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ORIGINAL ARTICLE

Zooplankton abundance trends and patterns in Shelikof Strait, western Gulf of Alaska, USA, 1990–2017

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A multivariate approach was used to analyze spring zooplankton abundance in Shelikof Strait, western Gulf of Alaska. abundance of individual zooplankton taxa was related to environmental variables using generalized additive models. The most important variables that correlated with zooplankton abundance were water temperature, salinity and ordinal day (day of year when sample was collected). A long-term increase in abundance was found for the calanoid copepod *Calanus pacificus*, copepodite stage 5 (C5). A dynamic factor analysis (DFA) indicated one underlying trend in the multivariate environmental data that related to phases of the Pacific Decadal Oscillation. DFA of zooplankton time series also indicated one underlying trend where the positive phase was characterized by increases in the abundance of *C. marshallae* C5, *C. pacificus* C5, *Eucalanus bungii* C4, *Pseudocalanus* spp. C5 and *Limacina helicina* and declines in the abundance of *Neocalanus cristatus* C4 and *Neocalanus* spp. C4. The environmental and zooplankton DFA trends were not correlated over the length of the entire time period; however, the two time series were correlated post-2004. The strong relationship between environmental conditions, zooplankton abundance and time of sampling suggests that continued warming in the region may lead to changes in zooplankton community composition and timing of life history events during spring.

KEYWORDS: Gulf of Alaska; zooplankton; abundance; trends; warming

INTRODUCTION

Zooplankton occupy a key position in pelagic food webs, serving as a critical link between primary producers and higher trophic levels. As such, this group has been the focus of intense research linking population level responses to climate variability (Beaugrand, 2003; Chiba *et al.*, 2006; Beaugrand and Kirby, 2018). Zooplankton are considered as indicators of ecosystem response to climate due to their strong biological response to temperature, short generation times and importance in the global carbon cycle (Beaugrand, 2005; Hays *et al.*, 2005; Steinberg and Landry, 2017; McQuatters-Gollop *et al.*, 2019). However, questions remain about how zooplankton respond to the interacting effects of large-scale and local climate (Kvile *et al.*, 2016). Changes in zooplankton population size are viewed as especially important to understand the potential for climate-driven changes in match–mismatch dynamics with fish (Edwards and Richardson, 2004; Sydeman and Bograd, 2009; Thackeray, 2012). Zooplankton population shifts are expected to operate differently across ecosystems and must be understood in the context of local oceanography and long-term trends (Ji *et al.*, 2010; Atkinson *et al.*, 2015). Here, we examined a time series in the western Gulf of Alaska (GOA) to determine if long-term trends were present in the zooplankton population and determine if trends related to regional climate and local oceanography. Climate-mediated changes in zooplankton community structure, life history timing and production have important ramifications for higher-trophic-level fishes, seabirds and mammals as bottom-up shifts have the potential to influence not only predator–prey synchrony but also reproductive success, migration, distribution and abundance and population density (Thompson *et al.*, 2012; Hollowed *et al.*, 2013; Salinger *et al.*, 2013).

The western GOA (Fig. 1A) is a large, coastal ocean system dominated by the Alaska Coastal Current (ACC), a current forced by alongshore winds and freshwater runoff (Royer, 1981a, b; Stabeno *et al.*, 2004; Weingartner *et al.*, 2005). Due to the ACC and winds, the GOA is predominantly a downwelling system but is productive due to the dynamic nature of the regional oceanography that is characterized by eddies, upwelling and flux in the surface Ekman layer (Stabeno *et al.*, 2004; Mordy *et al.*, 2019). The Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) program has been conducting research in the western GOA (Fig. 1A) since the late 1970s in order to investigate the early life history of *Gadus chalcogrammus* (walleye pollock), the focus of one of the largest commercial fisheries in the United States (Schumacher and Kendall, 1995; Kendall *et al.*, 1996; McClatchie *et al.*, 2014). Shelikof Strait and the area to

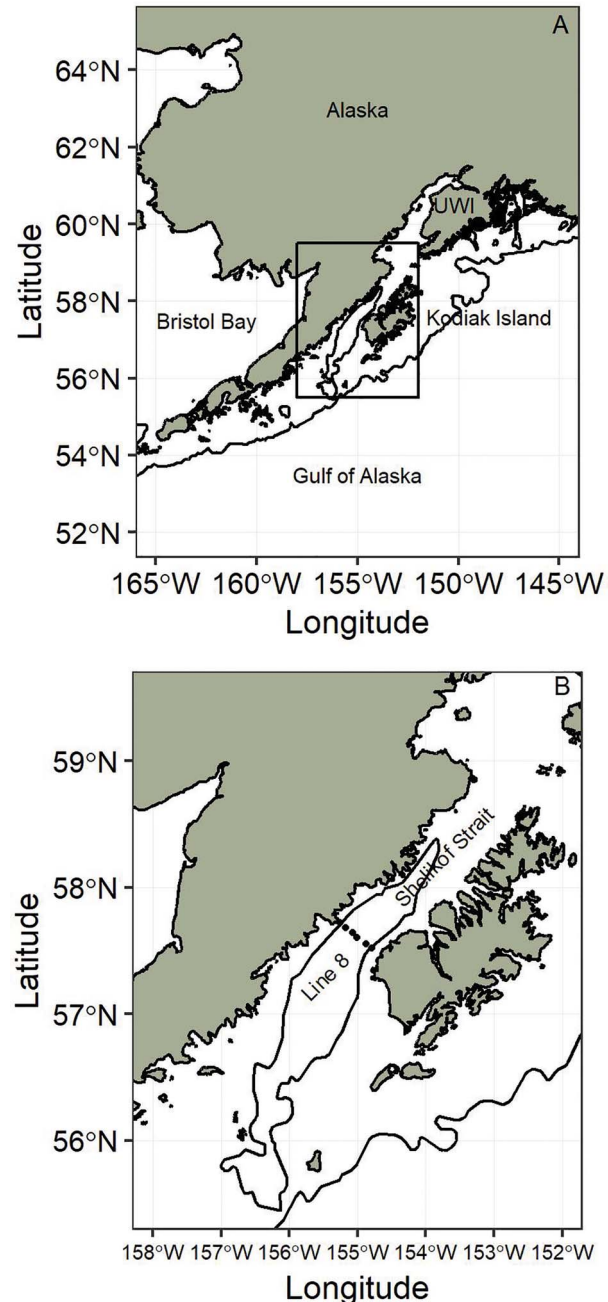


Fig. 1. Western GOA Region, USA, with box highlighting the study region (A) and location of Line 8 at the southwestern end of Shelikof Strait and Kodiak Island (B). UWI indicates the location used to calculate upwelling indices (A). Black circles indicate Line 8 sampling stations (B). Bathymetry line is the 200-m contour.

the southwest of Kodiak Island (Fig. 1B) are the locations of the largest spawning ground and nursery area for walleye pollock in the Gulf of Alaska. Sampling at Line 8 was designed to capture the oceanography and plankton abundances encountered by larval and juvenile walleye

pollock in this critical nursery area to provide insight into recruitment and population variability (Schumacher and Kendall, 1995; Kendall *et al.*, 1996).

The spring zooplankton community in the coastal, western Gulf of Alaska and Shelikof Strait is dominated by calanoid copepods, particularly *Neocalanus plumchrus* and *N. flemingeri* (hereafter, *Neocalanus* spp.), in terms of biomass, and *Neocalanus* spp., *Metridia pacifica*, *Pseudocalanus* spp., *Oithona* spp. and *Calanus marshallae* in terms of abundance (Cooney, 1986; Napp *et al.*, 1996; Incze *et al.*, 1997). Also present are euphausiids (primarily *Thysanoessa inermis* and *T. spinifera*), pteropods (*Limacina helicina* and *Clione limacina*), appendicularians (primarily *Oikopleura* spp.), chaetognaths (*Parasagitta elegans*, *Eukrohnia hamata*), amphipods (primarily *Themisto pacifica*) and cnidarians (Coyle and Pinchuk, 2003; Coyle and Pinchuk, 2005; Sousa *et al.*, 2016). Zooplankton abundance is typically higher in the nearshore region compared to offshore, and interannual variability of this community occurs in the context of a strong, seasonal signal (Napp *et al.*, 1996; Coyle and Pinchuk, 2003). Sousa *et al.* (2016) explored the relationships between oceanography and the zooplankton community along a cross-shelf transect in the northern Gulf of Alaska using a spring time series from 1998 to 2009. The study found changes in zooplankton community composition and abundance were likely the result of complex abiotic and biotic factors and their timing. In particular, the role of wind and transport was found to be important as well as oceanographic features that might enhance primary production, such as cross-shelf mixing (Sousa *et al.*, 2016). These findings showed many similarities with the conclusions of Napp *et al.* (1996) who highlighted the importance of mesoscale features (fronts, meanders and eddies) to zooplankton distribution and Coyle and Pinchuk (2005) who mentioned the role of freshwater discharge, wind and upwelling that drive transport and cross-shelf exchange of plankton communities.

The objective of this study was to determine if trends and patterns in zooplankton abundance could be detected at a long-term monitoring line in Shelikof Strait. Specific objectives were (i) to determine if individual zooplankton taxa correlated with environmental variables, (ii) to determine if individual zooplankton taxa have increased or decreased over time and (iii) to determine whether community-wide trends were evident. First, we related zooplankton abundance data to environmental variables to determine if individual taxa were correlated with environmental variables. We did this using a nonlinear approach, generalized additive models (GAM) (Wood, 2017). Next, we examined time series of individual taxa to determine if trends were present. Prior to testing for trend, we examined the time series for

potential bias due to differences in sampling time and the possible presence of serial autocorrelation. Finally, we used a dynamic factor analysis (Zuur *et al.*, 2003a, b) to estimate if common trends were present in multivariate environmental and zooplankton time series. We then compared these trends to determine if patterns in zooplankton community changes that occurred over time were related to multivariate environmental variability. We sought to use zooplankton response to ecosystem conditions to understand future patterns and inform ecosystem-based fisheries management of ecosystem productivity under a changing climate.

METHOD

Zooplankton data

Zooplankton were collected along Line 8 (Fig. 1B) during the months of May and June (Table SI). Zooplankton were collected using oblique tows of paired bongo nets (20 cm frame, 153 μ m mesh and 60 cm frame, 333 or 505 μ m mesh) (Napp *et al.*, 1996; Incze *et al.*, 1997). The tows were within 5–10 m of the bottom depending on sea state. Volume filtered was estimated using a General Oceanics Flowmeter mounted inside the mouth of each net. Samples were preserved in 5% buffered formalin/seawater. Zooplankton were identified to the lowest taxonomic level and stage possible at the Plankton Sorting and Identification Center in Szczecin, Poland, and verified at the Alaska Fisheries Science Center, Seattle, Washington, USA. We selected the taxa for inclusion in the analysis by choosing taxa that were most abundant in the system based on prior surveys (Napp *et al.*, 1996; Incze *et al.*, 1997). We identified taxa to multiple life history stages, and many of these life history stages show strong correlations with other life history stages within the same taxa, so we reported the abundances of one or two life history stages for each taxa. This was influenced by a methodological change in 2012, when the 60 cm frame net had its mesh changed to 505 μ m. The majority of taxa were not affected by this change; however, the potential for some differences to arise was noted. To minimize the effect of this change, we selected life history stages that were unlikely to be affected by the mesh size based on prior analyses of mesh retention (Seifert and Incze, 1989; Incze *et al.*, 1997). We then selected life history stages of taxa that did not differ between 333 and 505 μ m mesh (Table SII). The taxa and life histories affected by this change are listed in Table SIII.

Environmental data

We compiled environmental data for comparison to zooplankton time series placed into two categories:

broad-scale climate indices and local-scale atmospheric and oceanographic measurements (Table SIV). We did this to capture both interannual variability and decadal-scale forcing, evident in the GOA (Stabeno *et al.*, 2004; Hermann *et al.*, 2016). As with all multivariate analyses, a certain degree of collinearity among some variables was expected, and we provide a reference table of correlations between the environmental variables in the Supplementary Material (Table SV). We selected three broad-scale climate indices (Table SIV) that have been shown to link to biological shifts in the GOA (Litzow and Mueter, 2014). The Arctic Oscillation (AO) is the leading empirical orthogonal function of the winter (November–April) sea level pressure anomaly field over the domain poleward of 20°N (Thompson and Wallace, 1998) and has been shown to impact the winter weather of Alaska (Bond and Harrison, 2006). The North Pacific Index (NPI) is the area-weighted sea level pressure over the region 30–65°N and 160°E–140°W and is related to the intensity of the Aleutian Low (Trenberth and Hurrell, 1994). Finally, the Pacific Decadal Oscillation index is the leading principal component from an un-rotated EOF analysis of monthly residual North Pacific sea surface temperature anomalies poleward of 20°N (Mantua and Hare, 2002). The PDO has been related to widespread changes (regime shifts) in natural systems in the North Pacific (Hare and Mantua, 2000). We also considered the Multivariate El Niño–Southern Oscillation (ENSO) index (MEI) (Wolter and Timlin, 1993) as it has been shown to relate to GOA oceanography (Hermann *et al.*, 2016); however, the MEI was highly correlated to the PDO ($R = 0.71$, $P = 0$), thus representing a similar mode of variability. The same was also true of the East Pacific–North Pacific (EPNP) pattern anomaly. The EPNP has its center in eastern Alaska (60–65°N and 135–150°W) (Barnston and Livezey, 1987). The EPNP was also highly correlated to the PDO ($R = 0.69$, $P = 0$).

The atmospheric and water measurement sources are also in Table SIV. Monthly, mean alongshore and offshore upwelling indices were derived from atmospheric pressure at sea level and represent a proxy for the movement of water in the Ekman layer (Bakun, 1973). Upwelling indices were chosen because the strength of upwelling is linked to the likelihood of specific zooplankton taxa (e.g. more oceanic taxa, such as *N. cristatus* and *Neocalanus* spp.) being present on the shelf (Coyle and Pinchuk, 2005). The location of the upwelling station is 60°N, 149°W (Fig. 1A, UWI). Positive values indicate upwelling and negative values indicate downwelling. Temperature (°C) and salinity measurements were compiled from conductivity, temperature and depth (CTD; SeaBird SBE 911plus) data collected by the Pacific Marine Environmental Laboratory (PMEL)

over the time-period of 1990–2002. After 2003, the EcoFOCI Program deployed a CTD (SBE 19plus V2 SeaCAT or SBE 49 FastCAT) attached to the bongo net wire. The average temperatures of the <100 m and >100 m portions of the water column were calculated. One hundred meters was selected because most of the zooplankton taxa are found between this depth and the surface (Coyle and Pinchuk, 2005).

Surface wind was estimated using the NCEP/NCAR reanalysis U and V monthly wind data for an area bounded by 55–60°N and 150–160°W. Wind speed and direction are correlated to advection and are responsible for Ekman transport of zooplankton inshore, particularly in this downwelling system (Coyle and Pinchuk, 2005; Sousa *et al.*, 2016). We used the U and V wind components to calculate the wind vector, speed and direction. Wind vector was calculated as $\vec{WV} = \text{atan2}(V, U)$, wind speed was calculated as $WS = \sqrt{U^2 + V^2}$, and direction (°) was calculated as $WD = 270 - (\frac{180}{\pi} \cdot \vec{WV})$. We calculated the annual, mean wind vector, speed and direction for two time periods, winter (mean of January, February and March) and spring (April, May and June). For the GAM, we used the vector value \vec{WV} as the input variable in the model. We compared the NCEP/NCAR wind data to wind data measured by a surface buoy (46077) in Shelikof Strait (National Data Buoy Center (https://www.ndbc.noaa.gov/station_history.php?station=46077)). We found 48 and 52 buoy observations in winter and spring, respectively, that could be compared to NCEP/NCAR data. Buoy data were from the years 2006–2008, 2010–2014 and 2017–2018. We compared the monthly average U and V wind component values between the two data sets. The correlation (Pearson product moment) between the U component of the buoy measured and modeled wind was 0.92 ($P = 0$) in winter and 0.96 ($P = 0$) in spring. The correlation between the V component of the buoy measured and modeled wind was 0.25 ($P = 0.28$) in winter and 0.63 ($P = 0.001$) in spring. The strong correlations in the U direction reflect the dominant wind component near the Shelikof Strait.

We estimated surface current vector, speed and direction in Shelikof Strait using the output from the Hybrid Coordinate Ocean Model (HYCOM; Table SIV). Strength of advection has been shown to affect the abundance of zooplankton communities on the Gulf of Alaska shelf (Coyle *et al.*, 2013). HYCOM is a primitive equation ocean general circulation model with a 0.083° resolution in the horizontal and 40 standard depth levels (Bleck, 2002). The URL in Table SIV provides a general link to the HYCOM page where further documentation on the model may be located. For this application, we used

Table I: Generalized additive model (GAM) results for zooplankton taxa

Taxa	Adj. r^2	% Deviance	Alongshore upwelling	Offshore upwelling	Temp. < 100 m	Salinity < 100 m	Temp. > 100 m	Salinity > 100 m	Winter wind	Spring wind	Shelikof Transport	Ordinal day
<i>A. tonsa</i> spp. Adult	0.32	37.1										
<i>C. marshallae</i> C2	0.39	43.6										
<i>C. marshallae</i> C5	0.75	77.6										
<i>C. pacificus</i> C5	0.23	26.3										
<i>E. bungii</i> C4	0.86	87.9										
<i>M. pacifica</i> C5	0.32	34.7										
<i>N. cristatus</i> C4	0.63	66.3										
<i>Neocalanus</i> spp. C4	0.70	72.3										
<i>Oithona</i> spp. Adult	0.11	12.5										
<i>Pseudocalanus</i> spp. C5	0.27	30.2										
Amphipods	0.02	3.1										
Appendicularians	0.52	55.9										
Chaetognaths < 5 mm	0.19	23.0										
Euphausiid calyptopis	0.53	57.0										
Euphausiid furcilia	0.77	78.9										
<i>L. helicina</i> < 5 mm	0.30	33.4										

Each row summarizes the GAM for that particular taxa: the adjusted r^2 value (Adj. r^2), percent deviance explained (% Deviance), and significance of each environmental variable. Black squares represent P -values <0.0001, dark gray squares represent P -values <0.001, and light gray squares represent P -values <0.01.

velocity estimates as vector components, U (eastward water velocity) and V (northward water velocity), from several HYCOM model runs. The output represented one grid point (57.7 N, 155 W) at the exit of the Shelikof Strait, and we chose the depth to be 0 m to represent surface transport. We used the following model runs as output in order to generate a long enough time series: GOFS 3.0 expt_19.0, GOFS 3.1 expt_53.X, GOFS 3.1 expt_56.3, GOFS 3.1 expt_57.2, GOFS 3.1 expt_92.8, GOFS 3.1 expt_57.7 and GOFS 3.1 expt_92.9. We used the U and V components from 0 m depth to estimate surface current properties. Shelikof current vector was calculated as $\vec{CV} = \text{atan2}(V, U)$, current speed was calculated as $CS = \sqrt{U^2 + V^2}$, and direction ($^\circ$) was calculated as $CD = (\frac{180}{\pi} \cdot \vec{CV})$. We calculated the annual, mean current vector, speed and direction for the May and June time period to coincide with the zooplankton measurements. For the generalized additive models, we used the vector value \vec{CV} as the input variable in the model. In order to determine if the current estimates from HYCOM were representative of actual estimates from

the Shelikof Strait, we compared them to May transport estimates derived from mooring data from Stabeno *et al.* 2016. Based on 7 estimates reported in Table I (Stabeno *et al.*, 2016), we found a correlation of 0.75 (Pearson product moment correlation, $P = 0.05$).

A final variable of interest that we considered for inclusion in the analysis was chlorophyll a concentration. Chlorophyll a concentration is used as a proxy to estimate phytoplankton biomass, and these primary producers represent an important food source for the zooplankton community in addition to heterotrophic microzooplankton (Strom *et al.*, 2006, 2007). Direct observations of chlorophyll a and primary production on the shelf are limited (Brickley and Thomas, 2004; Waite and Mueter, 2013), and our own measurements of chlorophyll a included only 5 years of data collected along Line 8. In lieu of direct, *in situ* measurements, we could have included chlorophyll a estimates from satellites; however, this would have limited our ability to analyze more years of data as reliable satellite measurements began in 1998 with SeaWiFS and 2002 with MODIS-Aqua (Waite and Mueter, 2013). Furthermore, to generate a data set for

analysis, Waite and Mueter (2013) had to interpolate missing chlorophyll *a* data due to cloud cover, a significant issue with satellite measures in the Gulf of Alaska. Based on the limited data availability and the questionable reliability of satellite estimates of chlorophyll *a*, we chose not to include chlorophyll *a* as a variable in our analysis.

Statistical analysis

All statistical analyses were performed within the R computing environment, version 3.5.0 (R Core Team, 2019). We related zooplankton abundance to individual environmental variables using generalized additive models (GAM) (Wood, 2017). GAMs are generalized linear models that use a sum of smoothing functions of predictor variables. This allows for nonlinearity in the relationship between predictor variable and the response variable. GAMs are also nonparametric, avoiding the specification of parametric relationships between the response and predictor variables (Wood, 2017). We used the *mgcv* package in R (Wood, 2001; Wood *et al.*, 2016) to build the GAMs. For each particular taxon, we modeled the $\log_{10}(\text{abundance m}^{-3} + 1)$ as a function of environmental predictors, excluding climate indices (Table SIV). We excluded climate indices in the GAMs as we wanted to focus on the local environmental conditions only. We used the climate indices for the dynamic factor analysis performed on annually averaged data. The GAM was fit using the *gam* function with a Gaussian family, identity link function and a thin plate regression spline smoother. The inclusion of predictor variables in the model was determined using restricted maximum likelihood (REML) to compare model fits (Wood, 2011). We compared zooplankton data to environmental data resolved to the monthly timescale, as opposed to the trend and dynamic factor analyses that follow that compare zooplankton data to environmental data resolved to the yearly timescale, albeit only for the months of May/June. We included upwelling indices (offshore and alongshore), temperature (< and > 100 m), salinity (< and > 100 m), spring and winter wind vector and Shelikof transport as environmental variables.

We also included ordinal day (the day of year the sample was collected) to determine if a change in sampling timing related to the abundance of the zooplankton. If we discovered a relationship between taxa and ordinal day in the initial GAMs, a potential bias related to a shift in the sampling time between the earlier and later part of the zooplankton data record was possible. More samples were collected in the earlier part of May in the earlier years and in the later part of May in the later years, and the overall sampling date range was from 1 May to 8 Jun or from ordinal day 121 to ordinal day 159 (Table SI). To

eliminate this bias, we related zooplankton abundance to ordinal day and year using GAMs (Wood, 2017). We fit a GAM with year as a factor in the model and fit a smoothed function to ordinal day. We used the fitted GAM model to predict (*predict* function in R) abundances standardized to ordinal day 140 (midpoint between 1 May and 8 Jun). Therefore, we could test for trends on data standardized to the midpoint of collection, eliminating any potential bias of sampling date.

We computed the mean, annual abundance for each zooplankton taxa and tested these annual time series for autocorrelation and trend. We regressed each zooplankton and environmental annual time series against year and tested the residuals for lag-1 autocorrelation using the *durbinWatsonTest* function in the R package *car* (Durbin and Watson, 1971; Fox and Weisberg, 2019). If serial autocorrelation was present in the residuals, we removed it by fitting an autoregressive integrated moving average model (ARIMA) of the order (1, 0, 0) (lag-1 autocorrelation only) using the *arima* function in R. We tested for the presence of monotonic trends using the *Kendall* package in R, specifically the Mann–Kendall test for trend (Hipel and McLeod, 1994). The Mann–Kendall trend test is a nonparametric method to test for trend that uses rank correlation (Mann, 1945; Kendall, 1990). We applied the *Mann–Kendall* function to each zooplankton time series to compute the Kendall's τ (correlation) and *P*-value.

We used dynamic factor analysis (DFA) to estimate common trends in the multivariate time series (Zuur *et al.*, 2003a, b). DFA was designed to analyze short, nonstationary time series that may also contain missing values (Zuur *et al.*, 2003a). The goal of DFA was to reduce multidimensional time series into a preferably small number of common trends. The output was similar to other multivariate data reduction techniques, such as principal component analysis or factor analysis. As with factor analysis (Everitt and Hothorn, 2011), each dynamic factor identified in the DFA can be understood by examining how each variable loads onto the factor. The factor loading was interpreted like a correlation coefficient; the higher the value (positive or negative), the more strongly that individual variable relates to the dynamic factor. We used the *MARSS* package (Holmes *et al.*, 2012) to perform DFA and estimate multivariate time series for both the environmental data and the zooplankton data. First, we standardized each time series into \mathcal{Z} scores by subtracting the long-term mean and dividing by the standard deviation. Next, we fit a number of different DFA models and compared them using the Akaike information criterion (AIC). We selected the model with the lowest AIC score, rotated the factor loadings and plotted the trend(s) and loadings. We compared DFA time series using nonparametric correlations (Spearman's ρ) as well the

cross-correlation function (*ccf* function in R) to test for lagged responses.

RESULTS

Environmental time series

The PDO alternated between positive (1992–1998; 2002–2006; 2014–2017) and negative (1999–2001; 2007–2013) phases (Fig. 2A). The other two climate indices, the NPI (Fig. 2B) and AO (Fig. 2C), showed less evidence of phases, with the exception of two positive (2006–2008; 2001–2014) phases of the NPI (Fig. 2B). Shelikof Strait transport direction was always towards the southwest (data not shown) and speed varied interannually (Fig. 2D). Wind speeds showed minimal interannual variability (Fig. 2E and G) and were predominately from the east or northeast regardless of season (Fig. 2F and H). Alongshore upwelling showed greater variability in the earlier portion (1990–1999) of the data record and, after the year 2000, steadily increased over time (Fig. 3A). Offshore upwelling remained slightly below zero in most years, indicating persistent downwelling in May, with brief periods of upwelling in the late 1990s and stronger downwelling in 2008 (Fig. 3B). Temperature values in the upper 100 m (Fig. 3C) were variable over time and were out of phase with salinity <100 m (Fig. 3D), i.e. when temperature increased, salinity decreased. Temperatures >100 m mirrored those in the upper 100 m (Fig. 3E); however, salinity was much less variable >100 m (Fig. 3F).

Generalized additive models

The generalized additive models (GAM) found varying degrees of relationship between individual taxon abundances and environmental variables. The taxa that had the strongest relationship with environmental variables were *C. marshallae* C5, *E. bungii* C4, *N. cristatus* C4, *Neocalanus* spp. C4, appendicularians and euphausiid furcilia (Table I). The most important variables were temperature <100 m and salinity >100 m, and zooplankton taxa also showed relationships with temperature >100 m, salinity <100 m, winter wind, Shelikof transport and ordinal day (Table I). Larger body size copepods had the strongest relationships with environmental conditions. The copepods *C. marshallae* C5, *E. bungii* C4, *N. cristatus* C4 and *Neocalanus* spp. C4 as well as the early life history stages of euphausiids all had strong relationships with temperature <100 m (Fig. 4) and salinity >100 m (Fig. 5), albeit the nature of the relationships with temperature was not the same among species. Another important covariate was ordinal day, and this result suggested that there was

an influence of sampling time on taxon abundance for multiple species (Fig. 6).

Standardization of data to ordinal day 140

As several taxa had significant relationships with ordinal day, we chose to standardize the zooplankton abundance data to ordinal day 140, the midpoint of our data collections (see methods). For most species, this did not appreciably change the abundance time series; however, for taxa that did experience shifts in abundance related to day of sampling, differences between the two time series can be seen in Figs 7 and 8. For example, *Neocalanus* spp. C4 have lower abundances in the early part of the time series compared to higher abundances in the later portion (Fig. 7). The majority of abundance time series showed no response to time of sampling (Figs 7 and 8).

Serial autocorrelation and time series trends

We detected minimal evidence of serial autocorrelation in the annual, averaged time series. The only environmental variable that had evidence of serial autocorrelation was the PDO ($\rho = 0.55$, Durbin-Watson $d = 0.87$, $P = 0$). Three taxa showed evidence of serial autocorrelation, *C. marshallae* C2 ($\rho = 0.42$, $d = 1.06$, $P = 0.01$), *C. pacificus* C5 ($\rho = -0.44$, $d = 2.83$, $P = 0.04$) and amphipods ($\rho = 0.17$, $d = 1.31$, $P = 0.05$). We removed the serial autocorrelation in each of these time series by fitting an ARIMA model of the order (1, 0, 0). The residuals from the ARIMA model all had ρ values that were not different from zero and Durbin-Watson d statistics >1.6 and P -values >0.21, indicating that serial autocorrelation was removed from the time series.

We did not detect trends in any of the environmental time series (Mann-Kendall τ not different from 0, P -value >0.10). The copepod *C. pacificus* C5 (autocorrelation removed) had a positive trend ($\tau = 0.39$, $P = 0.007$), and both amphipods (autocorrelation removed) ($\tau = -0.45$, $P = 0.003$) and chaetognaths <5 mm had negative trends ($\tau = -0.33$, $P = 0.03$). Several other taxa had evidence of trends; however, these trends were not evident after standardization to ordinal day 140.

Dynamic factor analysis (DFA)

Dynamic factor analysis identified a single, multivariate trend in the environmental data (Fig. 9A). The model with the lowest AIC was an equal variance-covariance model, meaning variance values across the matrix diagonal were shared and estimated, and the population covariances were shared and estimated. One climate index, the PDO,

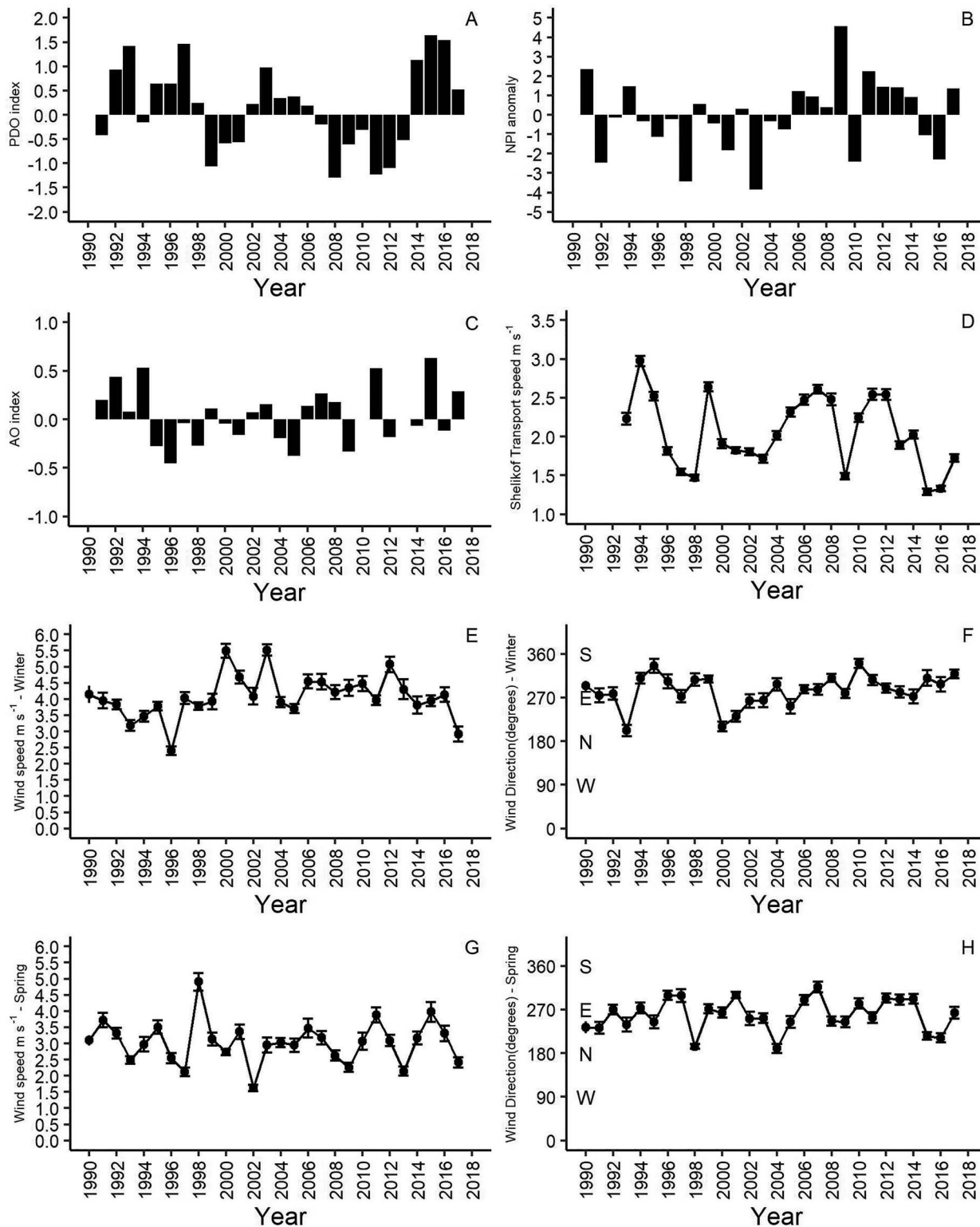


Fig. 2. Pacific Decadal Oscillation (PDO) index (A); North Pacific Index (NPI) anomaly (B); Arctic Oscillation (AO) index (C); mean Shelikof Strait transport speed as estimated by the HYCOM model (D); mean, winter wind speed (E); mean, winter wind direction (F) and letters on wind direction plot indicate the cardinal direction the wind is blow from the south (S), east (E), north (N) and west (W); mean, spring wind speed (G); mean, spring wind direction (H). Error bars represent ± 1 standard error of the mean.

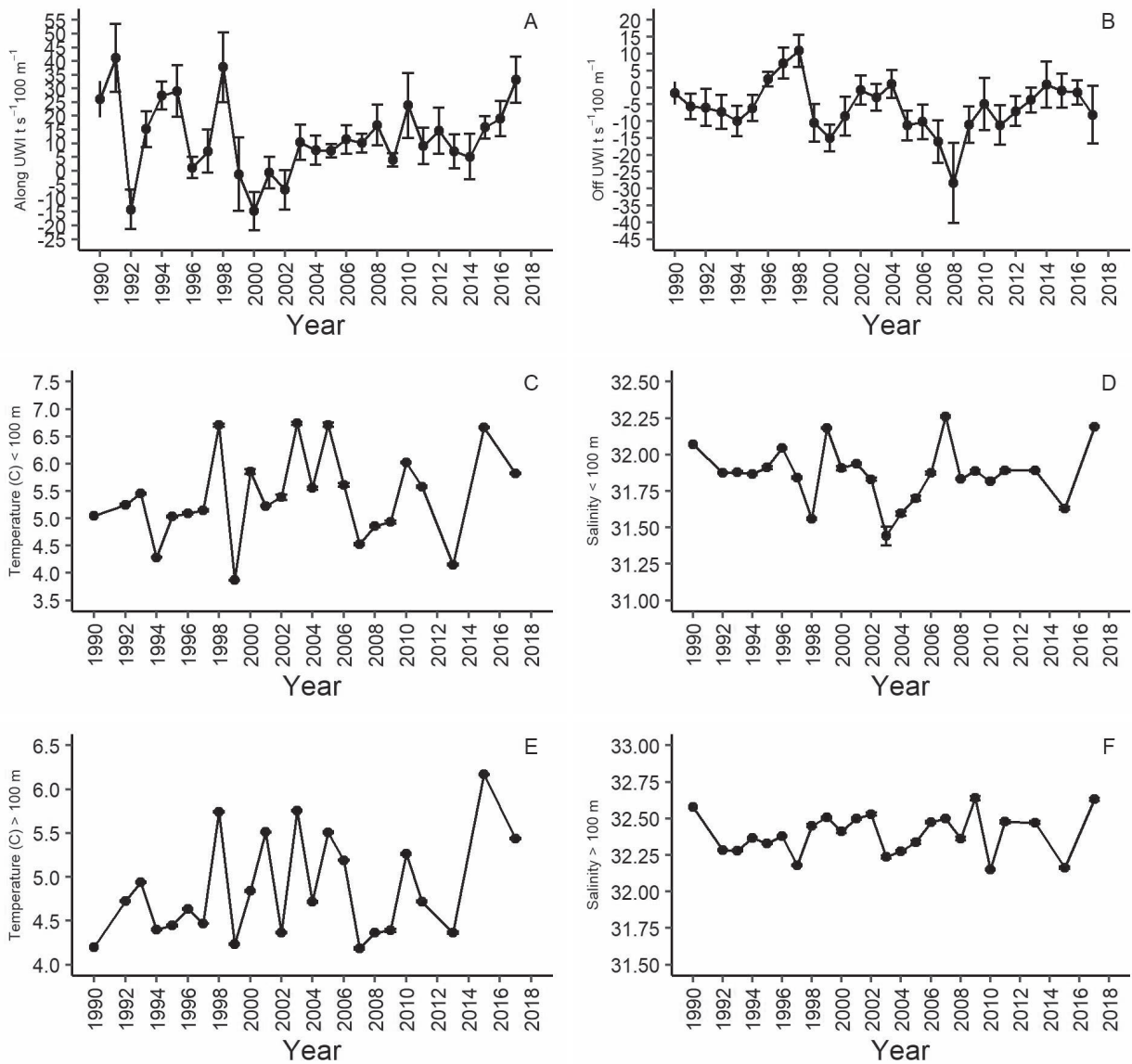


Fig. 3. Alongshore (along) upwelling index (UWI) (A); offshore (off) upwelling index (UWI) (B); mean temperature in the upper 100 m (C); mean salinity in the upper 100 m (D); mean temperature below 100 m (E); mean salinity below 100 m (F). Error bars represent ± 1 standard error of the mean.

had a positive loading >0.25 (Fig. 9B). Four local environmental variables also had positive loadings >0.25 : temperature $<$ and >100 m, spring wind and Shelikof Transport >0.25 (Fig. 9B). The climate indices NPI and AO as well as salinity $<$ and >100 m all had loadings <-0.25 (Fig. 9B). DFA values showed variability over time that included periods of positive or negative values (Fig. 9A). From 2000 to 2005 and 2014 to 2016, DFA values were positive (Fig. 9A). Based on the loadings, these years were characterized by a positive PDO phase with higher temperatures (Fig. 3C) and lower salinities (Fig. 3D). In contrast, the environmental DFA trend was

negative during 2006–2009, with a 1-year positive value in 2010 and a return to negative values from 2011 to 2013 (Fig. 2B). These years were characterized by a negative PDO phase (Fig. 2A), lower temperatures (Fig. 3C) and higher salinities (Fig. 3D).

Dynamic factor analysis identified a single multivariate trend in the zooplankton data (Fig. 9C). The DFA model with the lowest AIC had an equal variance and covariance structure. Taxa that positively loaded onto the DFA trend (>0.25) were *C. marshallae* C5, *E. bungii* C4, *M. pacifica* C5, euphausiids furcilia and *L. helicina* <5 mm (Fig. 9D). Taxa that negatively loaded onto the DFA trend

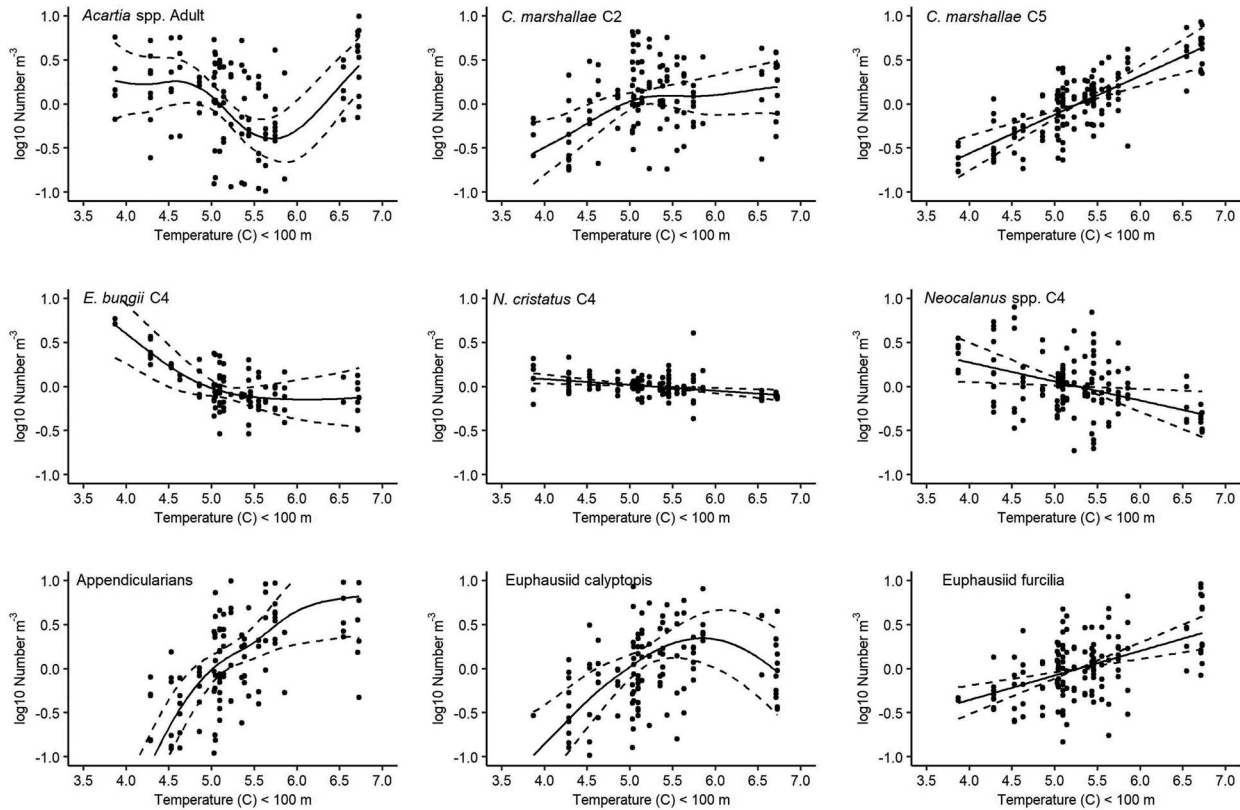


Fig. 4. Generalized additive model fits for selected taxa abundance and temperature ($^{\circ}\text{C}$) < 100 m. Black line represents thin plate spline fit by the GAM model and dashed lines represent the 95% confidence interval.

(< -0.25) were *C. marshallae* C2, *N. cristatus* C4, appendicularians, euphausiid calyptopis and chaetognaths < 5 mm (Fig. 7D). The zooplankton DFA trend (Fig. 9C) had less variability over time compared to the environmental DFA trend (Fig. 9A). The exceptions were two positive periods, 2004–2006 and 2016–2017, and one negative period, 2007–2009 (Fig. 9C). During the positive periods, *C. marshallae* C5, *Eucalanus* C4 and *L. helicina* < 5 mm abundances increased (Fig. 7). During the negative period, *C. marshallae* C2 and *N. cristatus* C4 abundances increased (Fig. 7).

The environmental DFA trend was not autocorrelated ($\rho = 0.29$, $d = 1.35$, $P = 0.06$), whereas the zooplankton DFA trend was autocorrelated ($\rho = 0.51$, $d = 0.65$, $P = 0$). We removed autocorrelation from the zooplankton DFA trend time series using ARIMA model of the order (1, 0, 0) as described above. Both the environmental ($\tau = 0.05$, $P = 0.71$) and zooplankton DFA trend (autocorrelation removed) ($\tau = 0.22$, $P = 0.11$) had no detectable trends. A direct comparison between the environmental DFA and zooplankton DFA trend (autocorrelation removed) showed little relationship (Spearman's $\rho = 0.33$, $P = 0.08$) (Fig. 10). A cross-correlation test (*ccf* function in R

showed no appreciable change in the correlation value for lagged data. Interestingly, the relationship between the environmental DFA trend and zooplankton DFA trend (autocorrelation removed) appeared to change around the year 2004 (Fig. 10). This was supported by correlations between the environmental DFA trend and the zooplankton DFA trend (autocorrelation removed) from 1990 to 2003 (Spearman's $\rho = -0.03$, $P = 0.91$) and from 2004 to 2017 (Spearman's $\rho = 0.70$, $P = 0.007$).

DISCUSSION

The multivariate environmental and zooplankton variability both exhibited a single, underlying trend in each time series. At first glance, these dynamic factor analysis time series were not related; however, when separated into two distinct time-periods (1990–2003 and 2004–2017), they appeared to be in phase from 2004 onward (Fig. 10). Shifts in the relationship between environmental forcing and biological responses over time have been well documented as regime shifts (Steele, 1998; Overland *et al.*, 2008), and it is likely that these relationships do

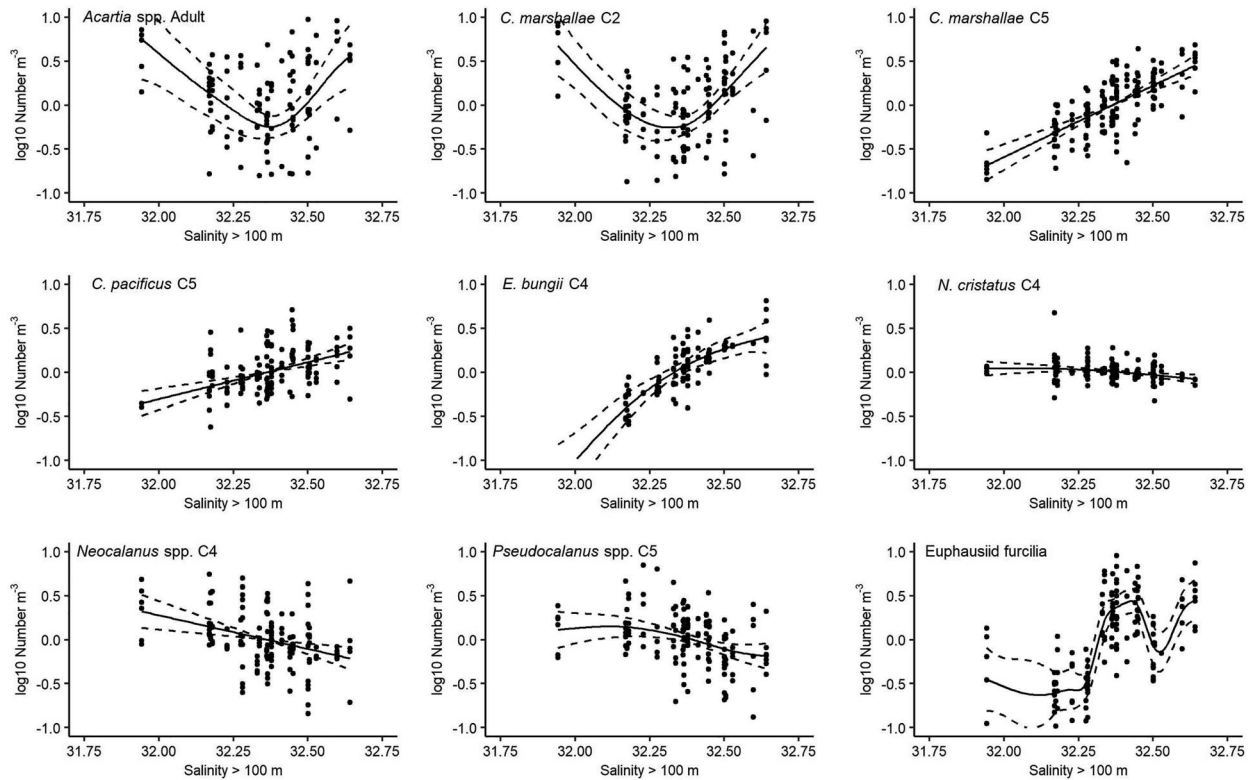


Fig. 5. Generalized additive model fits for selected taxa abundance and salinity > 100 m. Black line represents thin plate spline fit by the GAM model and dashed lines represent the 95% confidence interval.

not remain stationary over time (Litzow *et al.*, 2019). At present, we have no direct hypothesis as to why this shift occurred near 2004, except that the PDO entered into stronger negative and positive phases after this date (Fig. 2A). However, the relationship between the environmental and individual zooplankton taxa was more nuanced and varied than can be captured in a single, multivariate index (Gaichas *et al.*, 2011; Puerta *et al.*, 2019). Interestingly, Marshall *et al.* (2019) documented a shift in synchrony of GOA ichthyoplankton assemblages at roughly the same time. This suggests a large-scale, broader response of the planktonic community to an undetermined extrinsic forcing factor, perhaps a resurgence in abundance of young, walleye pollock. Nonlinear models helped identify specific environmental variables that were most strongly related to individual taxa abundance: temperature, salinity and ordinal day. The impact of sampling date was important as the relationship that several taxa had with ordinal day demonstrate that sample timing matters in the interpretation of the patterns and trends over time. Overall, our results indicate that the zooplankton community at Shelikof Strait Line 8 was strongly influenced by environmental variability. This suggested that ongoing changes in the ecosystem, most specifically climate

warming, will have a significant impact on the May zooplankton community with associated impacts on higher trophic levels, including fish, marine mammals and seabirds.

Zooplankton response to environmental variability

The environmental variability described and captured by the analysis has been observed and described in depth (Weingartner *et al.*, 2002; Stabeno *et al.*, 2004; Litzow *et al.*, 2014; Litzow and Mueter, 2014). The western Gulf of Alaska has been characterized as seasonally variable with a biological response to weak decadal signals, particularly the Pacific Decadal Oscillation (Hare and Mantua, 2000). Positive PDO phases were largely coherent with positive environmental DFA periods, resulting in warmer ocean temperatures, offshore downwelling relaxation and surface salinity declines due to increased freshwater runoff, with the opposite occurring in the negative PDO phases. The autocorrelation we found in the PDO (0.55) was similar to the 0.45 in winter–spring noted by Newman *et al.* (2016). The PDO explains little variance in sea surface temperature (Bond *et al.*, 2003; Stabeno *et al.*, 2004) and freshwater runoff (Weingartner *et al.*, 2005),

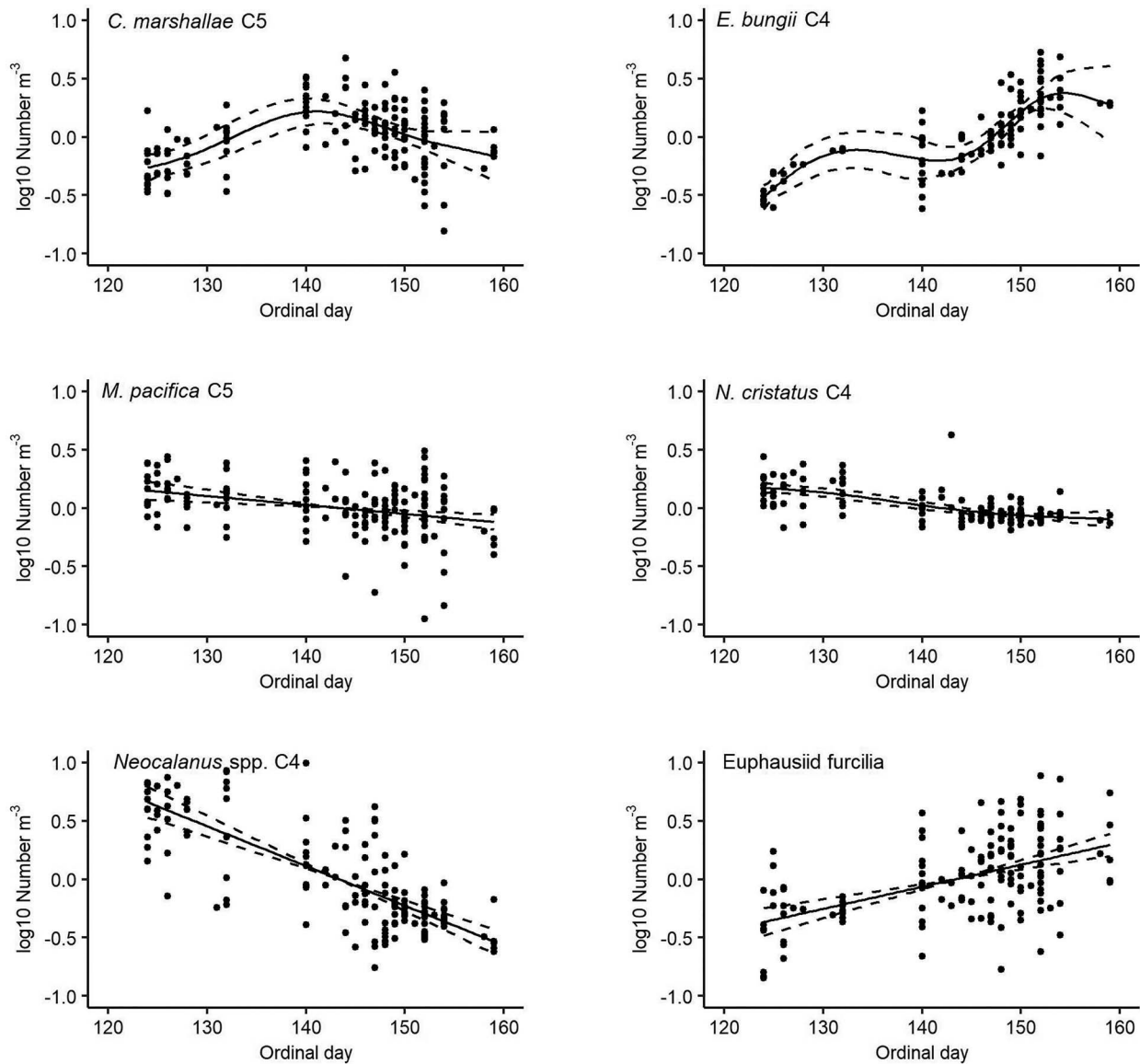


Fig. 6. Generalized additive model fits for selected taxa abundance and ordinal day. Black line represents thin plate spline fit by the GAM model and dashed lines represent the 95% confidence interval.

indicating that more local features influence the oceanography, namely, winds (Ladd *et al.*, 2005). Wind magnitude and direction during winter and spring determine the degree of cross-shelf exchange, the speed and volume transport of the ACC and timing of stratification preceding the spring phytoplankton bloom (Weingartner *et al.*, 2002; Stabeno *et al.*, 2004; Ladd *et al.*, 2005; Coyle *et al.*, 2013). This was particularly true for Shelikof Strait as the surface waters in the Strait were dominated by the ACC (Schumacher and Reed, 1986; Stabeno *et al.*, 2016). These factors are closely related to the variability in abundance of particular zooplankton taxa as evidenced in the GAM results.

Positive phases of the environmental DFA later in the data record (2002–2006 and 2014–2017) corresponded with increased abundances of zooplankton species, namely, the copepods *C. marshallae* C5 and *C. pacificus* C5 and the oceanic copepod *E. bungii* (Fig. 7). It has been suggested that periods of strong cross-shelf exchange and warmer temperatures result in higher abundances of *C. marshallae* (Coyle and Pinchuk, 2005; Sousa *et al.*, 2016). Our results supported this as well, as *C. marshallae* had positive relationships with temperature in the <100 m and salinity >100 m (Figs 4 and 5). The oceanic species *E. bungii* was hypothesized by Coyle and Pinchuk (2005) to correlate with higher salinities

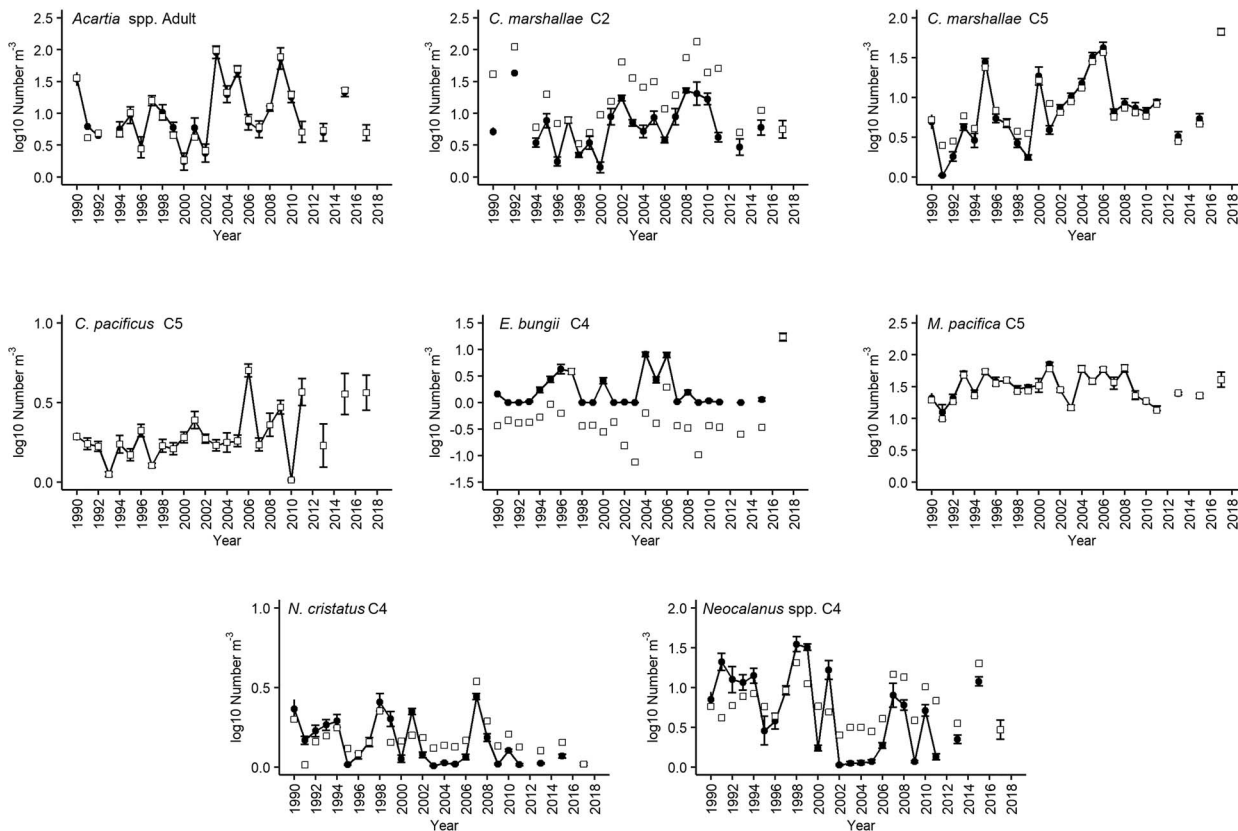


Fig. 7. Mean, annual \log_{10} abundance of selected zooplankton taxa over time (closed circles, black line) and mean, annual \log_{10} abundance standardized to ordinal day 140 (open squares). Error bars represent ± 1 standard error of the mean.

until upwelled along the shelf, whereby abundance would negatively correlate with salinity. This was exactly what we observed, in particular the strong relationship between *E. bungii* and alongshore upwelling (Table I). The increases in abundance of these species were thought to result from this cross-shelf exchange, which also brings nutrients that fuel phytoplankton production (Napp *et al.*, 1996; Coyle and Pinchuk, 2003, 2005; Sousa *et al.*, 2016).

The negative phase of the environmental DFA correlated with negative phase (2007–2013) of the zooplankton DFA, particularly after 2004 (Fig. 10). The abundance of *Neocalanus* spp. C4 and *N. cristatus* C4 increased during these time periods, and both species showed the strongest negative relationships with temperature in the <100 m (Table I). Coyle *et al.* (2013) noted that *Neocalanus* spp. biomass correlated negatively with salinity in May and hypothesized strong downwelling resulting in Ekman pumping of individuals onto the shelf where they upwell into the surface. If this was the case, we should have observed similar relationships between alongshore upwelling as was the case with *E. bungii*. We hypothesize two reasons why this was not observed. First, all

three species of *Neocalanus* are at the end of their annual cohort during May and enter diapause by June (Miller and Clemons, 1988; Miller, 1993). During the cooler periods associated with the negative environmental DFA, *Neocalanus* spp. C4 were more likely to be on the shelf and less likely to have advanced to the C5 stage or to diapause. During positive phases of the environmental DFA (2002–2005), *Neocalanus* spp. C4 were largely absent (Fig. 7). This was further supported by the negative relationship between temperature and ordinal day and abundance for *Neocalanus* (Table I). Downwelling and Ekman pumping may have brought *Neocalanus* onto the shelf, but warm temperatures could have accelerated development past the C4 stage, resulting in low abundances during the May survey period, as has been observed in other locations in the North Pacific (Miller and Clemons, 1988; Mackas *et al.*, 1998, 2007; Batten *et al.*, 2003). Also possibly was the advection of *Neocalanus* spp. out of Prince William Sound, where a population is present and subject to warmer temperatures (Cooney *et al.*, 2001). Secondly, the studies along the Gulf of Alaska (GAK) (Coyle and Pinchuk, 2003, 2005; Coyle *et al.*, 2013; Sousa *et al.*, 2016) sample a cross-shelf transect and were more able to

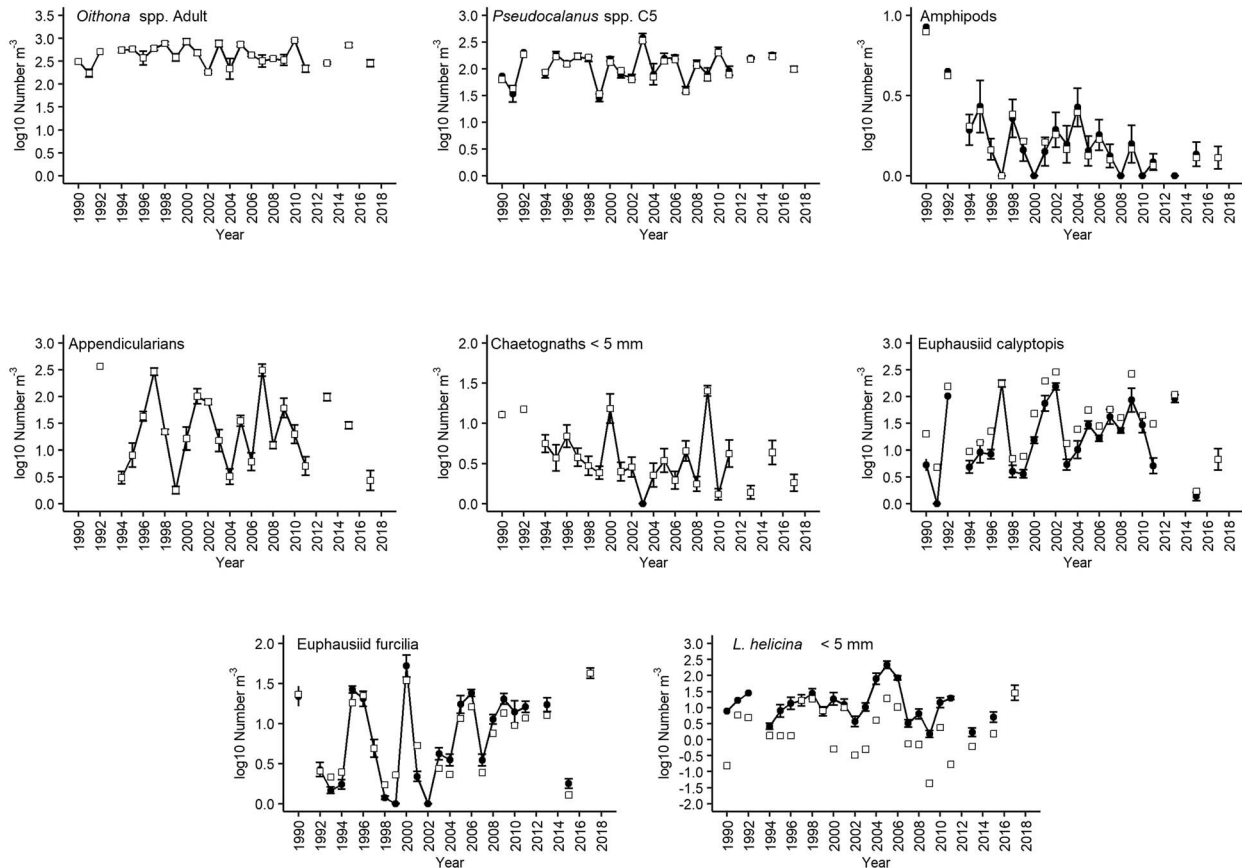


Fig. 8. Mean, annual \log_{10} abundance of selected zooplankton taxa over time (closed circles, black line) and mean, annual \log_{10} abundance standardized to ordinal day 140 (open squares). Error bars represent ± 1 standard error of the mean.

describe the cross-shelf dynamics, particularly for oceanic species, compared to Line 8 data.

Trends in zooplankton abundance

The only copepod that had a positive trend over the time series was *C. pacificus* C5. *Calanus pacificus* is more abundant in warmer waters (Batten and Welch, 2004; Batten and Walne, 2011); therefore the recent warming event of 2014–2016 (Bond *et al.*, 2015) likely resulted in the highest *C. pacificus* numbers observed (Fig. 7). Indeed, this was observed across the North Pacific (Fisher *et al.*, 2020) during the marine heatwave beginning in 2014 (Bond *et al.*, 2015). An increase in communities of warmer water zooplankton species, which included *C. pacificus*, was observed in Prince William Sound (McKinstry and Campbell, 2018) and in the North Pacific (Batten and Walne, 2011) during positive SST anomalies. An increase in more southern latitude larval fish species has also been reported (Marshall *et al.*, 2019). An increase in *C. pacificus* would be of interest if this species were to replace *C. marshallae* as the dominant copepod in the genus

Calanus. Compared to *C. marshallae*, *C. pacificus* is smaller in size and stores less lipids, e.g. 15.8% total lipid per dry mass (Ohman, 1988) at stage CV compared to *Calanus* spp. found in higher latitudes that often have >70% of dry mass as lipid (Vogedes *et al.*, 2010). We also found long-term trends in both amphipods and chaetognaths <5 mm. The amphipod trend was due to two high abundance measurements early in the data record (Fig. 8), and overall, abundance of amphipods were low over time. Chaetognaths also declined over time, a finding that was a bit surprising as chaetognaths were associated with warmer waters elsewhere (Baier and Terazaki, 2005) and in the Gulf of Alaska (Sousa *et al.*, 2016).

The trends for the other larger body size copepods (*C. marshallae*, *N. cristatus*, and *Neocalanus* spp.) were not significant; however, the strong relationships with temperature suggest future warming will likely impact abundances of copepod life history stages in the May/June time period. Copepod development times are strongly related to temperature (Kiørboe and Sabatini, 1995). Declines in *Neocalanus* spp. abundances over time could imply that *Neocalanus* spp. were developing beyond the C4 stage in

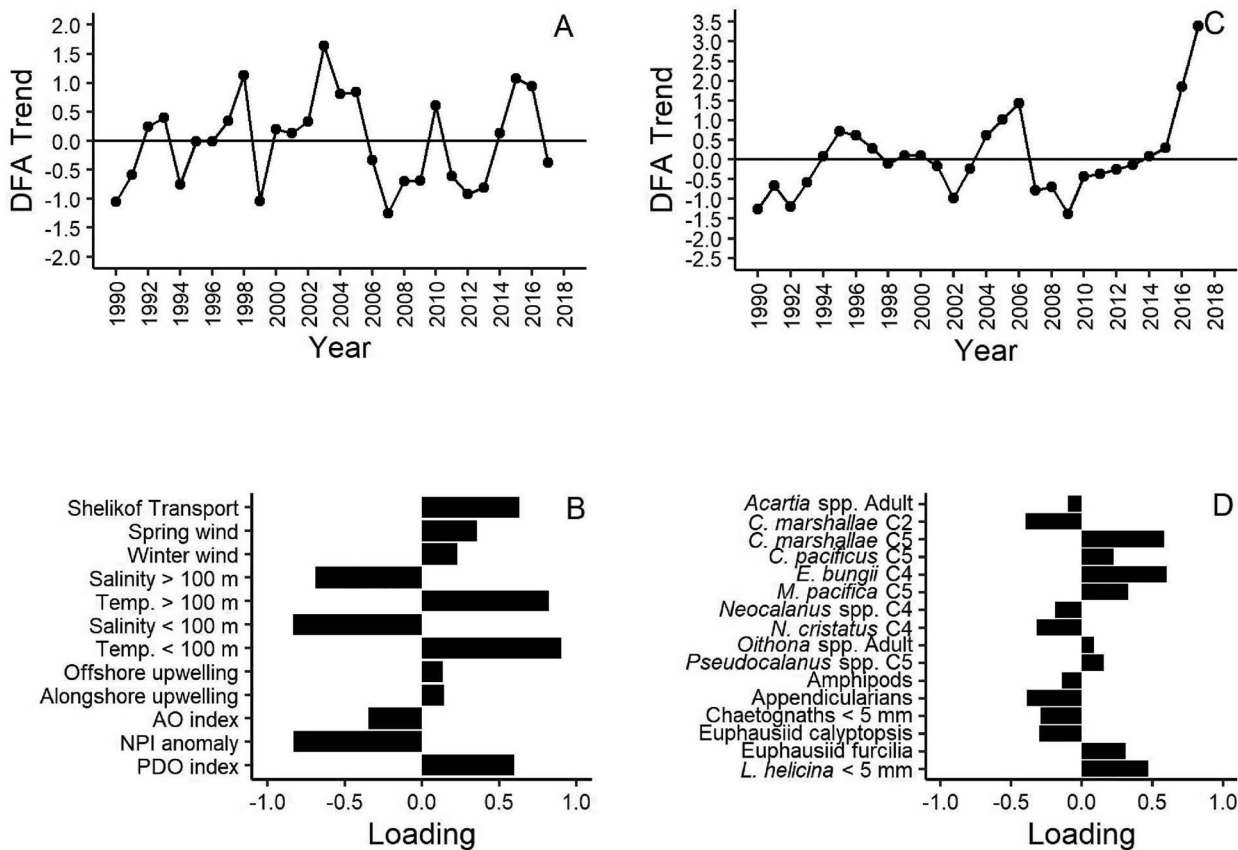


Fig. 9. Environmental dynamic factor analysis (DFA) trend (A) and loadings (B) and zooplankton DFA trend (C) and loadings (D).

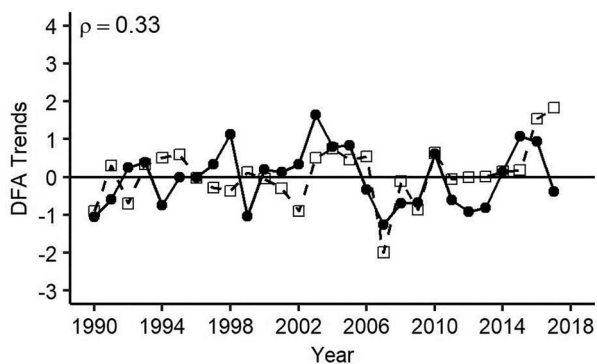


Fig. 10. Environmental dynamic factor analysis (DFA) trend (closed circles, solid line) and zooplankton DFA trend (open squares, dashed-line). Spearman's ρ correlation coefficient is shown in the upper left.

May during warm periods. This makes sense as both *N. cristatus* and *Neocalanus* spp. enter into diapause between May and July (Miller *et al.*, 1984; Kobari and Ikeda, 1999). The average stage duration for *Neocalanus* spp. C4 was found to be between 12 and 14 days at 5–6°C but under optimal conditions may be reduced to 10 days (Liu and

Hopcroft, 2006). These temperatures were similar to the range we observed, excepting recent warm years (Fig. 3). In a recent analysis, we found that development time to stage C5 in *N. cristatus* and *Neocalanus* spp. ranged from 120 to 134 and 113 to 123 days, respectively (Nielsen *et al.*, 2019).

Calanus marshallae development rates also increased with increasing temperature (Liu and Hopcroft, 2007), and this helps explain the overall abundance patterns observed. It is thought that *C. marshallae* exits diapause in winter (Dec–Feb) (Osgood and Frost, 1994; Peterson, 1998; Baier and Napp, 2003), and emergence is quickly followed by the terminal molt to the C6 stage to time reproduction to the spring bloom (Baier and Napp, 2003), as has been observed for congeneric species (Madsen *et al.*, 2001). The eggs produced then develop to the C5 stage, and development to this stage is completed by May in warmer Puget Sound (Osgood and Frost, 1994) and between July and September in the southeastern Bering Sea (Baier and Napp, 2003). Given the strong, linear relationship with *C. marshallae* C5 abundance and temperature in the <100 m as shown in the GAM model (Table I and Fig. 4), we hypothesize that *C. marshallae* was reaching the C5 stage

earlier during warm conditions. This indicates the possibility of a second generation occurring in the western GOA as the C5 in May could transition to adult stage and reproduce. In general, *C. marshallae* is thought to have only one cohort per year in higher latitude systems, for example, the southeastern Bering Sea (Baier and Napp, 2003), though Smith and Vidal (1986) reported a second cohort of *C. marshallae* in this region during warm conditions in 1981. This is in contrast to the Oregon coast, where *C. marshallae* has up to four generations per year (Peterson *et al.*, 1979). Using a life history model, Banas *et al.* (2016) showed that populations of *C. marshallae/glacialis* in the southeastern Bering Sea were likely to produce a second generation with warming, whereas those in the northern Bering Sea were not (note, *C. marshallae* and *C. glacialis* are difficult to tell apart, and their relative contribution to the *Calanus* on the Bering Sea shelf is unknown (Nelson *et al.*, 2009; Campbell *et al.*, 2016)). Differences in generation time with latitude have also been noted for *C. glacialis* across the Arctic (Daase *et al.*, 2013). Based on this information, the western GOA may support a second generation of *C. marshallae* during warmer than average periods, and this would have consequences for trophic interactions (see below).

Relevance to higher trophic levels

We found no long-term trend in temperature during the time series we analyzed. This was surprising as the Gulf of Alaska and North Pacific Ocean have been warming for some time (Bograd *et al.*, 2005; Janout *et al.*, 2010; Intergovernmental Panel on Climate Change, 2014). We suspect that our time series of *in situ* measurements was not long enough to detect a statistically significant warming trend, though the correlation values between temperature and year were positive. We expect a more comprehensive spatial and temporal analysis of our sampling data would show a warming trend. Given the strong relationships between the large copepods that dominate the spring biomass peak and temperature, it is reasonable to predict that future warming of this region will result in shifts in the spring zooplankton community driven by temperature and possibly a second generation of *C. marshallae*. These likely changes have ramifications for the ecosystem. The primary spawning ground for walleye pollock in the Gulf of Alaska is in Shelikof Strait (Kendall *et al.*, 1996), and the spring zooplankton community coincides with abundant walleye pollock larvae and larvae of other fishes (Doyle *et al.*, 1995; Doyle *et al.*, 2009; Marshall *et al.*, 2019). These larvae predominantly consume nauplii and copepod eggs (Incze and Ainaire, 1994; Theilacker *et al.*, 1996) as the majority of the dominant large plankton were too large for larvae to consume (Napp *et al.*, 1996;

Napp *et al.*, 2000). Nauplii were present from nearly all copepod species, though the main species consumed were thought to be mostly *Pseudocalanus* spp. (75%), *M. pacifica* (18%) and *C. marshallae* (4%) (Theilacker *et al.*, 1996). We found no major trends for *Pseudocalanus* spp. (Fig. 8) or *M. pacifica* (Fig. 7), thus the larval prey field for *G. chalcogrammus* does not appear to have changed, based on our data.

More relevant for walleye pollock would be the potential shift of *C. marshallae* abundance later in the year, when smaller (40–50 mm) age-0 walleye pollock rely on *C. marshallae* C4 and C5 stages as a primary food source (Wilson *et al.*, 2009). Development of *C. marshallae* to the C5 stage earlier in the year or the production of a second cohort may result in a mismatch with age-0 pollock. Walleye pollock were, on average, around 35 mm in length in late May/early June with a mouth gape of approximately 1 mm (Sogard and Olla, 1994), whereas *C. marshallae* C5 were 2.68 ± 0.17 SD mm in size (Liu and Hopcroft, 2007). Walleye pollock spawning times are occurring earlier (Rogers and Dougherty, 2019); thus the differential rates at which both populations respond to warming will be important to determining the potential for match–mismatch dynamics. For comparison, match–mismatch dynamics have been explored for the congener *C. finmarchicus* and Norwegian spring-spawning herring (*Clupea harengus*) predators in the Norwegian Sea. Varpe and Fiksen (2010) found that increases in herring body condition were decoupled from the main peaks in *C. finmarchicus* abundance; those emerging from diapause in late winter and early spring and their offspring born in spring and entering diapause in late summer and fall. Despite this, herring body condition correlated well with *C. finmarchicus* consumption, suggesting a match in timing was less important than other factors, namely, light availability that leads to greater foraging success (Varpe and Fiksen, 2010). It has been hypothesized that *C. finmarchicus* has only one generation per year in the Norwegian Sea due to strong predation leading to early (June) entry into diapause (Kaartvedt, 2000). However, a second generation of *C. finmarchicus* has been observed at Station M in the Norwegian Sea (Østvedt, 1955), suggesting that entry into diapause may be flexible. Therefore, match–mismatch dynamics are likely to be more complex than coincident timing of predator and prey peaks in the Gulf of Alaska.

Also of importance in the northwestern Gulf of Alaska are small, neritic fishes (capelin *Mallotus villosus*, eulachon *Thaleichthys pacificus*, Pacific herring *Clupea pallasii*, juvenile *G. chalcogrammus* and Pacific sand lance *Ammodytes personatus*) that consume zooplankton (Foy and Norcross, 1999; Wilson, 2009; Hipfner and Galbraith, 2014). These fishes are in turn consumed by a variety of piscivorous predators, including marine mammals such

as Steller sea lions (*Eumetopias jubatus*) (Sinclair, 2002), humpback whales (*Megaptera novaeangliae*) (Moran *et al.*, 2018) and seabirds (Hunt *et al.*, 2000). Climate-mediated shifts in the zooplankton community can propagate effects through the food web. As an example, earlier disappearance of *N. cristatus* and *Neocalanus* spp. from the water column could deprive forage fish of a critical trophic link to spring primary production, impacting the transfer of lipids and essential fatty acids to higher trophic levels (Litzow *et al.*, 2006). The pteropod *L. helicina* increases during warming events and is important in diets of some Pacific salmon (Aydin *et al.*, 2005; Karpenko *et al.*, 2007). Further, a shift to numerical dominance of smaller-sized copepods such as *C. pacificus* can have important effects on energy acquisition in young fish, including increasing prey search and handling time, reducing scope for growth and increasing mortality (Beaugrand *et al.*, 2003). It remains to be seen if changes in overall zooplankton productivity will result in either match–mismatch scenarios or declines in overall productivity, as has been posited with warming (Moore *et al.*, 2018). However, our results suggest a zooplankton assemblage that is susceptible to change through regional warming.

CONCLUSION

We found strong coherence between the climatic and environmental variability in the northwestern Gulf of Alaska and the May zooplankton community in Shelikof Strait. Contrasting environmental conditions were associated with specific zooplankton taxa, and the most important variables that described this variability were temperature, salinity and ordinal day. This was likely related to the dominant species of copepods that experience one cohort per year. The recent North Pacific warming event clearly affected the zooplankton community as it occurred at the end of the time series. The results suggest continued warming is likely to impact large-bodied copepods, i.e. all three species of *Neocalanus* may enter into diapause earlier in warmer conditions, *C. marshallae* developing to the C5 stage in greater numbers earlier in the year, leading to earlier entry into diapause or a second generation, and an increase in the less lipid-rich *C. pacificus*. If these trends persist, then changes in the zooplankton community have the potential to result in match–mismatch scenarios with predators and prey, both in the spring and later in the year, when many juvenile fish prey on larger-sized zooplankton.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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