevated chlorophyll events during these warm years occurred mainly as small cells, rather than large cells as are typical. In addition to these changes in community composition, satellite ocean color data indicate major (many weeks) alterations in bloom timing, with minor peaks observed earlier (early April 2016) and the main peak observed later (late May 2015 and 2016) than the typical early May timing.

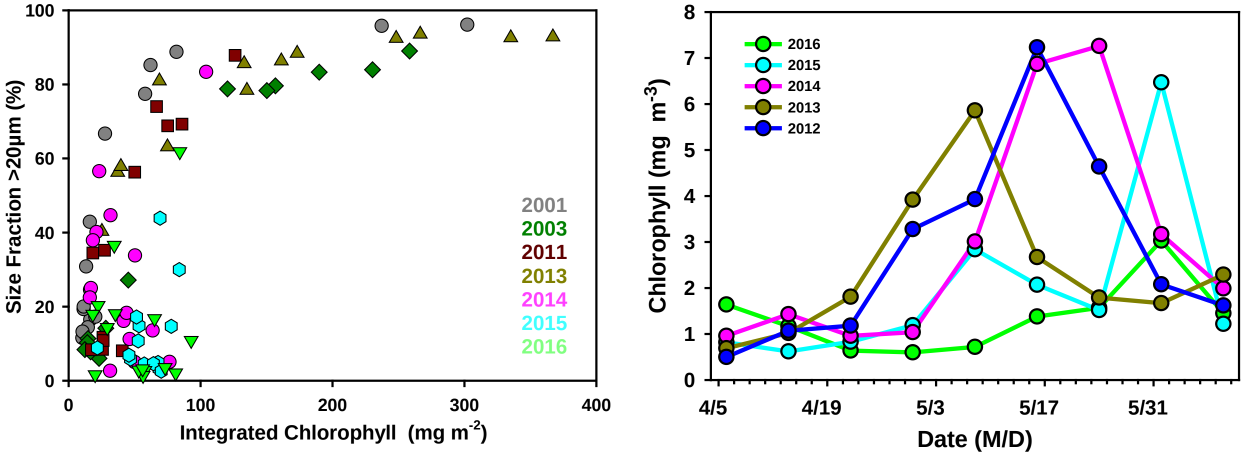

Figure 8. Contribution of the large phytoplankton size-fraction to total integrated chlorophyll a (left). MODIS Aqua satellite-derived surface chlorophyll for 8-day time intervals centered on midpoint of observation period (right).

Primary Production

During spring of 2012-2014, chlorophyll anomalies suggest high productivity, in contrast to 2015 and 2016 when productivity was low (Fig. 9). During summer, the pre-blob years had above average productivity while the blob years had low productivity. It is notable that low productivity during spring is often offset by a delayed summer bloom, however that was not the case during 2015 and particularly during 2016. The 2016 April through August time interval had the lowest average chlorophyll estimated for the Seward Line region over the 14-year observational life of the MODIS satellite. The only other year with comparable strong negative anomalies in both season was 2003 which was similar to 2016 in that it was characterized by a strong El Niño event.

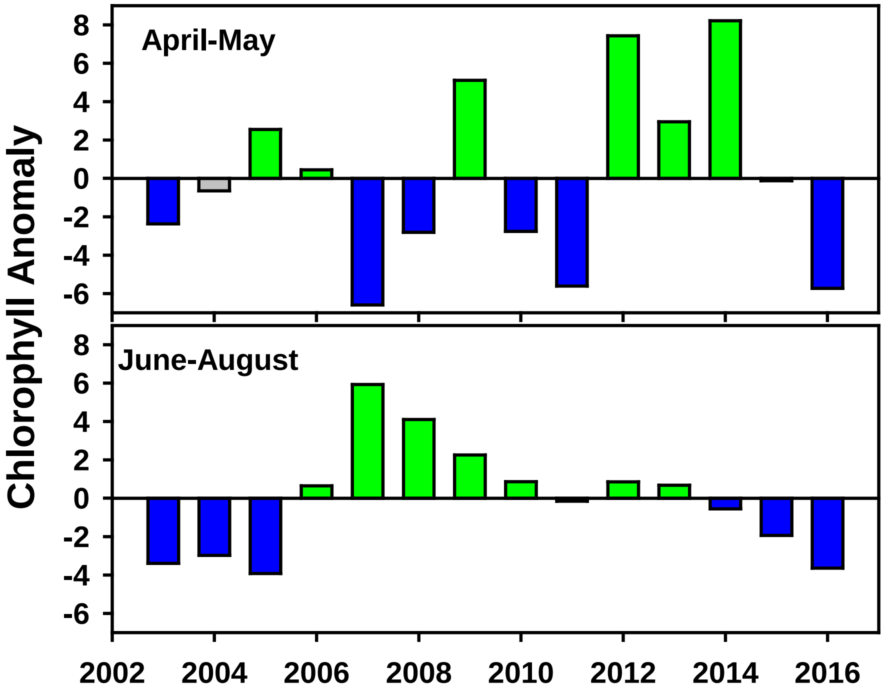

Figure 9. Seasonal chlorophyll anomalies observed along the Seward Line 2003-2016.

Microzooplankton

As for phytoplankton, microzooplankton biomass is typically higher in spring than fall (Fig, 10). It is notable that the "Blob" years of 2015 and 2016 showed very low spring biomass levels (even lower than in the low-bloom year of 2011; see Strom et al. 2017). The warm autumns of 2014 and 2015 also had exceptionally low biomass on all or part of the Seward Line. The coastal GOA tends to be a ciliate-dominated community, with dinoflagellates more important during high-production years (e.g., 2013) and in higher production regions (e.g., nearshore in fall). Although microzooplankton size data are not fully processed, the size composition of the community reflects the biomass trends, with low biomass springs of 2015 and 2016 mainly consisting of very small (≤20 µm) ciliates.

We are also finding that most large ciliates in the coastal GOA, and perhaps most ciliates of any size, retain chloroplasts from their ingested phytoplankton prey (termed 'stolen' chloroplasts). These chloroplasts remain functional inside the ciliate for days to weeks, and can contribute fixed carbon in substantial quantities to support respiration, a strategy thought to be important when phytoplankton production is intermittent.

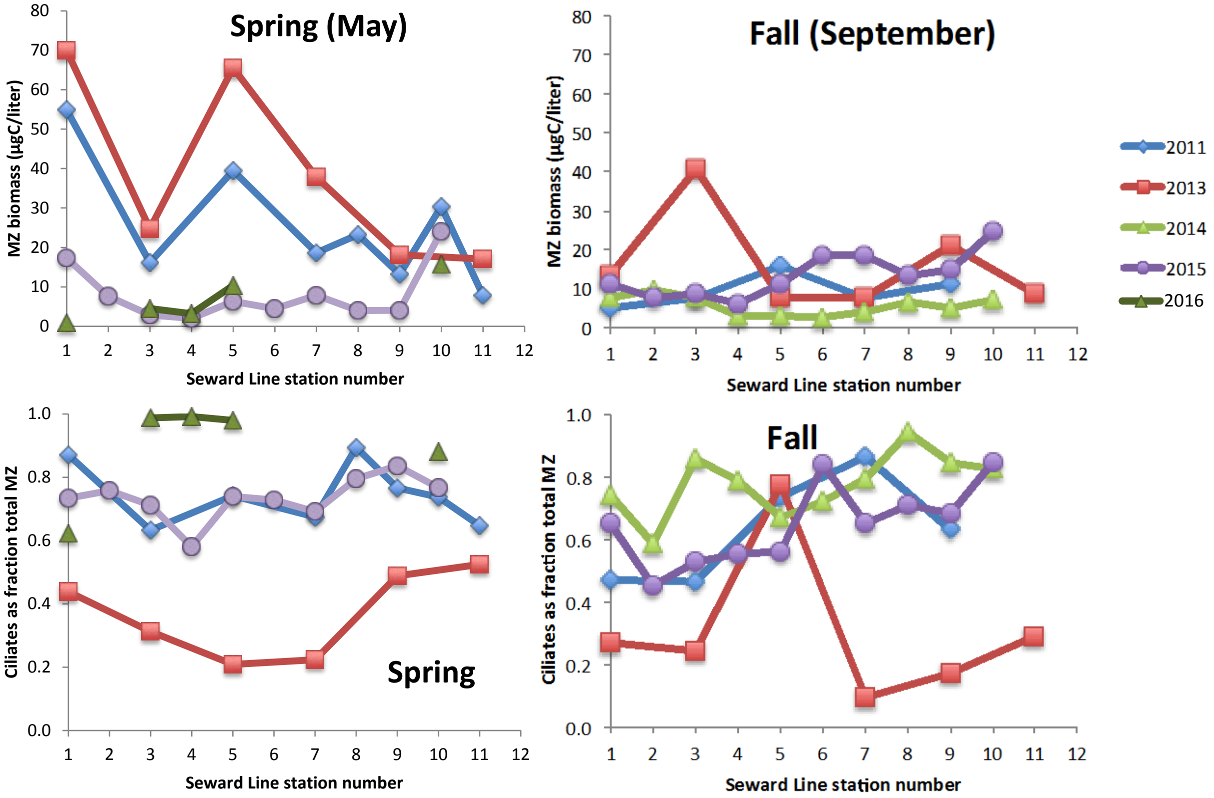

Figure 10. Microzooplankton biomass (top) and fraction of ciliates (bottom) along the Seward Line during May and September. Analysis of 2016 samples is still in progress.

Metazooplankton

The metazoan zooplankton community on the GOA shelf consists of over 200 recognized holoplanktonic species, of which about 3 dozen contribute the majority of the abundance and biomass (Appendix 2). The major suspension feeding groups captured by the 500-µm nets are the calanoid copepods and euphausiids, while the cnidarians (jellyfish and kin) and chaetognaths (arrow worms) are the major planktonic predators. Over the last 5 years, large calanoid abundance and biomass during May has increased steadily from below to above the long-term mean, while euphausiid abundance and biomass have been variable, with particularly low biomass during 2015-2016 (Fig. 11). Chaetognath abundance and biomass over this period have been at or below the long-term mean, except for 2016 when both exceeded the long-term mean. Cnidarian abundance increased significantly during 2015-2016, but without consistent correspondence to biomass.

The 150-µm nets better assess the abundance of the smaller calanoid copepods, the cyclopoid copepods, the larvaceans, and the shelled pteropods (Fig. 12). Over the past 5 years the abundance of these groups during May was typically near their long-term mean except for 2016 when abundances were generally significantly higher. Although very abundant, the smaller body size of these taxa meant their biomass was always relatively low in comparison to the larger-bodies species. It is notable that the long-term mean biomass of calanoids captured by the 150-µm nets during May was nearly the same as that estimated by the 500-µm nets; this demonstrates that spring biomass is dominated by the larger-bodied copepods.

By late summer, large calanoid abundance and biomass in the 500-µm nets have declined compared to May, while the abundance of euphausiids, chaetognaths and cnidarians remains similar to May, but with lower euphausiid biomass (Fig. 13). Large calanoid and chaetognath (and to a lesser extent euphausiid) abundance and biomass declined in 2015 compared to 2012-2014, while that of cnidarians increased in 2014 and 2015. Over the past 5 years the late summer abundance and biomass of the smaller calanoids, cyclopoids, larvaceans, and shelled pteropods in the 150-µm nets has been variable, with some years above the long-term mean (Fig. 14). The long-term mean abundance of small calanoids and cyclopoids was similar in fall to that of spring, while larvaceans and pteropods appear somewhat less abundant. It is notable that the long-term mean biomass of calanoids captured by the 150-µm nets during late-summer was nearly double that estimated by the 500-µm nets; this reflects the predominance of smaller-bodied copepod species during late summer.

During May, the predominant species within the larger copepods are *Neocalanus plumchrus/flemingeri, Metridia pacifica, N. cristatus*, and *Eucalanus bungii*, all of which have shown variability, but without systematic pattern. During May, the smaller copepods are numerically dominated by *Pseudocalanus* spp., *Oithona similis, Triconia borealis*, and to a lesser degree *Acartia* spp. The ontogenetic descent of the three *Neocalanus* species during late spring and early summer increases the relative importance of the remaining species, which show variability but no consistent patterns in their mean abundances during the fall. A notable trend within the copepods has been the increased prevalence and abundance of several California Current species, initially only observed during late-summer but most recently also observed during May albeit at extremely low abundances (Fig. 15). During 2016, these warm water species represented 10% of the calanoid community. Similarly, increases during the recent warm water years can be seen during May for the warm-water euphausiids *Thysanoessa inspinata* and *Euphausia pacifica* and during late-summer for the hydrozoan *Eirene indicans*.

Exploration of community structure using nMDS reveals a general cross-shelf patterning during spring, with PWS representing the most inshore habitat, but without a clear relationship to water temperature (Fig. 16). Late summer samples also show a clear cross-shelf structure, and while temperature does not appear to consistently relate to community structure, it is notable that the warm autumns of 2014-2016 all cluster closely along one edge of the projections – a pattern that is even clearer when the data are viewed as a 3-dimensional projection (not shown).

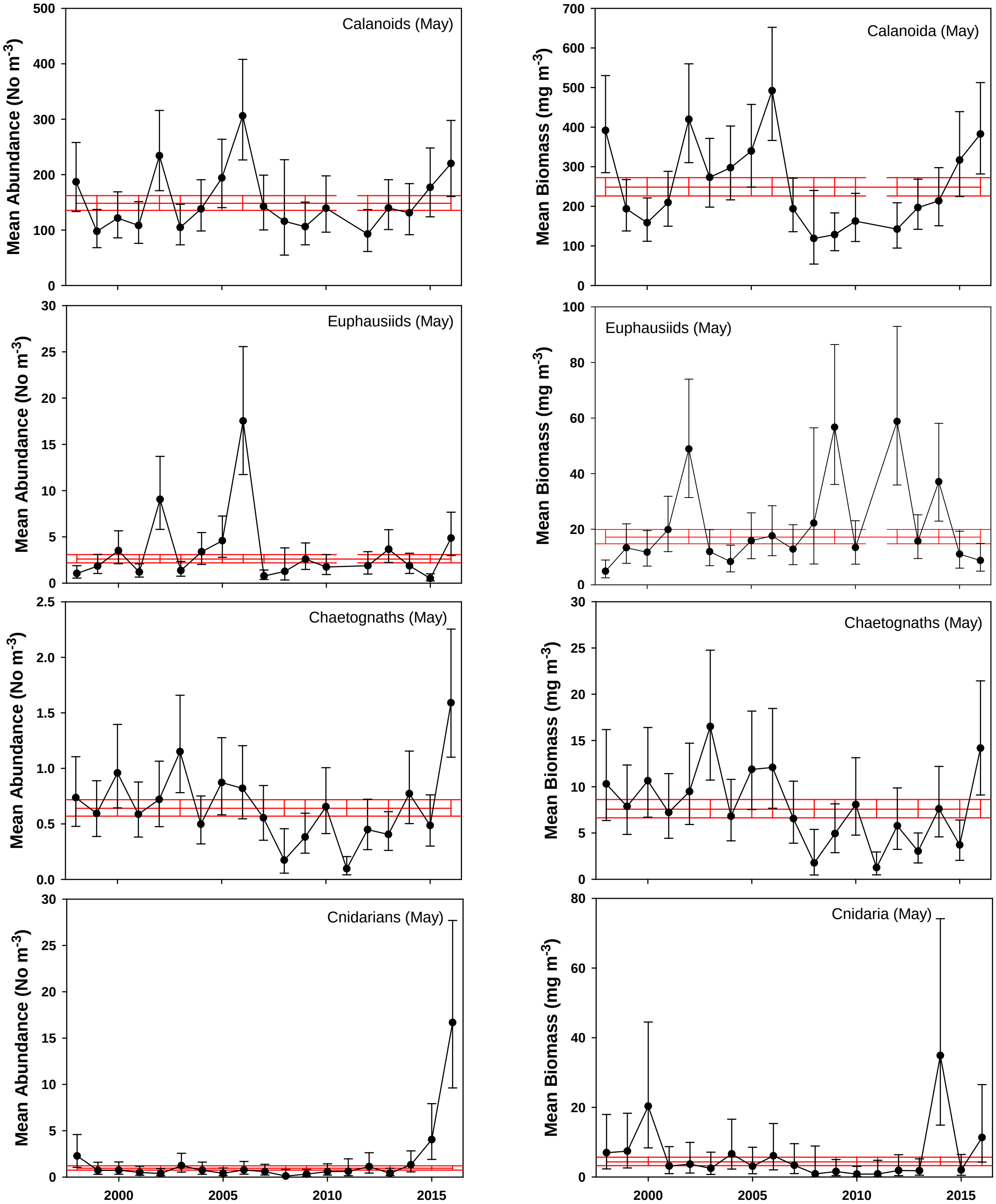

Figure 11. Abundance and wet-weight biomass of major zooplankton groups captured by 500µm-nets along the Seward Line during May 1998-2016. Error bars are 95% confidence intervals. Red line is the long-term mean bracketed by its confidence interval.

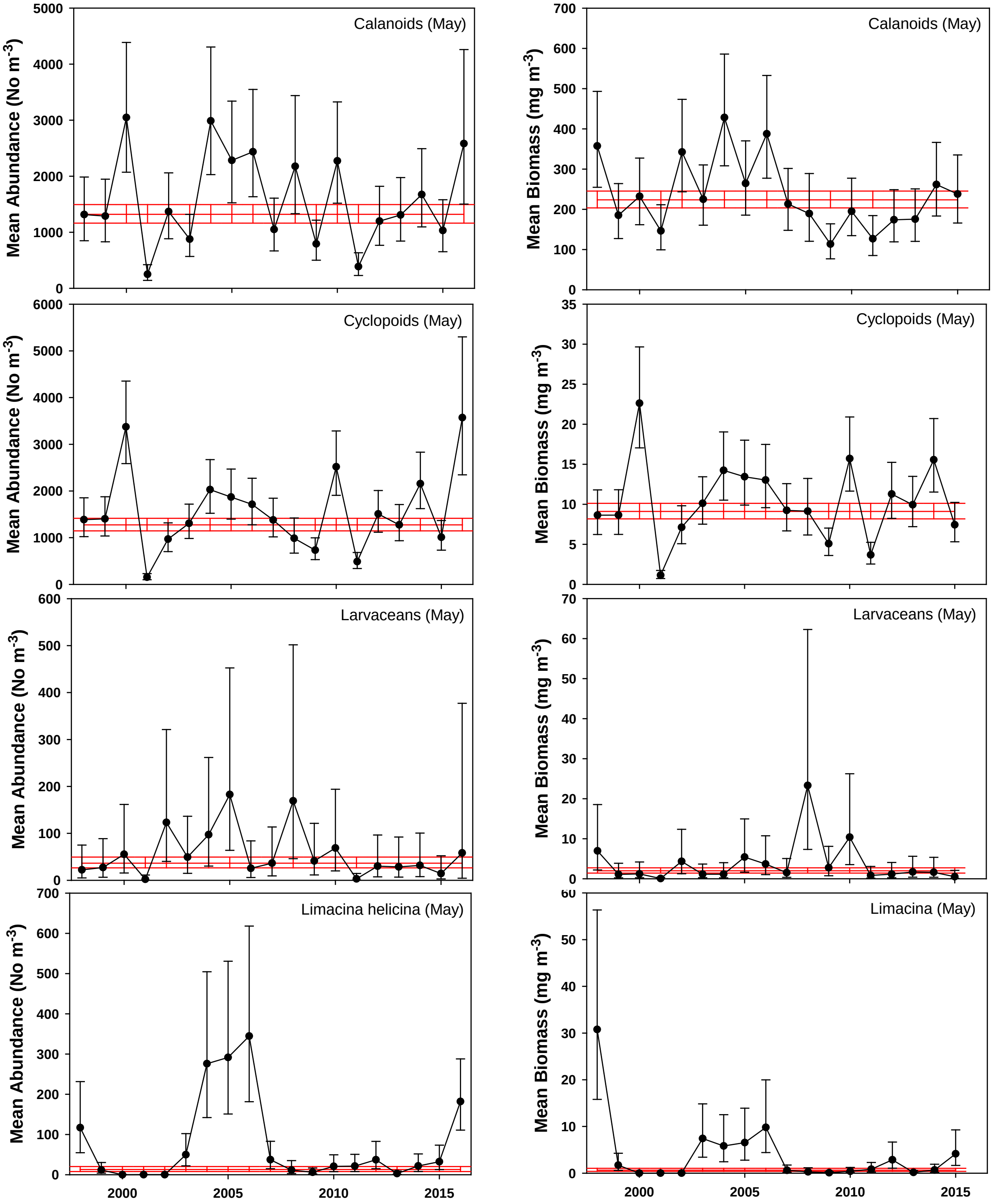

Figure 12. Abundance and wet-weight biomass of major zooplankton groups captured by 150µm-nets along the Seward Line during May 1998-2016. Error bars are 95% confidence intervals. Red line is the long-term mean bracketed by its confidence interval. Data for 2016 is preliminary and lacks biomass estimates.

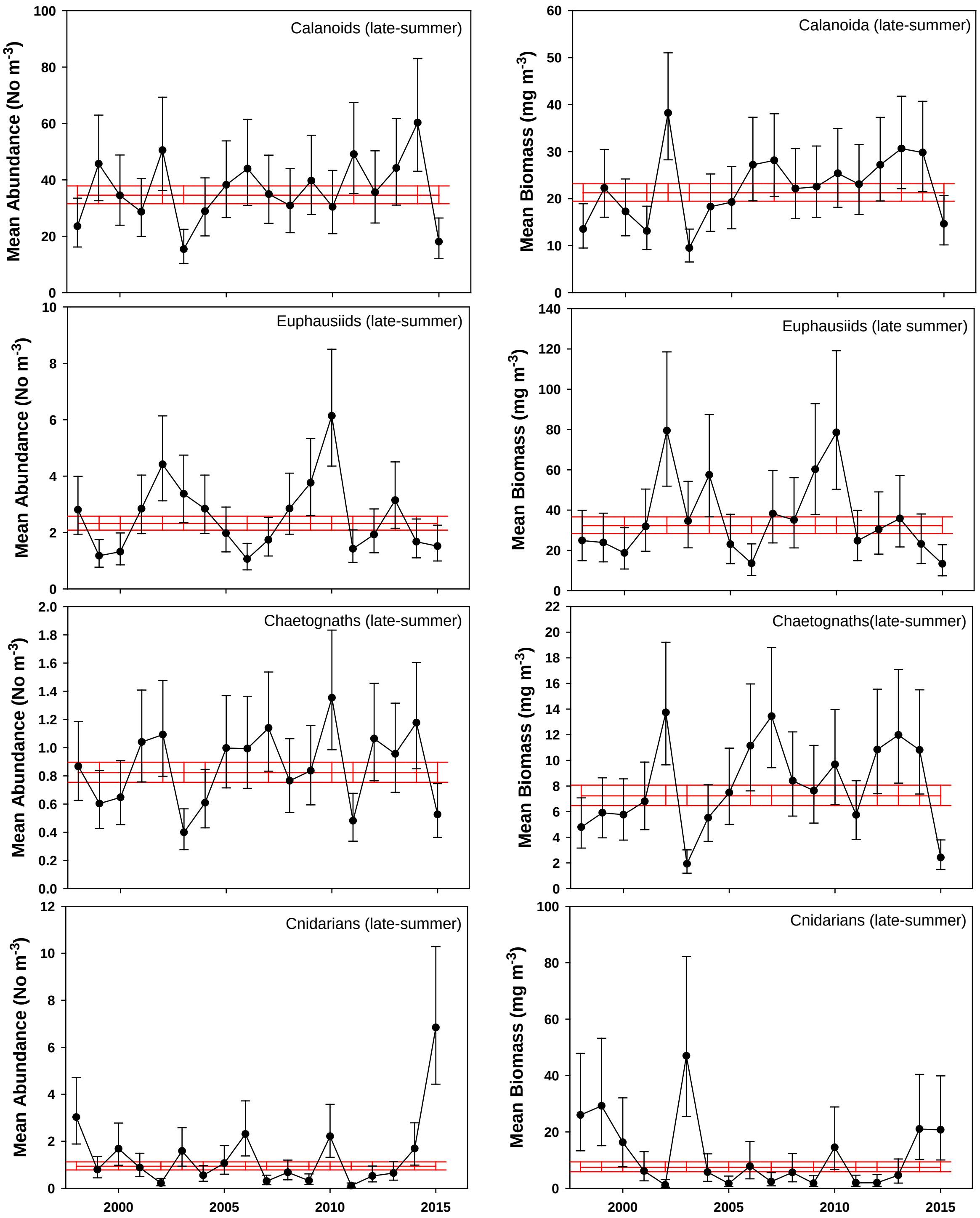

Figure 13. Abundance and wet-weight biomass of major zooplankton groups captured by 500µm-nets along the Seward Line during late-summer 1998-2015. Error bars are 95% confidence intervals. Red line is the long-term mean bracketed by its confidence interval. Data for 2016 is not yet available.

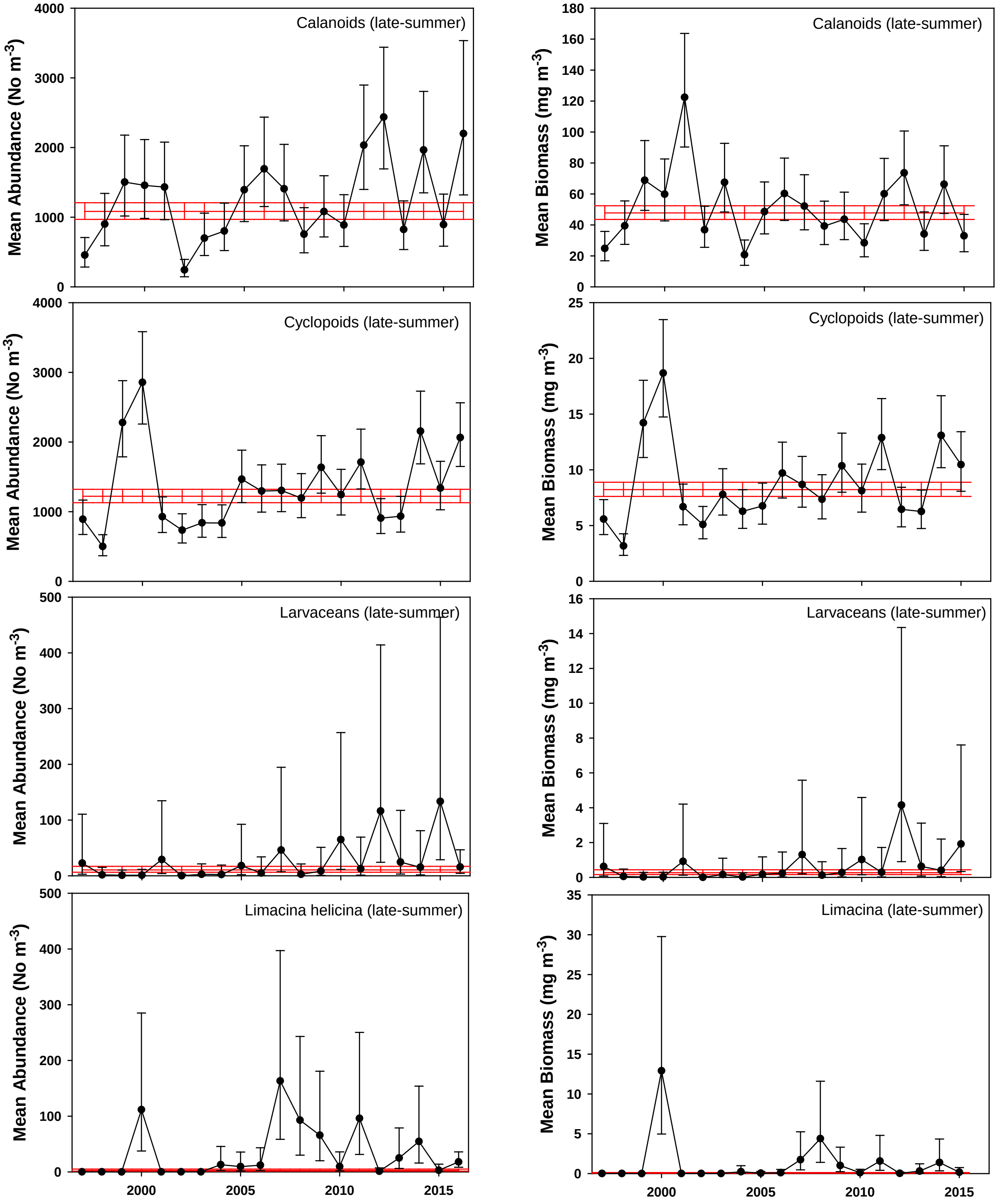

Figure 14. Abundance and wet-weight biomass of major zooplankton groups captured by 150μm-nets along the Seward Line during late-summer 1997-2016. Error bars are 95% confidence intervals. Red line is the long-term mean bracketed by its confidence interval. Data for 2016 is preliminary and lacks biomass estimates.

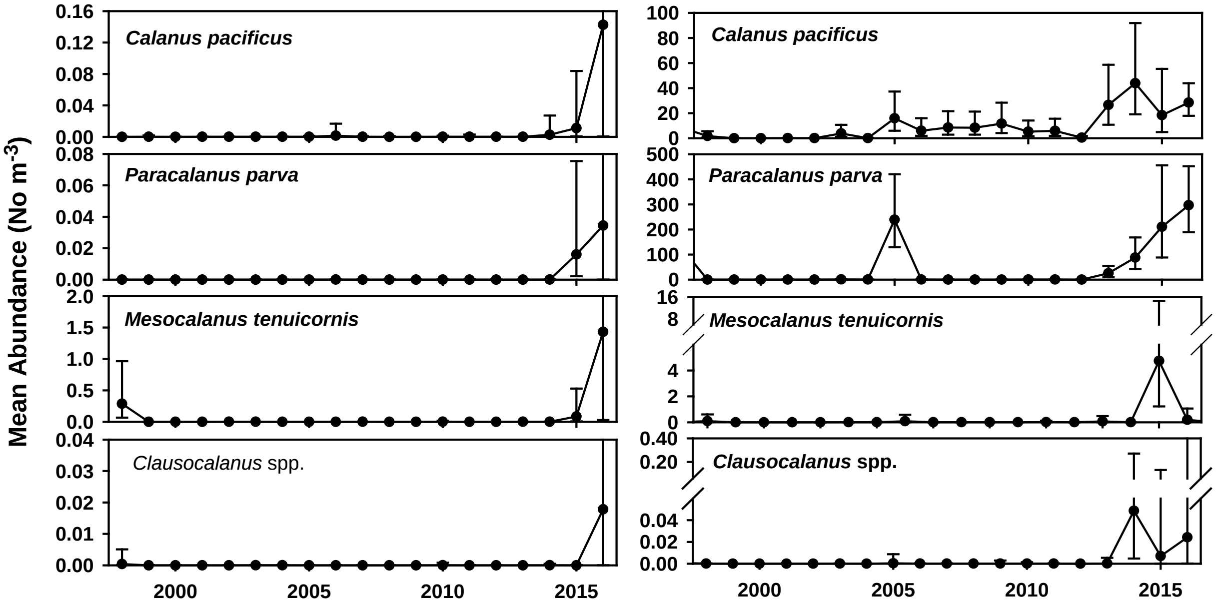

Figure 15. Abundance of four California Current calanoid copepods captured by 150µm-nets along the Seward Line during May (left) and late-summer (right) 1997-2016. Error bars are 95% confidence intervals.

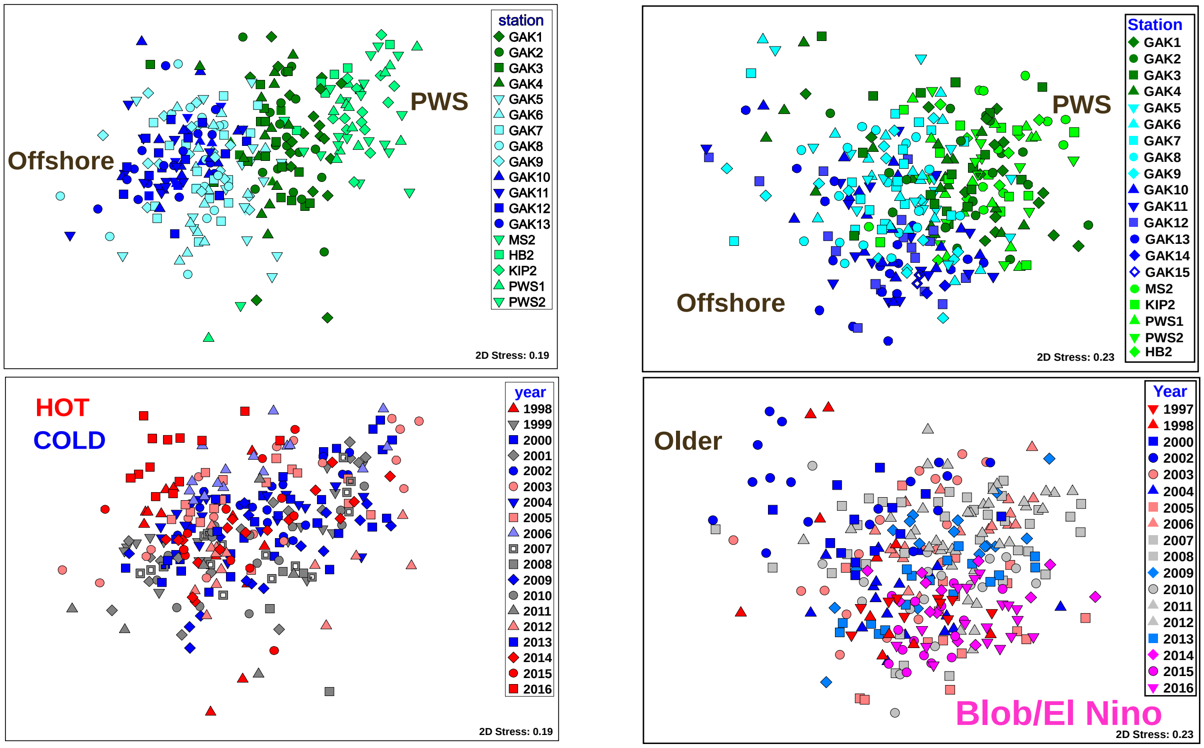

Figure 16. Two-dimensional projection of station similarity for 500-µm nets during May (left), and 150-µm nets during late summer (right). Color codes highlight cross shelf patterning and interannual patterning in relation to temperature (hot=red, warm=light red, neutral=gray, cool=light blue, cold=blue.

Seabirds and Marine Mammals

Survey effort for all cruises covered 7056 km in spring and 7420 km in fall. These surveys included transits from Homer to Resurrection Bay; transects used in analysis (2007-2015) within the Seward Line study area (Fig. 1) totaled 4241 km in spring and 4836 km in fall. For all surveys combined we observed 61 species of marine birds and 9 species of marine mammals. The numerically dominant species of marine birds were common murres (*Uria aalge*) and black-legged kittiwakes (*Rissa tridactyla*), both of which breed along the coast of the study area. Other abundant species included tufted puffins (*Fratercula cirrhata*), northern fulmars (*Fulmarus glacialis*), and fork-tailed storm-petrels (*Oceanodroma furcate*). In fall, sooty shearwaters (*Ardenna griseus*) and phalaropes (*Phalaropus* spp.) were also abundant. Shearwaters (*Ardenna* spp.) come from southern hemisphere breeding grounds to forage in Alaska during the northern summer and fall, while phalaropes are migrating south from northern Alaska breeding sites.

Overall, marine bird densities were higher during warm years, especially in fall (Fig. 17). PWS and the inner shelf showed the greatest differences between warm and cold years, particularly for ‘inshore’ species (larids, alcids, cormorants). ‘Offshore’ groups (fulmars, storm-petrels, albatrosses) always occupied mid-shelf and oceanic regions, although densities varied relative to temperature regimes. Shearwaters were more abundant during warm years, when they shifted from the mid-shelf and oceanic regions in spring to the inner shelf in fall.

Tests for differences between warm and cold years (Wilcoxon-Mann-Whitney rank-sum test with Holm-Bonferroni multiple comparison adjustment within seasons; $\alpha = 0.05$) indicated that the observed shift in distributions or abundance was significant for the following: shearwaters (higher in warm years from inner shelf to oceanic in fall); fulmars (higher densities during cold years in spring, but higher in warm years during fall); kittiwakes (higher in PWS during warm years for spring and fall); murres (higher in PWS and inner shelf in warm years, spring and fall); puffins (higher in cold years on mid-shelf in spring). For total birds combined (Fig. 18), densities were significantly higher in warm years in PWS and inner shelf waters in spring, and across all regions in fall.

Marine mammal observations suggest both baleen and toothed are broadly distributed throughout the survey area (Fig. 19). Baleen whales are dominated by fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) while toothed whales are dominated by Dall’s porpoise (*Phocoenoides dalli*). For pinnipeds, Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*) were most commonly observed, with both appearing to prefer coastal waters. Sea otters (*Enhydra lutris*) were entirely restricted to nearshore waters. The qualitative nature of mammal data precludes more in depth analysis.

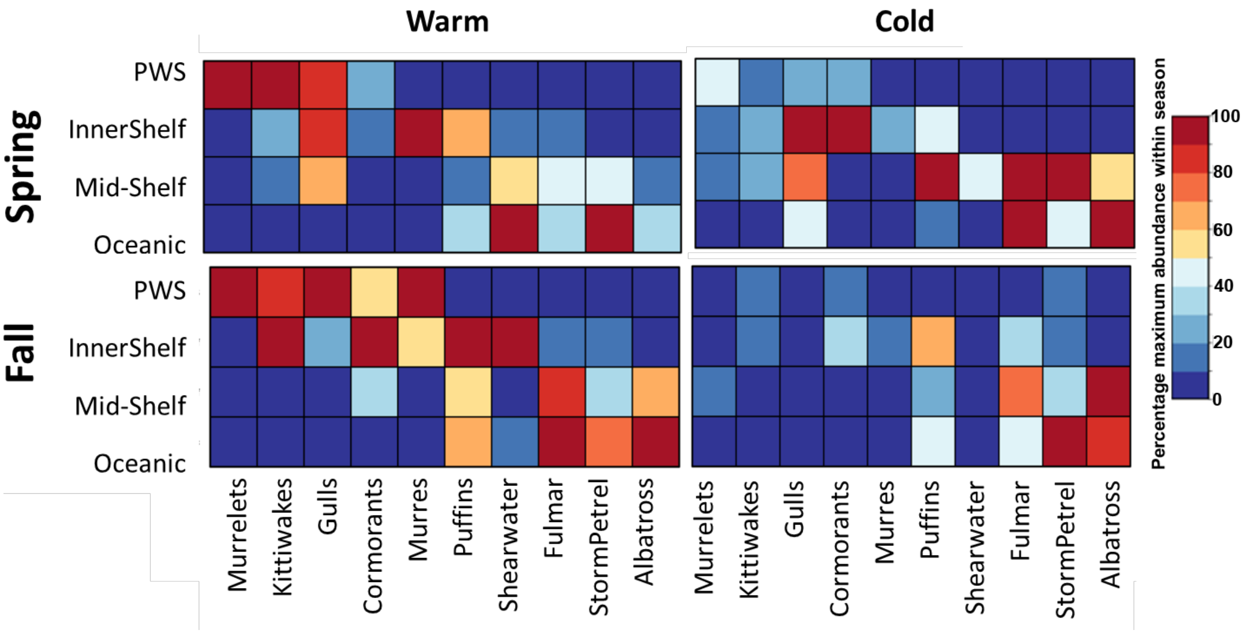

Figure 17. Cross-shelf distribution of 10 species-groups seasonally and between warm and cold years. Species groups on x-axis are arranged by tendency to be inshore to offshore foragers. Inshore species showed greatest differences between warm and cold years.

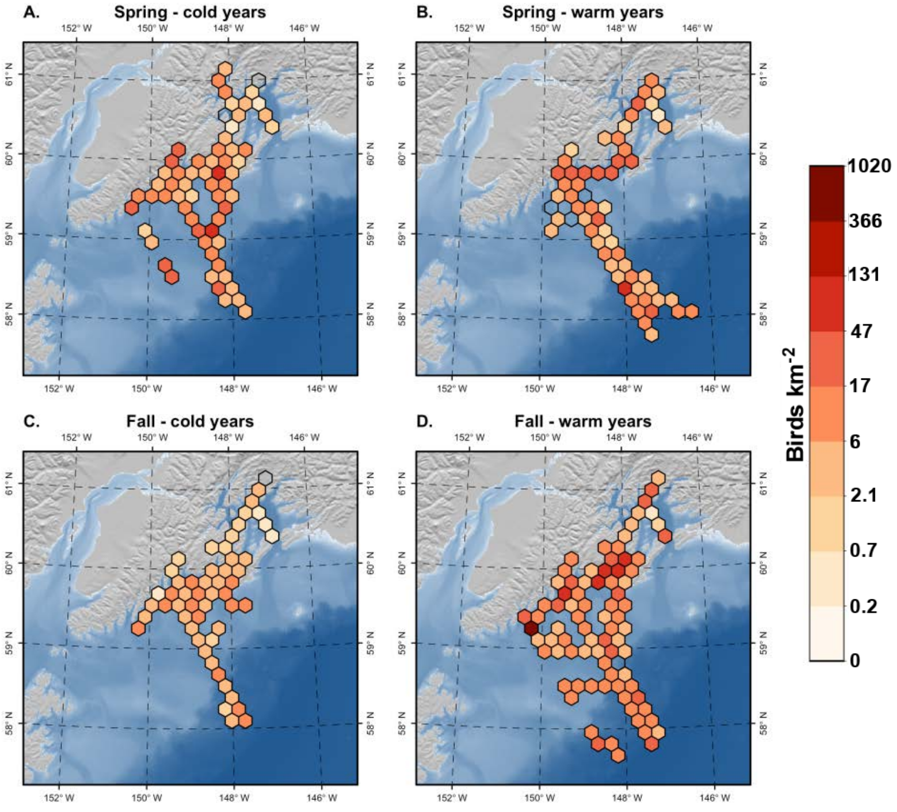

Figure 18. Distribution of total marine birds within the Seward Line study area, 2007-2015, for spring and fall during cold (2007-2009, 2013) and warm (2010, 2014, 2015) years.

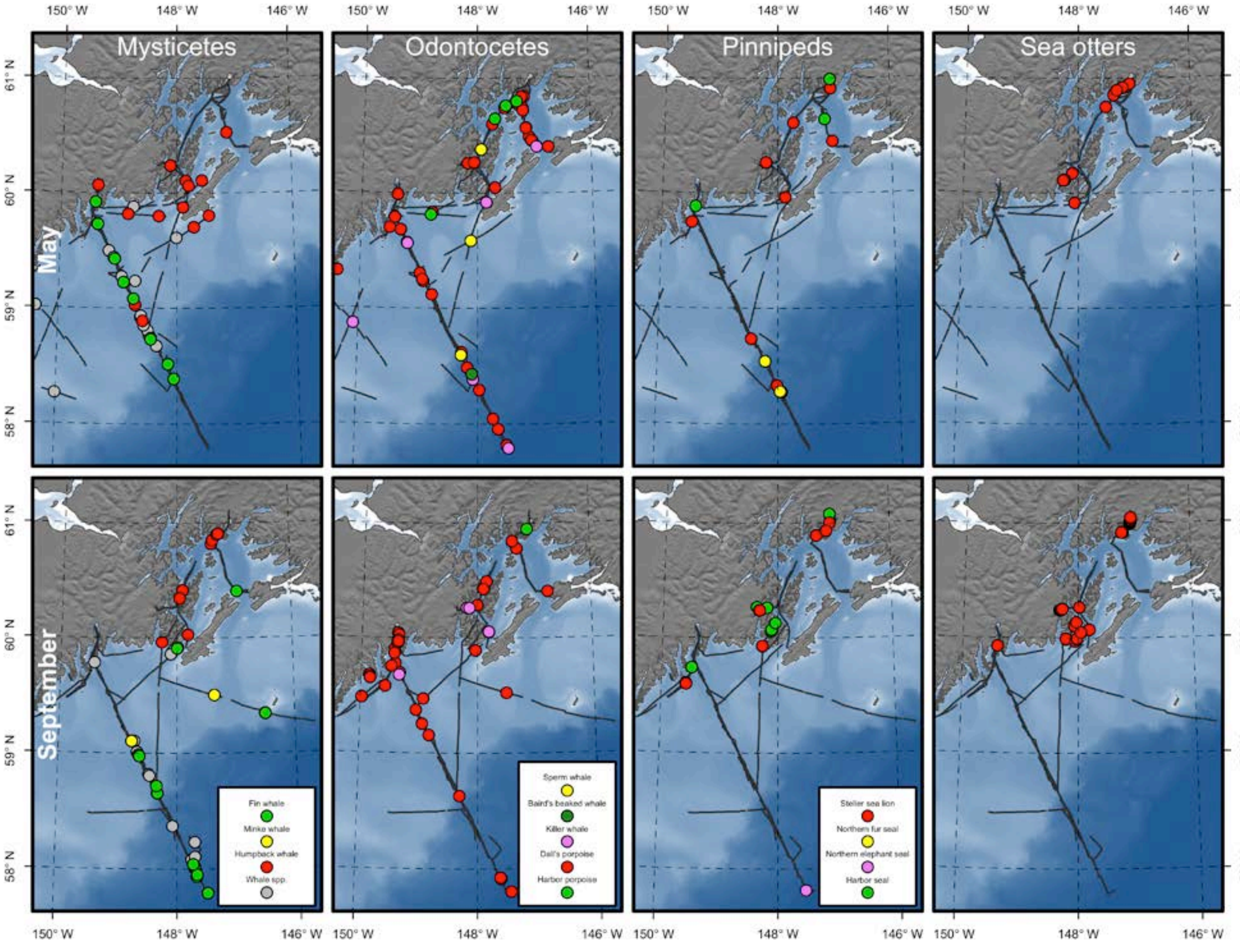

Figure 19. Distribution of marine mammals for Seward Line and Prince William Sound region during 2012-2016 cruises. Black lines represent survey effort.

DISCUSSION

For the most part our observations along the Seward Line are consistent with earlier observations regarding the major properties of this system in terms of its physics (Weingartner 2007), nutrient chemistry (Childers et al. 2005), phytoplankton (Strom et al. 2006), microzooplankton (Strom et al. 2007), and metazooplankton communities (Coyle and Pinchuk 2003, 2005). What this study adds is an increasing appreciation of the long-term mean values and particularly variability in response to environmental changes. Interannual differences in physical forcing within the GOA are readily manifested in the oceanographic environment (Janout et al. 2010), and these drive changes in both the phytoplankton response (Stabeno et al. 2016a,b, Strom et al. 2016), and the zooplankton communities (Doubleday and Hopcroft 2015, Sousa et al. 2016). Physical perturbations can result in unusual events at both lower trophic levels, such as the salp bloom during 2011 (Li et al. 2016), and at upper trophic levels, such as the recent murre mortality event (USFWS 2016).

The GOA is experiencing long-term warming and increased intensity of stratification (Weingartner and Danielson 2017). Nonetheless, the 2012-2016 period has seen considerable range in most of the observations made along the Seward Line: 2012 and 2013 were at or slightly below the climatological mean temperature, while late summer of 2014 and both seasons in 2015 and 2016 were well above the long-term mean temperatures. The synergistic effect of the 2016 El Niño building upon the Blob resulted in temperatures that exceeded those of both the 1997/98 and 2003 El Niño events. In recent decades the impact of El Niño on planktonic communities has been well documented along the North American coast (Peterson et al. 2002), with such events typically resulting in reduced primary production (Kahru and Mitchell 2000, Whitney and Welch 2002), increased coastal transport (Keister et al. 2011) and altered zooplankton species composition (Keister et al. 2005), all of which may impact higher trophic levels. Although the warm surface waters of the "Blob" in the GOA arose by a different mechanism (Bond et al. 2015), its ecological impacts in the GOA were similar to those associated with El Niño events, as has also been shown for the California Current System (Leising et al. 2015). Our observations reveal that the warm conditions reduced the mean cell size of the lowest trophic levels (phytoplankton and microzooplankton), and increased the contribution of smaller-bodied warm-water zooplankton species, as has been documented further to the south (i.e., Mackas et al. 2001, 2004, 2007).

Macronutrient, phytoplankton and microzooplankton time series all show a clear influence of the warmer 2015 and 2016 conditions. During 2013 and (on most of the shelf) 2014, the silicate:nitrate drawdown ratio in surface waters was 1.8, in agreement with the average reported by Strom et al. (2006) for May diatom-dominated communities on the Seward Line during the early 2000s. These nutrient ratios agree with chlorophyll data showing a bloom trajectory by which increases in chlorophyll are associated with increases in large cells (diatoms) on most of the shelf. In the recent warm years, however, silicic acid drawdown associated with spring production is more modest, with an overall silicate:nitrate drawdown ratio of 1.1. This is consistent with chlorophyll increases on the shelf in the springs of 2015 and 2016 being associated with smaller non-diatom phytoplankton. In addition to these changes in phytoplankton community composition, satellite ocean color data indicate delayed bloom timing and reduced magnitude.

Microzooplankton communities strongly reflected these interannual differences, with the warm springs of 2015 and 2016 having a low biomass community of small cells, mainly ciliates. Overall, the recent warm conditions have changed the spring protist assemblage from one dominated by chain diatoms, large ciliates and dinoflagellates (Strom et al. 2006, 2007, 2016), to one comprised mostly of small flagellate phytoplankton and small ciliates. This shift is likely to reduce the efficiency of production transfer to larger animals through the introduction of additional trophic levels near the base of the food web. However, the appearance of new, smaller mesozooplankton species adapted to warmer conditions may partially alleviate these reductions in efficiency. The question of why diatoms were less important in the recent warm years, despite growth-saturating spring concentrations of silicic acid and nitrate, awaits process studies that can address the mechanisms regulating spring production. Similarly, recent models (e.g., Ward and Follows 2016) also show that the presence of chloroplast-retaining ciliates has major implications for trophic transfer efficiency, overall primary production, and the resilience of planktonic food webs. We are in the process of developing quantitative approaches to the sampling and enumeration of these ciliates.

It is notable that despite high interannual thermal variability, many of the dominant zooplankton species in the GOA remain resilient to this variability, and do not show variability easily attributable to simple temperature forcing. This is particularly true during spring, when the keystone large-bodied species are generally uncoupled from ambient thermal conditions because their recruitment has been fueled by egg production dependent on lipids stored the previous year (Mackas and Tsuda 1999). For these species, factors that affect cross-shelf transport may be of greater consequence in determining local abundance (Mackas and Coyle 2005), and this in part maintains the strong cross-shelf gradients in the Gulf (Brickley and Thomas 2004, Coyle and Pinchuk 2005, Waite and Mueter 2013) that are apparent in our data. Nonetheless, in contrast to the spring, changes in the lowest trophic level composition and community structure are apparent during the fall, and likely related to increased survival of warm-water species that are normally seeded into the coastal waters where the North Pacific Current bifurcates (Mackas et al. 2007). The 2014-2016 samples during a period of extreme upper mixed layer heating suggests that the community structure is shifting toward a new domain not simply reflective of prior El Niño events. Other Gulf Watch Alaska investigators also observed shifts in zooplankton community structure associated with the warm anomaly (Batten et al. 2018, McKinstry and Campbell 2018). Thus, zooplankton may serve as important sentinels of ecosystem change (Richardson 2008), and their time-series collectively provide a means to examine change at global scales (Ji et al. 2010, Mackas et al. 2012). If the heat of the multiyear anomalous warm “Blob” dissipates, then lower trophic species compositions may return to those more typically observed during the past 15 years along the Seward Line.

At higher trophic levels, observations indicate that ‘inshore’ species of marine birds were most affected by changes in conditions in the northern GOA. PWS and the inner shelf became concentrated with inshore seabird species during warm years, including large numbers of migrant shearwaters (typically found farther offshore) into the inner shelf. Although seabirds increased inshore during warm years, recent seabird die-offs (from starvation) suggest that the shift in distribution may not have provided favorable foraging conditions in those regions for all birds. Rather, the shift inshore may reflect a response to more highly stratified waters throughout the GOA shelf during warm years. Based on oceanographic data, a typical pattern for a cold year, such as 2009, shows deeper, complex layers of low salinity waters. In warm years like 2015, the extension of high salinity offshore waters into the mid and inner shelf may have influenced the displacement (and concentration) of marine birds into the inshore regions, presumably because of changes to prey distribution. During warm years, the mixed layer depth is also typically shallower and the water column more strongly stratified than during cold years. Weak water-column mixing then affects primary productivity and prey, ultimately impacting upper trophic-level foragers like seabirds.

CONCLUSIONS

Many aspects of the GOA ecosystem show interannual variability, but notable changes have occurred since the fall of 2014 due to warm-water anomalies generated by a combination of the “Blob” and El Niño. These changes foreshadow the production regime that could be expected if the frequency and/or intensity of such warm events were to increase. If current long-term warming and stratification trends continue in the GOA this will likely result in a seasonally earlier and altered composition of the spring bloom, followed by a longer oceanographic summer with higher temperatures and reduced productivity. Based on our recent observations, we can expect increased contributions of warm water planktonic species and changes to energy and nutrient flux pathways. This would contribute to a further shoreward distribution of and reduced abundances of seabirds. Negative consequences to fisheries are also likely, with higher temperatures increasing fish metabolic demand, while at the same time the zooplankton prey available may be of reduced size and energetic quality. Continued observations along the Seward Line, improved collaborations with NOAA Fisheries, and expanded observations in the GOA by the National Science Foundation’s Long-Term Ecological Research Network should ensure we are better poised to study future ecosystem responses to climatological change.

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APPENDIX 1. OCEANOGRAPHIC RESOURCES

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Compiled SST data: the Extended Reconstructed SST datasets (currently version 4): https://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v4

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APPENDIX 2. HOLOZOOPLANKON TAXA

Phylum	Class	Order	Family	Scientific Name
Annelida	Polychaeta	Phyllodocida	Syllidae	*Myrianida*
			Tomopteridae	*Tomopteris*
			Typhloscolecidae	*Typhloscolex muelleri*
Arthropoda	Branchiopoda	Diplostraca	Podonidae	*Evadne nordmanni*
			Podonidae	*Podon leuckarti*
	Hexanauplia	Calanoida	Acartiidae	*Acartia clausi*
			Acartiidae	*Acartia danae*
			Acartiidae	*Acartia longiremis*
			Acartiidae	*Acartia tumida*
			Aetideidae	*Aetideus armatus*
			Aetideidae	*Aetideus pacificus*
			Aetideidae	*Bradyidius saanichi*
			Aetideidae	*Chiridius gracilis*
			Aetideidae	*Chiridius obtusifrons*
			Aetideidae	*Chiridius polaris*
			Aetideidae	*Chirundina streetsii*
			Aetideidae	*Euchirella pseudopulchra*
			Aetideidae	*Euchirella pulchra*
			Aetideidae	*Euchirella rostrata*
			Aetideidae	*Gaetanus campbellae*
			Aetideidae	*Gaetanus minutus*
			Aetideidae	*Pseudochirella obtusa*
			Aetideidae	*Undeuchaeta intermedia*
			Arietellidae	*Arietellus setosus*
			Augaptilidae	*Pseudhaloptilus pacificus*
			Calanidae	*Calanus marshallae*
			Calanidae	*Calanus pacificus*
			Calanidae	*Mesocalanus tenuicornis*
			Calanidae	*Neocalanus cristatus*
			Calanidae	*Neocalanus flemingeri*
			Calanidae	*Neocalanus plumchrus*
			Candaciidae	*Candacia bipinnata*
			Candaciidae	*Candacia columbiae*
			Centropagidae	*Centropages abdominalis*
			Clausocalanidae	*Clausocalanus lividus*
			Clausocalanidae	*Clausocalanus parapergens*
			Clausocalanidae	*Microcalanus pygmmaeus*
			Clausocalanidae	*Pseudocalanus minus*
			Clausocalanidae	*Pseudocalanus newmanii*
			Clausocalanidae	*Pseudocalanus minutus*
			Clausocalanidae	*Pseudocalanus acuspes*

Phylum	Class	Order	Family	Scientific Name
			Eucalanidae	*Eucalanus bungii*
			Euchaetidae	*Paraeuchaeta elongata*
			Heterorhabdidae	*Heterorhabdus clausi*
			Heterorhabdidae	*Heterorhabdus pacificus*
			Heterorhabdidae	*Heterorhabdus papilliger*
			Heterorhabdidae	*Paraheterorhabdus robustus*
			Heterorhabdidae	*Heterorhabdus tanneri*
			Heterorhabdidae	*Heterostylites longicornis*
			Heterorhabdidae	*Heterostylites major*
			Lucicutiidae	*Lucicutia curta*
			Lucicutiidae	*Lucicutia flavicornis*
			Lucicutiidae	*Lucicutia ovalis*
			Metridinidae	*Gaussia princeps*
			Metridinidae	*Metridia okhotensis*
			Metridinidae	*Metridia ornata*
			Metridinidae	*Metridia pacifica*
			Metridinidae	*Metridia princeps*
			Metridinidae	*Pleuromamma abdominalis*
			Metridinidae	*Pleuromamma scutullata*
			Metridinidae	*Pleuromamma xiphias*
			Paracalanidae	*Calocalanus styliremis*
			Paracalanidae	*Paracalanus parvus*
			Phaennidae	*Onchocalanus magnus*
			Pontellidae	*Epilabidocera amphitrites*
			Scolecitrichidae	*Lophothrix frontalis*
			Scolecitrichidae	*Pseudoamallothrix emarginata*
			Scolecitrichidae	*Pseudoamallothrix inornata*
			Scolecitrichidae	*Pseudoamallothrix ovata*
			Scolecitrichidae	*Racovitzanus antarcticus*
			Scolecitrichidae	*Scaphocalanus brevicornis*
			Scolecitrichidae	*Scaphocalanus echinatus*
			Scolecitrichidae	*Scaphocalanus magnus*
			Scolecitrichidae	*Scolecithricella minor*
			Scolecitrichidae	*Scolecithrix*
			Scolecitrichidae	*Scottocalanus persecans*
			Temoridae	*Eurytemora*
			Tharybidae	*Tharybis fultoni*
			Tortanidae	*Tortanus discaudatus*
		Cyclopoida	Oithonidae	*Oithona similis*
			Oithonidae	*Oithona setigera*
		Harpacticoida	Ectinosomatidae	*Microsetella*
			Tisbidae	*Tisbe*

Phylum	**Class**	**Order**	**Family**	**Scientific Name**
		Monstrilloida	Monstrillidae	*Monstrilla*
		Poecilostomatoida	Corycaeidae	*Corycaeus*
			Lubbockiidae	*Lubbockia wilsonae*
			Lubbockiidae	*Pseudolubbockia dilatata*
			Oncaeidae	*Oncaea*
		Siphonostomatoida		
	Malacostraca	Amphipoda	Atylidae	*Atylus*
			Cyphocarididae	*Cyphocaris challengeri*
			Dairellidae	*Dairella*
			Eusiridae	*Rhachotropis*
			Hyperiidae	*Hyperia medusarum*
			Hyperiidae	*Hyperia*
			Hyperiidae	*Hyperoche medusarum*
			Hyperiidae	*Themisto libellula*
			Hyperiidae	*Themisto pacifica*
			Lanceolidae	*Lanceola clausii*
			Paraphronimidae	*Paraphronima crassipes*
			Pardaliscidae	*Nicippe tumida*
			Phronimidae	*Phronima sedentaria*
			Phrosinidae	*Primno macropa*
			Scinidae	*Scina borealis*
			Vibiliidae	*Vibilia caeca*
		Decapoda	Pasiphaeidae	*Pasiphaea pacifica*
			Pasiphaeidae	*Pasiphaea tarda*
			Sergestidae	*Eusergestes similis*
		Euphausiacea	Euphausiidae	*Euphausia pacifica*
				Nematoscelis difficilis
				Stylocheiron maximum
				Tessarabrachion oculatum
				Thysanoessa inermis
				Thysanoessa inspinata
				Thysanoessa longipes
				Thysanoessa raschii
				Thysanoessa spinifera
		Isopoda	Munnopsidae*	
		Isopoda	Microniscidae	
		Lophogastrida	Gnathophausiidae	*Neognathophausia gigas*
		Mysida	Mysidae	*Caesaromysis hispida*
				Acanthomysis stelleri
				Meterythrops robustus
				Neomysis mercedis
				Neomysis rayii

Phylum	**Class**	**Order**	**Family**	**Scientific Name**
				Pacifacanthomysis nephrophthalma
				Pseudomma
				Stilomysis grandis
				Xenacanthomysis pseudomacropsis
	Ostracoda	Halocyprida	Halocyprididae*	
Chaetognatha	Sagittoidea	Aphragmophora	Sagittidae	*Parasagitta elegans*
				Pseudosagitta lyra
		Phragmophora	Eukrohniidae	*Eukrohnia hamata*
Chordata	Larvacea	Copelata	Fritillariidae	*Appendicularia sicula*
			Fritillariidae	*Fritillaria borelais*
			Fritillariidae	*Fritillaria pellucida*
			Oikopleuridae	*Oikopleura dioica*
			Oikopleuridae	*Oikopleura labradorensis*
			Oikopleuridae	*Oikopleura*
	Thaliacea	Doliolida	Doliolidae	*Dolioletta*
		Salpida	Salpidae	*Cyclosalpa bakeri*
				Salpa aspera
				Salpa fusiformis
Cnidaria	Hydrozoa	Anthoathecata	Boreohydridae	*Plotocnide borealis*
			Bougainvilliidae	*Bougainvillia principis*
				Bougainvillia superciliaris
				Bougainvillia
			Bythotiaridae	*Calycopsis nematomorpha*
			Corymorphidae	*Euphysa flammea*
			Corynidae	*Sarsia princeps*
				Sarsia tubulosa
			Pandeidae	*Pandea*
				Stomotoca atra
			Proboscidactylidae	*Proboscidactyla flavicirrata*
			Rathkeidae	*Rathkea octopunctata*
			Tubulariidae	*Hybocodon prolifer*
		Leptothecata	Aequoreidae	*Aequorea victoria*
			Campanulariidae	*Clytia gregaria*
				Obelia longissima
				Staurophora mertensii
			Eirenidae	*Eutonina indicans*
			Laodiceidae	*Ptychogena lactea*
			Melicertidae	*Melicertum octocostatum*
			Mitrocomidae	*Mitrocoma cellularia*
				Mitrocomidae
			Tiaropsidae	*Tiaropsidium kelseyi*
				Tiaropsis multicirrata

Phylum	Class	Order	Family	Scientific Name
		Limnomedusae	Olindiidae	*Eperetmus typus*
				Gonionemus vertens
		Narcomedusae	Aeginidae	*Aegina citrea*
				Aeginopsis laurentii
			Cuninidae	*Cunina*
				Solmissus marshalli
		Siphonophorae*		
			Diphyidae	*Dimophyes arctica*
			Prayidae	*Praya*
		Trachymedusae	Halicreatidae	*Halicreas*
			Halicreatidae	*Haliscera*
			Rhopalonematidae	*Aglantha digitale*
	Scyphozoa	Coronatae	Atollidae	*Atolla*
			Periphyllidae	*Periphylla periphylla*
		Semaeostomeae	Cyaneidae	*Cyanea capillata*
			Pelagiidae	*Chrysaora melanaster*
			Ulmaridae	*Aurelia aurita*
			Ulmaridae	*Phacellophora camtschatica*
Ctenophora	Nuda	Beroida	Beroidae	*Beroe cucumis*
	Tentaculata	Cydippida	Pleurobrachiidae	*Pleurobrachia*
			Pleurobrachiidae	*Hormiphora*
Mollusca	Gastropoda	Gymnosomata	Clionidae	*Clione limacina*
		Gymnosomata	Pneumodermatidae	*Pneumodermopsis macrochira*
		Gymnosomata*		
		Littorinimorpha	Carinariidae	
		Thecosomata	Cavoliniidae	*Cavolinia*
			Cliidae	*Clio*
			Creseidae	*Creseis*
			Cymbuliidae	*Corolla spectabilis*
				Cymbulia
			Limacinidae	*Limacina helicina*
Nemertea*				
Cercozoa*	Thecofilosea			

* indicates a taxa where finer taxonomic resolution in not normally attempted and multiple species are known to be encompassed