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# Pink Salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands

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## Abstract

We examined the hypothesis of top-down (predator) control of plankton populations around the Aleutian Islands and in the southern Bering Sea using a 15 year time series (2000–2014) of plankton populations sampled during summer by Continuous Plankton Recorders. Our analyses reveal opposing biennial patterns in abundances of large phytoplankton and copepods. This pattern is likely caused by the predation pressure on copepods from biennially abundant eastern Kamchatka Pink Salmon that results in a trophic cascade. In odd years, Pink Salmon are exceptionally abundant, large copepod abundance is low, and abundance of large diatoms grazed by copepods is high. Furthermore, large copepod abundance was inversely correlated, and diatom abundance was positively correlated, with Pink Salmon abundance. In addition to influencing the abundance of diatoms and large copepods we also report an effect on phytoplankton taxonomic composition. We find regional differences in the expression of these effects with alternating odd/even year patterns being strongest in the central Southern Bering Sea and eastern Aleutians and reduced, or absent, in the western Aleutians. When the abundance of 2013 Pink Salmon was unexpectedly low, there were consequent changes in the plankton populations, with highest recorded numbers in the time series of large copepods and microzooplankton (hard-shelled ciliates). These findings emphasise the importance of variability in predator abundance and its effect across the ecosystem, which in this case was greater than physical oceanographic variability.

KEYWORDS
Aleutian Islands, Bering Sea, biennial pattern, continuous plankton recorder, copepods, ocean ecology, Pink Salmon, trophic cascade

## 1 | INTRODUCTION

The disparity in odd and even year class strengths of Pink Salmon (*Oncorhynchus gorbuscha*) in the North Pacific is a well known phenomenon which has shown ecological impacts in some regions; for example, on seabirds across the Aleutian Islands and southern Bering Sea (Springer & van Vliet, 2014), on Sockeye Salmon (*Oncorhynchus nerka*; Ruggerone, Zimmermann, Myers, Nielsen, & Rogers, 2003; Ruggerone et al., 2016), and other species of salmon (Ruggerone & Nielsen, 2004; Shaul & Geiger, 2004). Pink Salmon have a distinct 2 year life cycle and represent nearly 70% of the combined wild and hatchery salmon species found throughout the North Pacific (Ruggerone, Peterman, Dorner, & Myers, 2010).

Commercial ships have towed Continuous Plankton Recorders (CPRs) on a great circle route from the west coast of North America to ports in Asia to provide taxonomically resolved abundance data on larger phytoplankton and robust, mostly crustacean, zooplankton as part of a large-scale monitoring program in the North Pacific. Summer observations have been collected each year from 2000 to 2014 around the Aleutian Island chain as the vessels entered and exited the southern Bering Sea. Interannual variability in plankton populations at large (regional to basin) scales has often been linked to ocean climate forcing with warm or cool conditions causing a change in species composition and often abundance (e.g., Chiba, Batten, Sasaoka, Sasai, & Sugisaki, 2012; Chiba et al., 2015; Mackas et al., 2012). However, preliminary analyses of the plankton data from around the Aleutians showed a striking alternating odd/even year pattern in major groups of plankton rather than lower frequency, “stanza-like”, patterns of variability. The most likely explanation for an alternating pattern in the marine ecosystem is from the influence of Pink Salmon.

Japanese surveys have found large numbers of Pink Salmon in the southern Bering Sea in June and July (1972–1998), south of 62°N (Azumaya & Ishida, 2000). Furthermore, odd year densities were five times higher than even year densities here. During a more recent period (1991–2000), Pink Salmon densities in the central Bering Sea were approximately 40 times greater in odd years than in even years (Davis, 2003). Effects of Pink Salmon on zooplankton biomass and chlorophyll-*a* concentration have also been reported for North Pacific waters just south of the Aleutian Islands from 1989 to 1994 (Shiomoto, Tadokoro, Nagasawa, & Ishida, 1997) and from 1979 to 1998 (Kobari et al., 2003). For this period, high Pink Salmon densities in odd years were suspected of reducing the zooplankton biomass through grazing, which then allowed chlorophyll-*a* levels to be higher because of a lack of grazing pressure in these years. The reverse pattern was found in the even years (high zooplankton biomass and low chlorophyll-*a* concentrations).

In this study, we describe the likely impact of alternating high and low Pink Salmon densities on the zooplankton and phytoplankton around the Aleutian Islands (AI) as sampled by the CPR. We examine regional differences in the plankton populations and also examine the impacts on the plankton of unusual eastern Kamchatka Pink Salmon runs in 2013 and 2014. Our investigation of top-down effects of salmon on the offshore pelagic food-web has important implications for conservation and management of species of commercial, societal, and ecological importance because large numbers of hatchery salmon are released into the North Pacific each year and these fish could influence the marine ecosystem (Holt, Rutherford, & Peterman, 2008; Malick, Rutherford, & Cox, 2017).

## 2 | MATERIALS AND METHODS

The CPR was towed behind a commercial ship through Unimak Pass and across the southern Bering Sea on route to Asia each summer (1 June to 31 August) from 2000 to 2014 (Figure 1). Sampling occurred over just a few days in each summer, usually between 2 June and 14 July. In 2009 and 2011 sampling also occurred in August. Several vessels conducted the sampling over the time series but in each case the CPR was towed in the wake of the ship at a depth of about 7 m. Water and associated plankton entered the front of the CPR through a small square aperture (1.27 $\text{cm}^2$), and then through silk filtering mesh (with a mesh size of 270 μm) which retained the plankton and allowed the water to exit at the back of the machine. The movement of the CPR through the water turned an external propeller which, via a drive shaft and gear-box, moved the filtering mesh across the tunnel at a rate of approximately 10 cm per 18.5 km of tow. As the filtering mesh left the tunnel it was covered by a second band of mesh so that the plankton were sandwiched between these two layers. This mesh and plankton sandwich was then wound into a storage chamber containing buffered 40% formaldehyde preservative (which diluted in the seawater to a concentration of about 4%, sufficient to fix and preserve the plankton).

The towed mesh was processed according to standard CPR protocols (Batten et al., 2003). It was first cut into separate samples (each representing 18.5 km of tow and about 3 $\text{m}^3$ of seawater filtered) and every 4th sample was randomly apportioned amongst the analysts for plankton identification and counting. The ship’s log was used to determine the mid-point latitude and longitude of each sample (shown in Figure 1), along with the date and time.

The formaldehyde preservative used in the CPR does not fix athecate dinoflagellates so it is not possible to quantify their abundance. Hard-shelled phytoplankton were assessed under a purpose built microscope by viewing 20 fields of view (diameter 295 μm) across each sample under high magnification (×450) and recording the presence of all the taxa in each field. Presence in 20 fields is assumed to reflect a more abundant organism than presence in two fields, for example. Cell abundances per sample ($H$) were then estimated for each taxon according to Robinson and Hiby (1978):

$$H = -\ln\left(\frac{k}{20}\right)$$

Where $k$ is the number of empty microscope fields (out of 20) observed. Multiplication by the proportion of the sample examined gave cell counts per sample. Total diatom abundance was calculated by summing the estimated abundances of each diatom taxon recorded, per sample, and averaging for all samples in each year/sub-region.

Small zooplankton (less than about 2 mm) were identified and counted from a sub-sample by tracking across the filtering mesh with the microscope objective (a 2 mm diameter field of view = 2% of the sample width) and counting all zooplankton organisms encountered within the sub-sample.

All zooplankton larger than about 2 mm were removed from the mesh and counted without sub-sampling. Identification in all cases was carried out to the most detailed practicable taxonomic level and was a compromise between speed of analysis and scientific interest. For example, since copepods make up the majority of the zooplankton and remain mostly intact after sampling, most copepods were identified to species level whilst rarer groups, or those more fragile and not preserved well by the sampling mechanism (such as chaetognaths), were identified to a lower level of resolution such as phylum.

Every fourth sample collected was processed to give plankton abundance data and the mid-point of the 18.5 km sample allocated

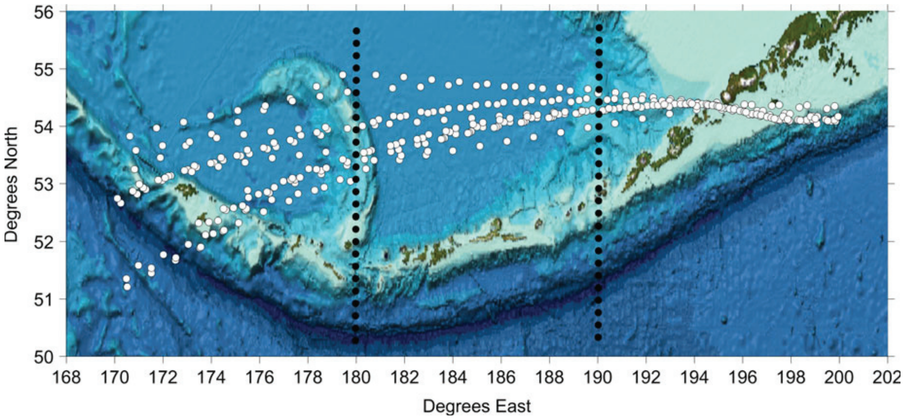

**FIGURE 1** Location of the mid-point of the Continuous Plankton Recorder samples used in this study. Dashed lines indicate the regional subdivisions (Western Aleutian Islands, Central southern Bering Sea and Eastern Aleutian Islands) [Colour figure can be viewed at wileyonlinelibrary.com]

a time, date and position. Figure 1 shows the location of all sample mid-points between 170°E and 160°W. All transects entered the Bering Sea through Unimak Pass, but the western exit varied more extensively between transects, depending on the Asian port travelled to. The region was subdivided along longitudinal lines (at 170°W and 180°) into three equal regions to examine spatial patterns in the plankton data. The eastern-most region sampled shelf and slope waters either side of Unimak Pass, while the central and western-most regions were more deep-water.

### 2.1 | Community composition

For each year/region combination a mean abundance of each phytoplankton taxon was calculated (99 taxa in total). Means were transformed (log $x + 1$) to reduce the impact of the most common taxa, and then Bray-Curtis dis-similarities were calculated between each pair of year/region means. The first analysis was a non-Multi Dimensional Scaling analysis of all three regions, and all sampled years. Then, each region was subjected to hierarchical clustering to examine similarities between years but within a region.

Broad groupings of mesozooplankton and microzooplankton taxa were made (such as large and small copepods, pteropods, euphausiids, ciliates, etc.) and mean abundances calculated for each region/year. Speed of the vessel did vary with sea conditions, but to cross one of the sub-regions typically took 18–24 hr. At these latitudes, in summer, most of the samples were therefore collected during daylight, but year/sub-region combinations each also contained 1–3 night samples. Night-time CPR samples often have higher zooplankton abundances of some taxa (such as euphausiids) and some taxa that show strong diel vertical migration (such as *Metridia* spp.) only occur in night-time samples. No sub-region/year combination consisted of wholly night or wholly day samples, therefore comparison of mean abundances (day and night together) between years and regions is valid.

### 2.2 | Plankton relationships with Pink Salmon

Pink Salmon originating from the eastern Kamchatka Peninsula is the primary population occurring in the central and eastern regions of our plankton sampling area, based on tagging studies and conceptual models of salmon migrations (Myers, Aydin, Walker, Fowler, & Dahlberg, 1996; Takagi, Aro, Hartt, & Dell, 1981). In the western region, Pink Salmon originating from other regions of Russia (western Kamchatka, Okhotsk Sea, Sakhalin and Iturup Islands) are present along with both juvenile and maturing Pink Salmon from eastern Kamchatka. Annual abundances (catch plus spawning escapement) of maturing pink salmon from these regions were provided by Ruggerone and Irvine (2018).

To evaluate the potential effect of Pink Salmon on plankton populations, we first searched for biennial patterns in zooplankton and phytoplankton counts because maturing Pink Salmon are especially abundant in odd years, owing in part to their fixed 2-year life cycle (Ruggerone & Irvine, 2018). A single factor ANOVA was used to quantify whether copepod abundance was low and diatom abundance was high in odd years, as anticipated in regions where Pink Salmon abundance is especially high in odd years, i.e., the central and eastern plankton sampling regions. Secondly, we used linear regression to evaluate whether copepod abundances declined and diatom abundances increased in years of abundant Pink Salmon, 2000–2014. Plankton counts in the eastern and central regions were regressed on Pink Salmon abundances from the eastern Kamchatka Peninsula, the primary population occurring in those areas. In the western region, plankton counts were regressed on Pink Salmon abundances from the eastern Kamchatka Peninsula and from the combined abundances of salmon from other areas of Russia that inhabit this region. A Durbin–Watson test was used to evaluate first-order serial autocorrelation in the residuals of the regression models.

## 3 | RESULTS

### 3.1 | Sampling

A total of 368 samples from 2000 to 2014 (Figure 1) were processed representing summer plankton populations in the eastern Aleutian Islands, central southern Bering Sea and western Aleutian Islands. Number of samples per year, per sub-region, was typically 9 but owing to occasional detrimental effects of debris in the water, or weather delays in deploying the instrument, was sometimes 3–5.

In 2008 only the eastern region was sampled, and in 2003 the central region was only represented by one sample and so was excluded. 2011 was sampled twice during summer in June and August and data were combined.

## 3.2 | Phytoplankton

Diatoms were by far the largest group of phytoplankton recorded from CPR samples, averaging 94% of total cell counts. For each region, the mean diatom abundance in each odd year was significantly greater than the mean abundance in the preceding or succeeding even year, resulting in an alternating-year pattern until 2012 in the Western region and 2013 in the Eastern and Central region (Figure 2). The Eastern region spans Unimak Pass so that samples to the east of 165°W were geographically in the Gulf of Alaska while samples to the west were in the Bering Sea. Conceivably, this could present a natural boundary that might influence the data and so we compared the mean annual diatom abundances either side of Unimak Pass. Although treating these two portions of the Eastern region separately reduces the sample density to only 4–5 at most per portion, both the Gulf of Alaska side and the Bering Sea side retained a clear alternating-year pattern to 2012, and there was a highly significant positive correlation between the two time series ($R^2 = .71$, $p < .001$). We therefore continued to treat the Eastern region as one continuous region, rather than two.

Community composition analyses (using all phytoplankton taxa, e.g., dinoflagellates, silicoflagellates, as well as diatoms) revealed firstly that there were some regional gradients in community structure (Figure 3). There was overlap between some years of all three regions but generally there was more separation between the Western and Eastern regions, with the Central region intermediate. With the exception of the outlying 2010 point from the Eastern region the *y* axis likely represents longitude (positive to the east, negative to the west). The Western region showed the tightest clustering, with less variability on both *x* and *y*-axes. For the Eastern and Central regions the *x*-axis reflects an odd-even year pattern with odd years (and 2014) to the right, and even years to the left.

Individual regions were subjected to hierarchical clustering of the dis-similarity matrices and the results are shown in Figure 4. The Western region shows no discrete clusters. The Central region shows two main clusters, one containing the even years from the earlier half of the time series (2000, 2002, 2004, 2006) plus 2005

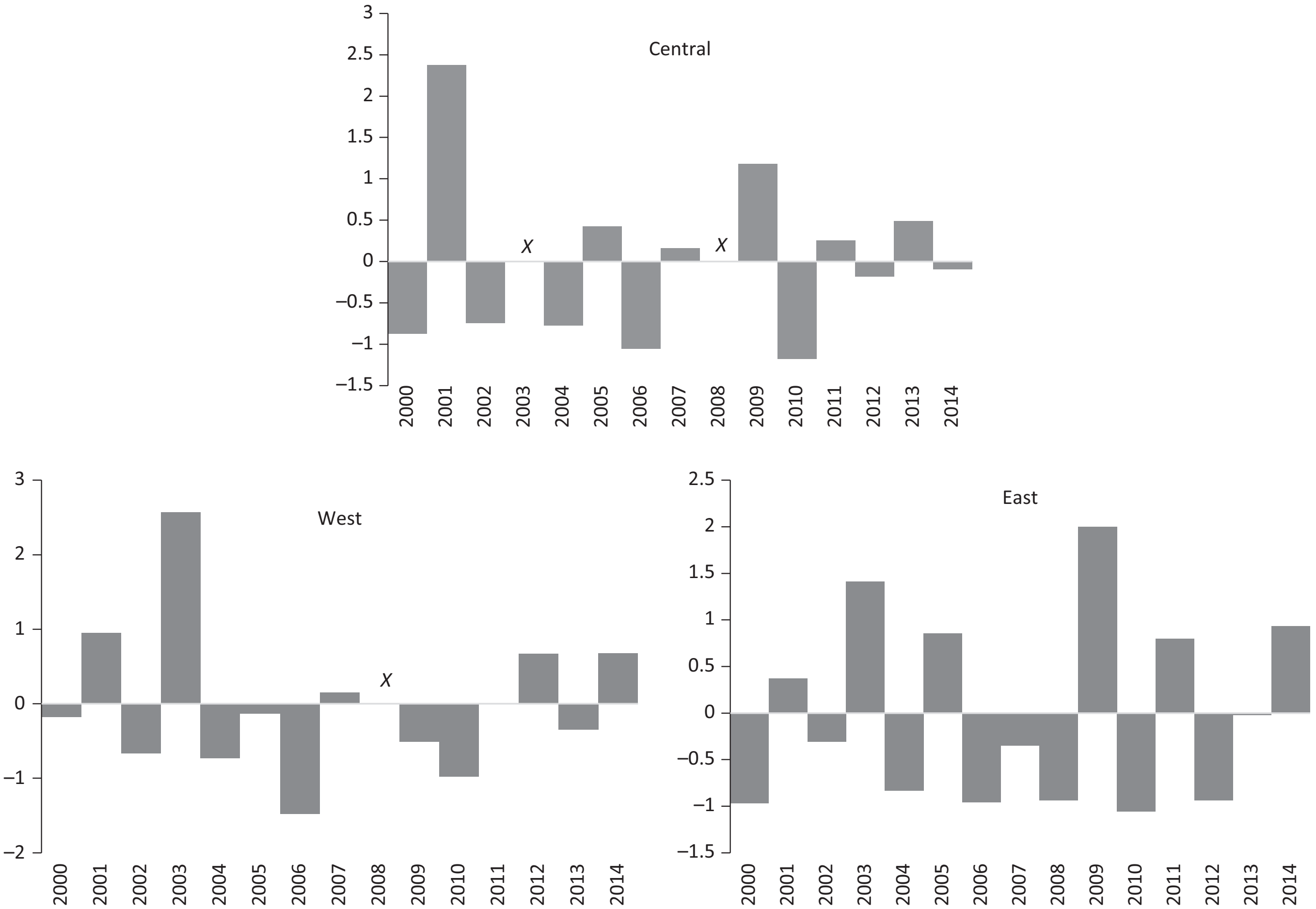

**FIGURE 2** Normalised annual abundance of diatoms per sample for each year and sub-region. *X*, no samples that year. ANOVA, significant differences in diatom abundances in the Central southern Bering Sea region ($df = 1,9$, $p = .002$) and Eastern region ($df = 1,12$, $p < .001$) prior to 2013, and marginally significant differences in the Western region ($df = 1,10$, $p = .08$)

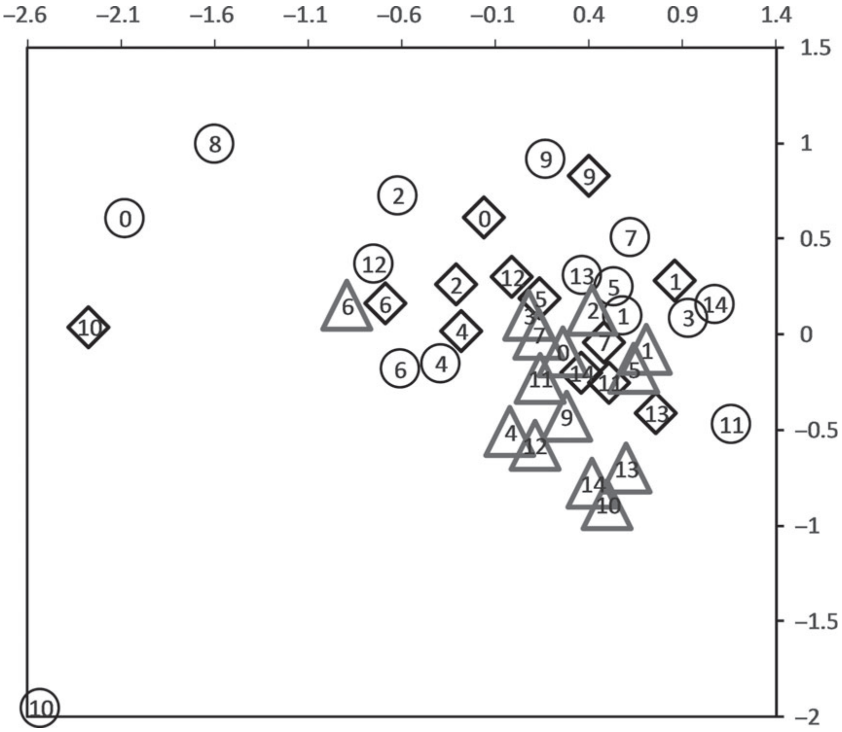

**FIGURE 3** Non-Metric Multidimensional Scaling analysis of transformed phytoplankton abundance data. Circles = Eastern AI region, Diamonds = Central southern Bering Sea region, Triangles = Western AI region. Year is shown in the centre of each symbol. Stress value of the ordination was 0.18

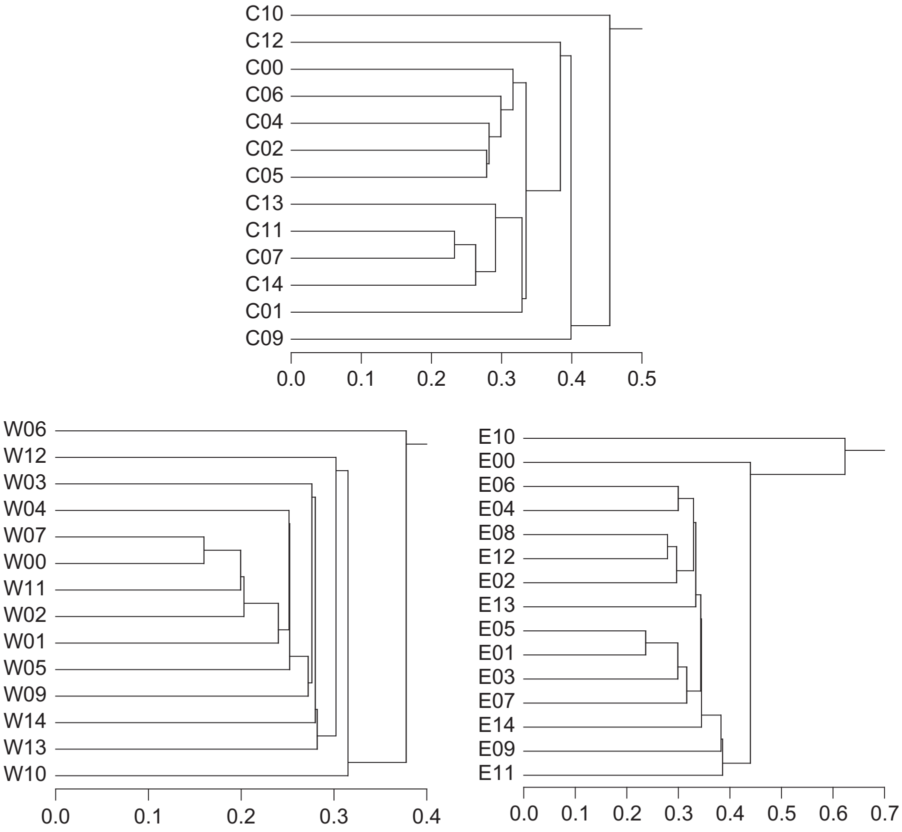

**FIGURE 4** Hierarchical clustering of mean phytoplankton composition per year for the Central southern Bering Sea (C top), Western Aleutian Island (W lower left) and Eastern Aleutian Island (E lower right) regions. Years are indicated after the C, W or E on the *y* axes labels. Distance is along the *x* axes

and the second containing mostly odd years (2001, 2007, 2011, 2013) plus 2014. The 3 years of 2009, 2010 and 2012 did not cluster with any group but were somewhat distinct. For the Eastern region separation into odd and even year groupings is very obvious. 2000 and 2010 are distinct years, otherwise one cluster contains all even years plus 2013 and the other contains all odd years plus 2014.

There was no noticeable effect of timing of the sampling within the summer season on the odd-even year patterns described above (e.g., years 2001–2005 and 2007 were sampled in early June while years 2006, 2008, 2010, 2013 and 2014 were sampled in the first 2 weeks of July and 2009 and 2011 sampled in July and August).

### 3.3 | Zooplankton

The mean composition by broad taxonomic groups is shown in Figure 5. The primary difference between regions is in the number of pteropods (mostly *Limacina* sp., but also includes *Clione*, *Clio*, *Thliptodon* spp.) which were much higher in the Western region. Otherwise regions showed similar numbers of each group. Copepods dominated numerically (accounting for 78%, on average, of the mesozooplankton individuals per sample), particularly those smaller than 2 mm total length. However, large copepods (>2 mm) dominated the zooplankton biomass because they are typically an order of magnitude greater in individual biomass, but only about one quarter as abundant as the small copepods. The large copepods showed a significant alternating odd/even year pattern of abundance in the Central southern Bering Sea and Eastern regions through 2012, but this biennial pattern was not significant in the Western region (Figure 6). In the Central and Eastern regions, the copepod pattern was opposite to that of diatoms, being high in even years and low in odd years (Figures 2 and 6).

### 3.4 | Eastern Kamchatka Pink Salmon

Abundances of eastern Kamchatka Pink Salmon, which is the primary population occupying the Central and Eastern regions, were eight times higher in odd years (122 million salmon) compared with even years (15 million salmon), from 2000 to 2012 (Figure 7). In 2013, abundance of eastern Kamchatka Pink Salmon unexpectedly declined 73% compared with previous odd years and their abundance (33 million salmon) was more similar to that in even years. The 2014 run size (48 million salmon) was relatively large for an even year cycle, though still less than the mean odd year run size. In contrast, Pink Salmon originating from other regions of Russia (western Kamchatka, Okhotsk Sea, Sakhalin and Iturup Islands), which are known to be distributed west of eastern Kamchatka Pink Salmon and overlapping the Western region in Figure 1 (Myers et al., 1996; Takagi et al., 1981), did not exhibit a strong alternating-year pattern of abundance (Figure 7).

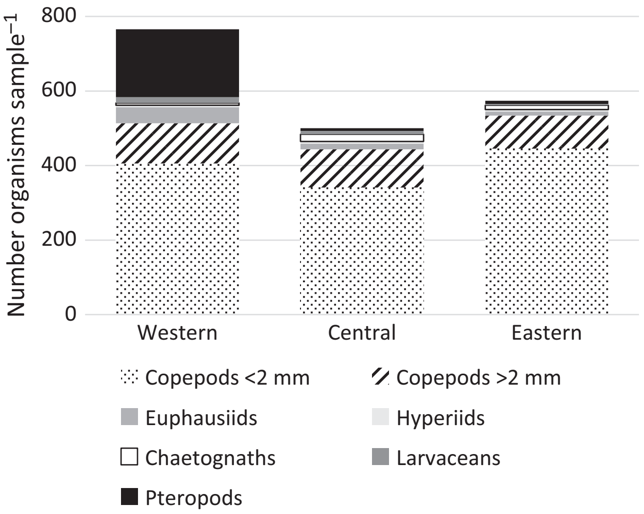

**FIGURE 5** Mean sample abundances for broad taxonomic categories of zooplankton, per region shown in Figure 1 for samples taken from 2000 to 2014

### 3.5 | Plankton-Pink Salmon relationships

In the Central and Eastern regions during odd-numbered years, Pink Salmon abundance was high, large copepod abundance was low, and large diatom abundance was high. Furthermore, abundances of large copepods ($\log_{10}$ transformed) in the Central and Eastern regions were negatively correlated with abundance of eastern Kamchatka Pink Salmon, 2000–2014 (Figure 8; $r^2 = .32$, $p = .04$; $r^2 = .61$, $p < .001$, respectively). In contrast, diatom counts in the Central and Eastern regions were positively correlated with abundance of eastern Kamchatka Pink Salmon ($\log_{10}$ transformed; $r^2 = .32$, $p = .04$; $r^2 = .50$, $p = .003$, respectively). Serial autocorrelation was non-significant among residuals in each model ($p > .05$). Copepod abundance and diatom counts in the Western Region were not significantly correlated with Pink Salmon abundances from (i) eastern Kamchatka, (ii) the combined abundances of other Pink Salmon populations that inhabit the Western Region, or (iii) Pink Salmon from all areas ($p > .05$).

In Figure 9 we show the 2013 and 2014 plankton data (years when the abundance of eastern Kamchatka Pink Salmon deviated from the normal odd/even run sizes) for the Central and Eastern regions alongside the mean odd/even data for 2000–2012. Large copepods would typically be low in numbers in an odd year, but in 2013 they were very abundant. In the Eastern region 2013 was the highest, and in the Central region the second highest, mean annual abundance of any year in the time series (odd or even). Diatoms would typically be high in an odd year, but given the very high numbers of large copepods in 2013 we would expect low numbers of diatoms in the Central and Eastern regions. However, for both regions diatom abundances in 2013 were high; not as high as a typical odd year (with high salmon and low copepod abundances) but higher than in a typical even year (with low salmon and high copepods; Figure 9). 2013 also had a dramatic change in the numbers of hard-shelled ciliates which comprise the only part of the microzooplankton community that is sampled by the CPR. These organisms are similar in size to the larger diatoms, and not a food source for Pink Salmon. Odd years up to 2011 typically had a slightly higher abundance of microzooplankton than even years up to 2012, suggestive of enhanced grazing pressure on microzooplankton by large copepods in the low Pink Salmon years as occurred with diatoms (ANOVA, $p = .02$ for the Central, southern Bering Sea region, $p = .05$ for the Eastern region). In both the Eastern and Central regions microzooplankton numbers were at least an order of magnitude higher in 2013 than in any year previously (Figure 9).

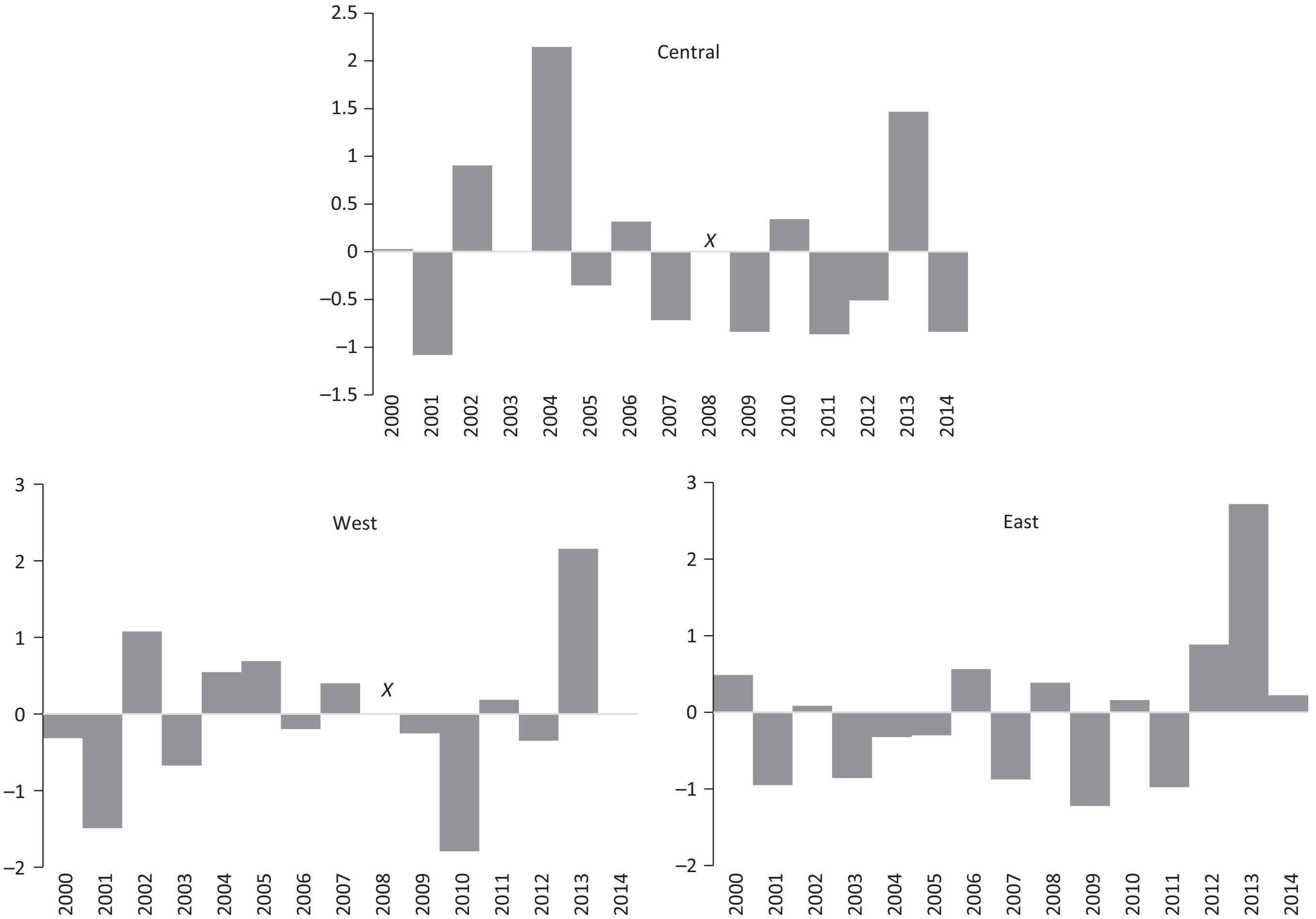

**FIGURE 6** Normalised annual abundance of large copepods (>2 mm total length) per sample for each year and sub-region (in Figure 1). *X*, no samples that year; ANOVA, significant differences in copepod abundances in the Central southern Bering Sea region ($df$ = 1,9, $p$ = .01) and Eastern AI region ($df$ = 1,11, $p$ < .001) prior to 2013, but no difference detected in the Western AI region ($df$ = 1,10, $p$ = .95)

## 4 | DISCUSSION

Our results provide evidence for a trophic cascade caused by Pink Salmon from eastern Kamchatka on the plankton populations near the Aleutian Island chain: (i) clear biennial patterns in the summer abundance of large diatoms and copepods which alternate in opposing directions, (ii) significant correlations with Pink Salmon abundance (negative in the case of large copepods, positive in the case of diatoms) for the Central and Eastern regions, (iii) biennial patterns in the community composition of the phytoplankton in the Central and Eastern regions, and (iv) clear and consistent changes to these biennial patterns in 2013 and 2014 when the Pink Salmon runs deviated from their normal pattern. Furthermore, the patterns in the plankton do not reflect the lower frequency ocean climate variability of the region.

As with all plankton sampling devices, the CPR has biases; small phytoplankton cells are vastly under-sampled and naked flagellates are not able to be resolved at all. Gelatinous zooplankton are also only discernible either at a low taxonomic resolution (as in the case of chaetognaths and salps), or as presence/absence data only (such as jellyfish) and very small copepods (including young stages of larger species) and large euphausiids are significantly under-sampled. However, the CPR is a consistent sampler of larger diatoms, hard-shelled dinoflagellates and (especially crustacean) mesozooplankton, therefore, changes in the data for these groups likely reflect real changes in the ecosystem. Richardson et al. (2006) describe the strengths and limitations of CPR data analysis in more detail.

The striking alternating patterns of high and low annual abundances seen in the diatoms (high in odd years, low in even years, Figure 2) and in large copepods (low in odd years, high in even years, Figure 6) between 2000 and 2012, particularly in the Central and Eastern regions, is strongly suggestive of a trophic-cascade caused by Pink Salmon. Diet studies show copepods comprise an increasing portion of maturing Pink Salmon diet since the 1960s, contributing 10% or more in the 1990s and 2000s in the Bering Sea (Davis, Fukuwaka, Armstrong, & Myers, 2005; Karpenko, Volkov, & Koval, 2007), with the remainder being mostly fish, squid and euphausiids. High maturing Pink Salmon abundances (odd years, Figure 7) appear to exert a heavy grazing pressure on large copepods which in turn exert a lower grazing pressure on the diatoms with the reverse being true in even years when Pink Salmon abundance is low (Figure 8).

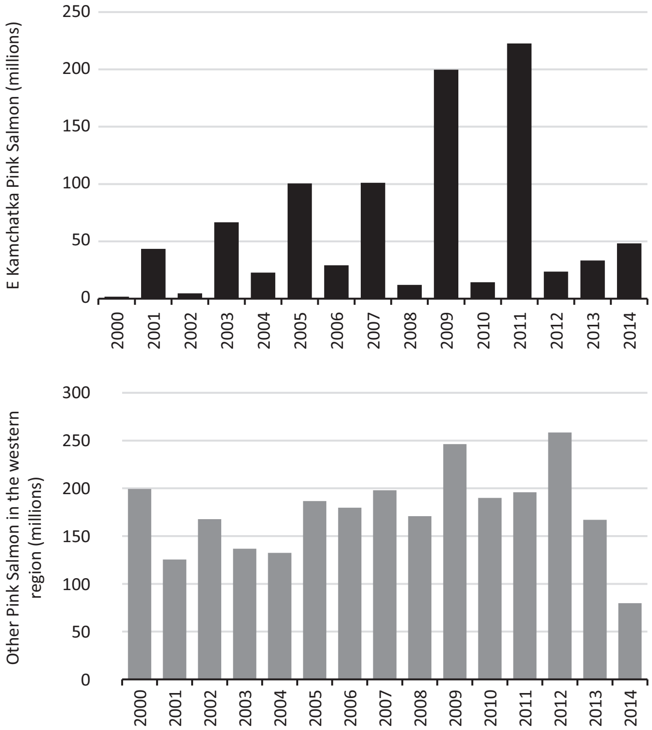

**FIGURE 7** Abundances of adult Pink Salmon from eastern Kamchatka that overlap the Western and Eastern Aleutian Island and southern Central Bering Sea regions (top). Combined Pink Salmon abundances from western Kamchatka, Okhotsk Sea, and Sakhalin and Iturup islands that primarily overlap the Western Aleutian Island Region but not regions farther east (bottom). Source: Ruggerone and Irvine (2018)

The data for the Western region show weaker biennial patterns in both copepod and diatom abundances (Figures 2 and 6) and in the phytoplankton community structure (Figures 3 and 4). The lack of a strong alternating year pattern in the plankton of the Western region may reflect the presence of both post-smolt (juvenile) and maturing Pink Salmon, including those originating from other regions of Russia (Myers et al., 1996; Takagi et al., 1981) where the odd/even abundance pattern is weak (Figure 7). Furthermore, Russian scientists have suggested that the western Bering Sea is approximately 30% more productive than the eastern Bering Sea (Davis et al., 2009) which may reduce the impacts of Pink Salmon if there is sufficient productivity to support their numbers. Our data also indicated zooplankton abundance was 53% and 33% greater in the Western region compared with the Central and Eastern regions, respectively (Figure 5).

Phytoplankton taxonomic composition appears subtly different between the Western Aleutian Island, Central southern Bering Sea and Eastern Aleutian Island regions (Figures 3 and 4), although there is overlap. Most common taxa (e.g., *Thalassiosira* spp. and *Chaetoceros* spp.) occurred in all three regions, but there were some differences in relative abundances. Dinoflagellates appeared to be less common and less diverse in the Western region and taxa associated with shallow waters (such as *Paralia* spp.) were only found in the Eastern region or had higher abundances. There is some evidence that the phytoplankton community structure (as sampled by the CPR) was influenced by the alternating weight of grazing pressure (Figure 4) with clear clustering into two groups of mostly odd and even years in the Central and Eastern regions.

The unusually low 2013 run of eastern Kamchatka Pink Salmon and the resulting influence on plankton provides further evidence for a trophic cascade effect. Plankton communities did not show their expected odd-year relative abundances in 2013. Large copepods were unusually high, diatoms were also relatively high and microzooplankton (hard-shelled ciliates only) were high (Figure 9). The most likely explanation for higher numbers of large copepods is reduced grazing pressure by Pink Salmon from eastern Kamchatka. However, the high numbers of diatoms and hard-shelled microzooplankton was unexpected given the high numbers of large copepods and as yet we have no explanation. Pink Salmon returning to Southeast Alaska and Prince William Sound were exceptionally abundant in 2013 (about 265 million fish), but tagging data indicate these stocks are distributed primarily east of our Eastern sampling region (Myers et al., 1996; Takagi et al., 1981). The 2015 odd year run to eastern Kamchatka returned in very high numbers (Ruggerone & Irvine, 2018) so their decline in 2013 did not persist.

In 2014 Pink Salmon abundance was high for an even year, higher than all other even years between 2000 and 2012 and similar in magnitude to the 2001 odd year run. The effect on large copepods was clear, with relatively low numbers for an even year, especially in the Central region where abundances were close to the odd-year mean (Figure 9). Diatoms were high for an even year especially in the Eastern region, which would be expected from the lower copepod abundances. Microzooplankton numbers reverted to normal in the Central region, but remained high in the Eastern region. The northeast Pacific experienced anomalously warm conditions in 2014 (DiLorenzo & Mantua, 2016) and the so-called “marine heat-wave” was widespread. This may have caused Pink Salmon to shift further north so that more salmon were in the southern Bering Sea, thus leading to a higher grazing pressure than typical for an even year.

The start of the CPR plankton time series (2000) coincided with a shift in the frequency of physical variability in the Bering Sea (Duffy-Anderson et al., 2017) from short term (1–2 years) before 2000 to longer, persistent periods of warm or cold (4–6 years) after 2000, known as “stanzas”. The years 2001–2005 covered a warm stanza, and were followed by a cold stanza lasting from 2007 to 2013 before a return to warm conditions in 2014. On the Bering Sea shelf warm periods had noticeable effects on Pollock recruitment (previously little-impacted by single warm years) through changes in their zooplankton prey (Coyle et al., 2011), in a strongly bottom-up driven system (Stabeno et al., 2017). The more oceanic regions of the southern Bering Sea in our study may function differently to the productive shelf to the north-east, as recent analysis from model outputs show gradients in zooplankton and phytoplankton phenology, as well as in the frequency of the interannual variability characterized by 1–2 years inshore and 2–4 years off shelf (Hermann et al., 2016; Ortiz et al., 2016). There are no obvious

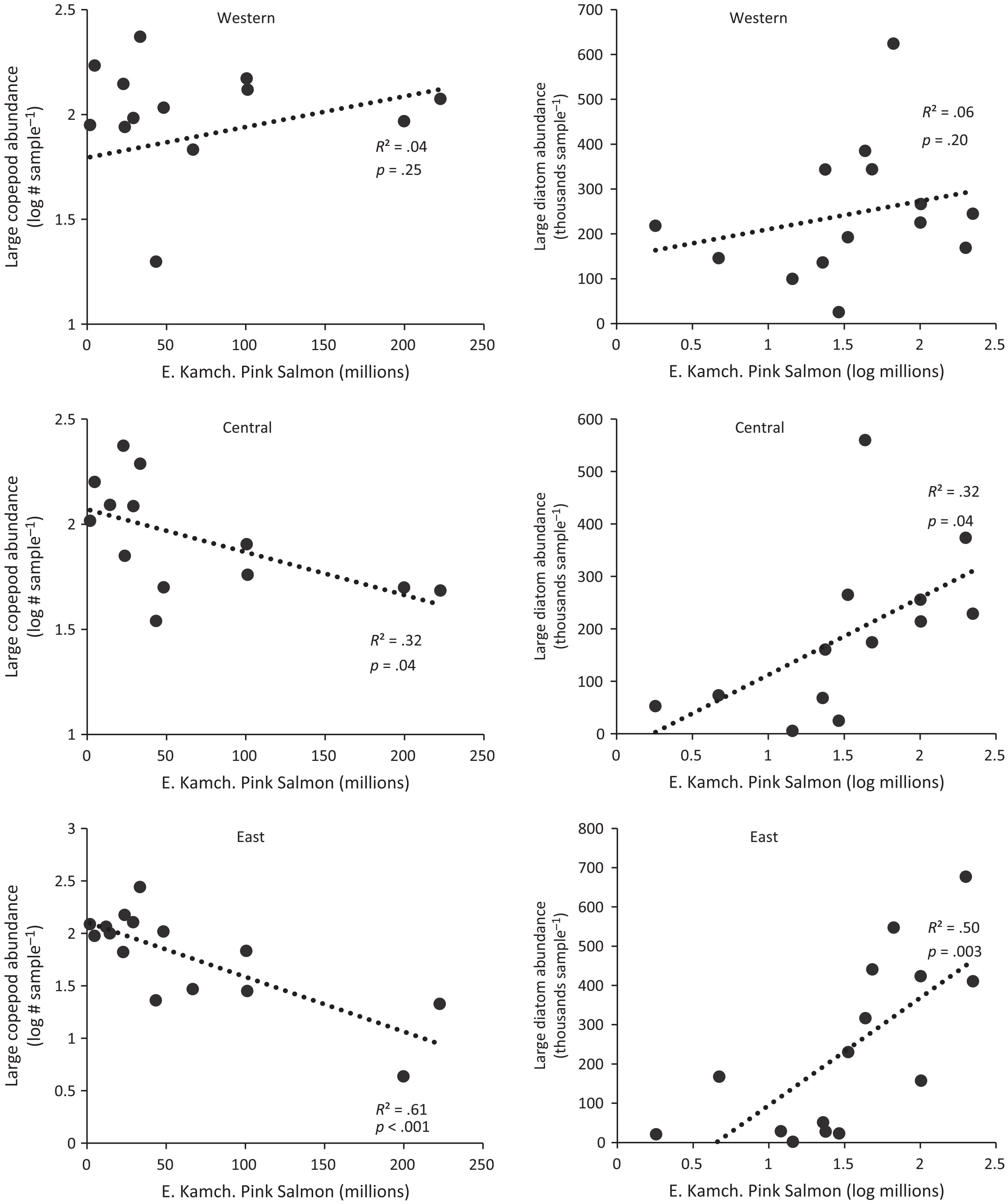

**FIGURE 8** Correlations between eastern Kamchatka Pink Salmon and large copepods (left) and large diatoms (right) for the Western Aleutian Island, Central southern Bering Sea and Eastern Aleutian Island regions. $R^2$ and $p$ values are shown on each graph

impacts of the multi-year warm and cold stanzas in the plankton time series (Figures 2 and 6). Perhaps the reduced frequency of physical variability highlighted the biennial Pink Salmon signal.

Examples of trophic cascades in marine ecosystems are rare but can be found (Essington, 2010; Pershing et al., 2015). For example; Frank, Petrie, Choi, and Leggett (2005) describe the effects of the

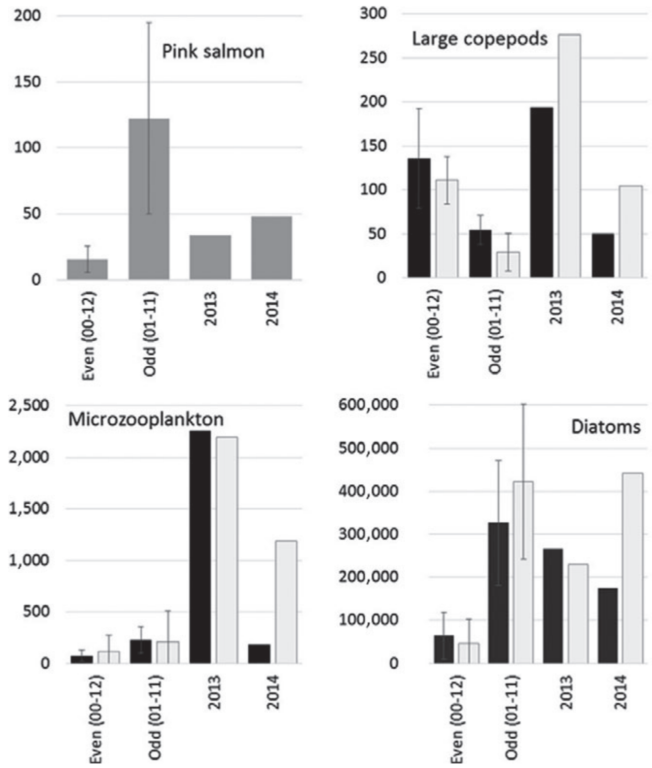

**FIGURE 9** Comparison of mean odd and even year abundances with 2013 and 2014 values for different trophic levels. Pink Salmon data are estimated from run size data from Ruggerone and Irvine (2018) in millions of fish, plankton data are numbers of organisms per sample. Error bars indicate standard deviation in each case. Black bars indicate plankton data for the Central southern Bering Sea, grey bars plankton data for the Eastern Aleutian Island region

collapsed cod (*Gadus morhua*) fishery on the Scotian Shelf where the removal of the top predators caused an increase in benthic macro-invertebrates and small fish, a decline in larger zooplankton and an increase in phytoplankton. Similarly, the effect of sea otter predation on sea urchins leading to increased kelp forests was described by Estes and Palmisano (1974), and indirectly affected bald eagles (*Haliaeetus leucocephalus*; Anthony, Estes, Ricca, Miles, & Forsman, 2008). While examples of trophic cascades are much rarer than studies reporting the bottom-up effects of oceanographic variability, the results described here show that top-down effects need to be considered where large numbers of predators occur. The influence of Pink Salmon on the summer plankton around the Aleutian Islands and in the southern Bering Sea was a much stronger signal than environmental variability caused by the cold/warm stanzas experienced by the Bering Sea during the same time period.

Our findings support other studies indicating consequences for predators that directly or indirectly rely on plankton in the Bering Sea in summers when Pink Salmon are numerous. Growing evidence indicates that foraging Pink Salmon affect feeding and reproduction of seabirds (Springer & van Vliet, 2014; Sydeman et al., 2017; Zador, Hunt, TenBrink, & Aydin, 2013) and growth and survival of Sockeye Salmon (Ruggerone & Connors, 2015; Ruggerone et al., 2016), Chinook Salmon (*Oncorhynchus tshawytscha*; Ruggerone et al., 2016; Ruggerone & Nielsen, 2004), Coho Salmon (*Oncorhynchus kisutch*; Shaul & Geiger, 2016), and Chum Salmon (*Oncorhynchus keta*; Azumaya & Ishida, 2000; Ruggerone & Nielsen, 2004; Agler, Ruggerone, Wilson, & Mueter, 2013). The trophic cascade caused by Pink Salmon has important societal implications, especially to the extent that Pink Salmon may have influenced the declining size-at-age and abundance of Chinook Salmon throughout Alaska (Lewis, Grant, Brenner, & Hamazaki, 2015). Our work supports the expanded inclusion of annual indicators, trophic effects, and interactions within the larger context of marine resource management, both as ecosystem status indicators and as a way to track population abundance and ecosystem processes.

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