

# Large-scale climate control of zooplankton transport and biogeography in the Kuroshio-Oyashio Extension region

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[1] We studied decadal-scale climate control of zooplankton biogeography driven by Kuroshio Extension (KE) dynamics using long-term zooplankton data and an advection model driven with currents from the Earth Simulator eddy-resolving ocean model. Passive tracer model experiments indicated that warm-water species transported from the south were retained in the Kuroshio-Oyashio Extension (KOE) region during years with a weak KE. A 2.5 year lag in the North Pacific Gyre Oscillation (NPGO) index was significantly correlated with the KE strength and with warm-water species abundance. These findings indicate that climate signals from the central and eastern North Pacific propagated westward, influencing not only transport in the KOE region but also regional ecosystem variability. Because the NPGO controls important aspects of the transport dynamics and ecosystem variability in the eastern North Pacific, this study provides additional evidence that large-scale climate patterns drive coherent changes in ecosystems throughout the North Pacific by impacting regional-scale transport dynamics. **Citation:** Chiba, S., E. Di Lorenzo, A. Davis, J. E. Keister, B. Taguchi, Y. Sasai, and H. Sugisaki (2013), Large-scale climate control of zooplankton transport and biogeography in the Kuroshio-Oyashio Extension region, *Geophys. Res. Lett.*, 40, 5182–5187, doi:10.1002/grl.50999.

## 1. Introduction

[2] Biogeographical changes in zooplankton communities related to large-scale climatic events over the past several decades have been reported in the world's oceans. A multidecadal trend observed in the North Atlantic and related to North Atlantic Oscillation involves a northward shift of warm-water species associated with regional warming [Beaugrand *et al.*, 2002]. The alternating dominance of cold-water and warm-water species driven by oceanic current dynamics has been reported in the eastern North Pacific [Batten and Freeland, 2007]. Understanding the regionally specific mechanisms of how climatic forcing influences the biogeography of zooplankton is crucial for the sustainable

management of local fisheries, because changes in the regional zooplankton community structure could impact recruitment success of commercially important fish species [Beaugrand *et al.*, 2003; Peterson and Schwing, 2003].

[3] Peterson and Keister [2003] observed a significant correlation between the interannual variation in copepod species composition off the Oregon coast and the Pacific Decadal Oscillation index (PDO). They subsequently hypothesized that interannual variation in the strength of alongshore transport in the California Current driven by the dynamics of the Aleutian Low (AL) pressure systems determines the extent of latitudinal advection of zooplankton and, consequently, local copepod biogeography. This hypothesis was supported by passive tracer experiments using a Regional Ocean Modeling System that showed a significant correlation between the model output and the observed data [Keister *et al.*, 2011].

[4] In the western North Pacific, Chiba *et al.* [2009] studied the geographical shift of the copepod community in the Transition region of the Kuroshio and Oyashio currents during the 1960s–1990s. Although they hypothesized that variation in advection transport by the Kuroshio was the major driver of the observed interannual variation in the occurrence of warm-water species in the study region, the mechanism was not fully investigated. The Kuroshio turns eastward to reach around 35°N and forms inertial jet, the Kuroshio Extension (KE) (Figure 1a). The decadal-scale dynamics of the KE have been linked to large-scale modes of decadal climate variability over the North Pacific sector. Qiu *et al.* [2007] shows that sea-surface-height anomalies in the central North Pacific associated with the PDO travel westward as Rossby waves toward the KE, giving rise to decadal variations in the mean-latitudinal position of the KE jet. A more recent study shows that large-scale Rossby waves excited by the North Pacific Gyre Oscillation (NPGO) also travel westward and impact strength of the KE upon reaching the KE with a delay of about 2.5 years [Ceballos *et al.*, 2009].

[5] Using a passive tracer model experiment, this study aimed to test the hypothesis that the dynamics of the Kuroshio Current and KE influence decadal-scale zooplankton biogeography and, furthermore, aimed to investigate large-scale climate control of lower-tropic-level ecosystems in the Kuroshio-Oyashio Extension (KOE) region.

## 2. Materials and Methods

### 2.1. Zooplankton Analysis

[6] We used copepod species composition data from the Odate Collection zooplankton data set [Odate, 1994]. All zooplankton were collected by vertical towing of a ring net (mesh size, 330  $\mu$ m) between the surface and 150 m depth.

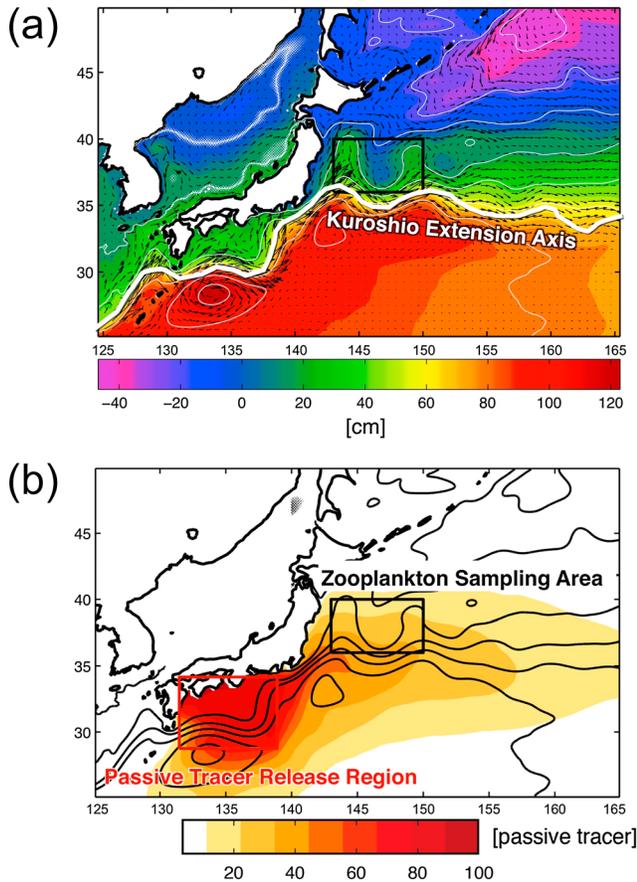
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**Figure 1.** (a) Map of mean sea surface height (SSH) obtained by Ocean General Circulation Model for the Earth Simulator (OFES) and currents for the period 1950–2008. Thick white line shows the mean position of the Kuroshio Extension (KE) axis during those years. (b) Mean tracer concentration over the same period. The tracer is released in the region outlined by the red box and is advected by the 3 day average currents of the OFES model and decays to zero with a timescale of 6 months. Therefore, Figure 1b can also be interpreted as the probability distribution function of the tracer from the red box at a 6 month lag. The black box in Figure 1b outlines the boundaries of the Odate zooplankton sampling grid.

Detailed descriptions of the sampling methods and data sources were provided by Odate [1994]. We used zooplankton data sampled between May and September for 1966–1999, as the sampling frequency for other months was not sufficient to examine interannual variation. As zooplankton biomass is highest from spring to summer and remains small during late autumn and winter in this region [Odate, 1994], we assumed that the May–September average biomass represented interannual biomass variation. The compositions of copepod species in a total of 1164 samples were analyzed in the area within  $36^{\circ}00'–40^{\circ}00'N$ ,  $143^{\circ}00'–150^{\circ}00'E$  (Figures 1a and 1b, black boxes) in the area north of the KE axis, which roughly covers the transition region lying between the Oyashio and Kuroshio.

[7] Copepod compositions in this research area are mixtures of northern, cold-water species and southern, warm-water species, which are mainly distributed in the Oyashio

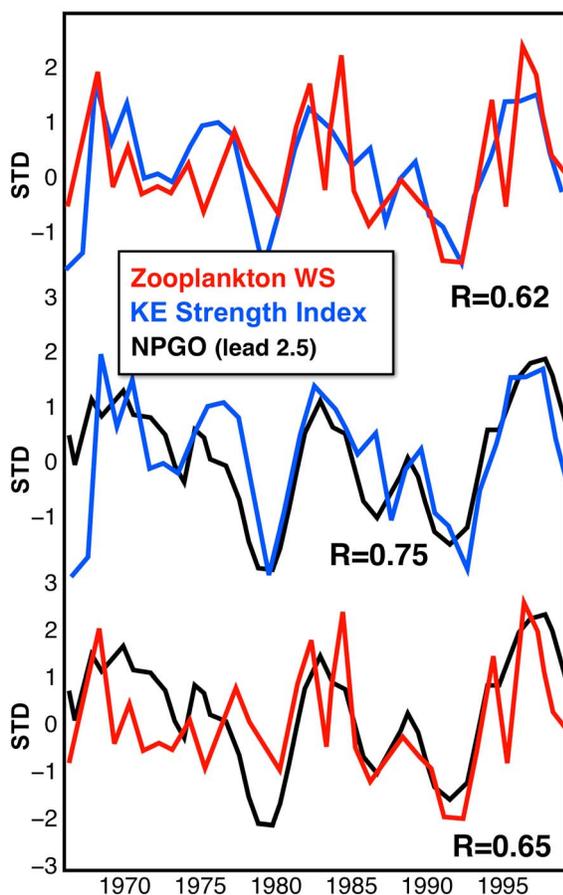
and Kuroshio, respectively. Among the major species occurring in  $>30\%$  of all samples, we selected warm-water species according to the scheme established by Chihara and Murano [1997] and estimated the interannual variation of their area-mean abundance (number of individuals per  $1000\text{ m}^{-3}$ ). The warm-water species group consisted mainly of small species in comparison with the cold-water species group (mean total length, 1.3 mm and 4.1 mm, respectively).

## 2.2. Advection Model Using the Ocean General Circulation Model for the Earth Simulator

[8] Warm-water species in the KOE region are found mainly within the upper 50 m of the water column ( $>90\%$ ) [Shimode *et al.*, 2006]. This depth is within the mix layer depth of 150–200 m [Ohno *et al.*, 2009] during the months when the zooplankton is being transported. To model the horizontal advection of zooplankton, we treated the upper ocean 50 m as a uniform 2-D layer and used an offline 2-D horizontal advection model to track a passive tracer released in the hypothesized source regions of the warm-water zooplankton species over the Kuroshio pass ( $29^{\circ}00'–34^{\circ}00'N$  and  $132^{\circ}00'–139^{\circ}00'E$ ) (Figure 1b, red box), in which the warm-water copepods species are abundant [Nakata and Hidaka, 2003].

[9] The model used a simple Euler scheme for the time derivatives and a second-order up-wind scheme to discretize the spatial derivatives where the upper ocean velocity field (0–50 m) is prescribed from the 3 day average hindcast of the global eddy-resolving Ocean General Circulation Model for the Earth Simulator (OFES) over the period 1950–2008 [Sasaki *et al.*, 2008]. No explicit diffusion term is added in the advection model because the second-order up-wind scheme introduces already numerical diffusion that is sufficient to make the scheme stable. The OFES ocean model horizontal resolution is  $1/10^{\circ}$  with 54 vertical level (5 m interval for the surface 0–330 m). The OFES topography is computed from the  $1/30^{\circ}$  bathymetry data set of the Ocean Circulation and Climate Advanced Modelling Project. The OFES hindcast was forced by surface wind stress, heat, and freshwater fluxes derived from daily reanalyses by the National Centers for Environmental Prediction–National Center for Atmospheric Research [Kalnay *et al.*, 1996]. This hindcast has successfully been used in previous studies to analyze different aspects of decadal variability in the KOE region [Nonaka *et al.*, 2006; Taguchi *et al.*, 2007].

[10] The passive tracer was continuously released from the source region. To avoid accumulation of the tracer with time, we introduced a decay or dissipation term in the advection model with a timescale of 6 months. This implies that taking the long-term mean of the tracer will provide information on the average spread of the tracer from the release region over a period of 6 months (Figure 1b). Given that the tracer concentration in the release area is set to 100, the tracer concentration is also representative of the probability distribution function (PDF) of the tracer (0–100%) from the release region at lag 6 months. This PDF (Figure 1b) shows that on average over a period of 6 months, the tracer is transported from the source region along the main axis of the Kuroshio to the region where the zooplankton data were collected (Figures 1a and 1b, black box). The timescale of 6 months for the decay was selected in order to compute a PDF that is consistent with the timescale of advection of the particles estimated by Noto and Yasuda [1999], which shows that



**Figure 2.** Time series abundance of warm-water zooplankton species (Zooplankton WS) in the study area, Kuroshio Extension (KE) Strength Index (sign reversed), and North Pacific Gyre Oscillation (NPGO). The NPGO is plotted with a lead time of 2.5 years consistent with the time takes for the NPGO sea surface height anomaly (SSHa) to reach the Kuroshio-Oyashio Extension (KOE) region. Zooplankton data are May–September averages; the KE Strength Index and NPGO were averaged over March–June period when the zooplankton is transported from the southern source region. All time series are normalized by their standard deviations (SDs) so that the y axis indicates units of SD.

it takes 1 to 5 months for Kuroshio transport to carry fish eggs/larvae from its spawning region, which overlaps the source region in this study, to 150–160°E along the KE axis. As the life cycles of the warm-water species are generally shorter than 3 months [Mauchline *et al.*, 1998], we assumed that population of multiple generations of these species expanded their distribution northward and reached the observation region with a couple of months lag.

### 2.3. Indices of KE Dynamics

[11] We investigated the influence of KE dynamics on the distribution of the warm-water species by comparing the KE indices [Taguchi *et al.*, 2007] to the observed zooplankton time series. The decadal variability of the KE is driven by the arrival of westward-propagating large-scale Rossby waves from the central and eastern North Pacific at the western Pacific boundary [Qiu *et al.*, 2007; Ceballos *et al.*, 2009]. The response of the KE to this remote wave

forcing can be separated into two dominant modes of variability [Taguchi *et al.*, 2007]: the first mode is associated with a southward/northward shift in the axis of the KE (KE Axis Index), which is defined by the zonal mean of the midlatitude between the northern and southern KE fronts, and the second mode is associated with a strengthening and weakening of the mean KE (KE Strength Index), which is defined by difference in sea surface height (SSH) between 34.5 and 37°N.

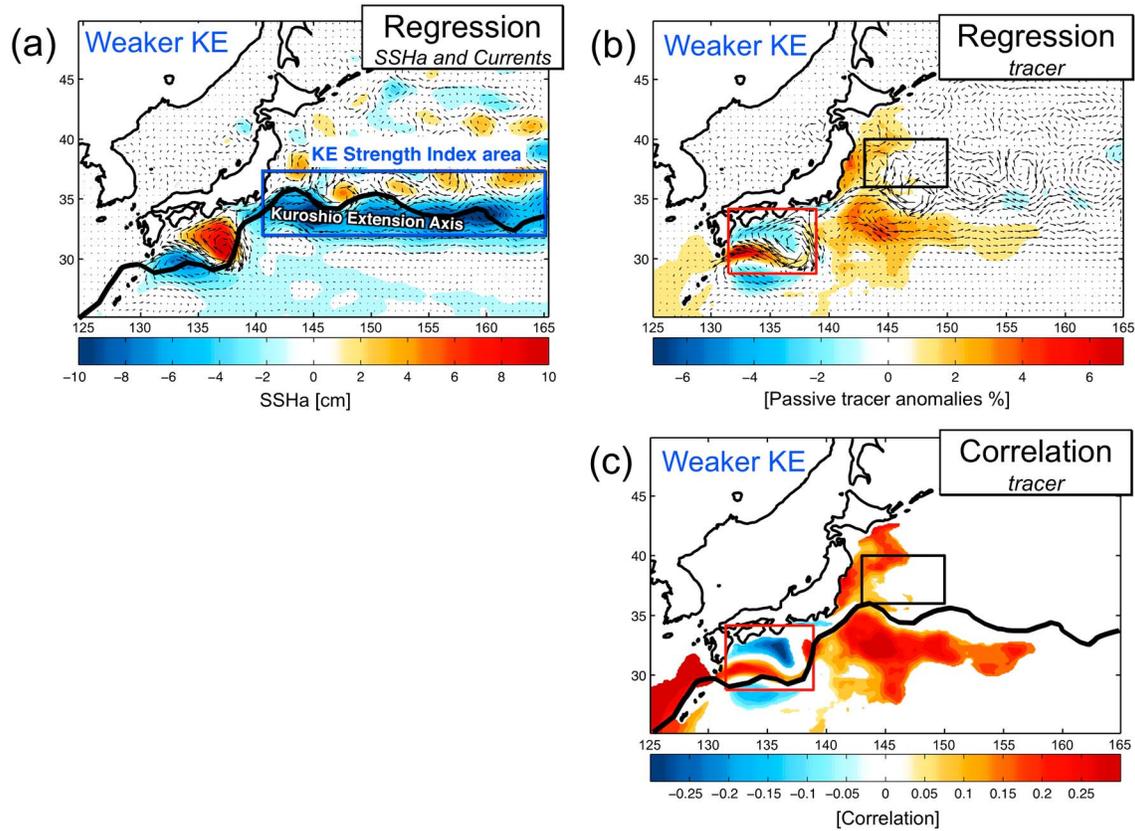
[12] The correlations between the KE Indices and zooplankton time series were computed using the KE indices values averaged over the months of March–June assuming the several month timescale when the zooplankton is transported from the southern source region toward the northern sampling region [Noto and Yasuda, 1999]. Because the PDO and NPGO are closely related to the KE Axis Index and KE Strength Index, respectively [Taguchi *et al.*, 2007], we also compared these indices and zooplankton time series to the March–June average PDO index and NPGO index. As the NPGO signal reaches the KE with a delay of about 2.5 years [Ceballos *et al.*, 2009], NPGO time series was plotted with a lead time of 2.5 years. All time series are normalized by their standard deviations.

## 3. Results and Discussion

### 3.1. Advection Transport and Impact on Zooplankton

[13] The observed warm-water zooplankton abundance, which peaked in the late 1960s, early 1980s, and mid-1990s, was significantly correlated with the KE Strength Index ( $R=0.62$ ,  $p < 0.05$ ; KE Index was reversed in Figure 2), indicating more warm-water species in years with a weak KE. Similar high correlations were found between the NPGO and KE Strength Index ( $R=0.75$ ,  $p < 0.01$ ), as well as the NPGO and the zooplankton time series ( $R=0.65$ ,  $p < 0.05$ ) (Figure 2). The results evidence that the KE dynamics driven by NPGO can determine the biogeography of the zooplankton community in the KOE region. In contrast, we detected no significant correlations between the KE Axis Index and either zooplankton time series or the PDO.

[14] The strong correlation between weak KE years and the zooplankton suggests that during weaker KE years, the reduced offshore advection of southern waters along the KE axis generates retention of these waters in the region of zooplankton observation. To verify this hypothesis, we examined the circulation regimes and passive tracer dispersions calculation (see section 2.2) during years of weaker KE Strength Index. A regression map between the KE Strength Index and the OFES model SSH anomalies (SSHa) and currents (Figure 3a) reveals that weaker states of the KE are characterized by strong recirculating meanders along the KE axis. By performing the same regression analyses on the passive tracer monthly anomalies, we examined how the spread of waters from the southern region (Figure 3b, red box) into the KE is affected during the weak KE regime. Figure 3b shows that during weak KE, a significantly higher than usual concentration of tracer is found both to the south and north of the KE axis (Figure 3c). These positive correlation and tracer concentration values follow closely the structures of the ocean meanders. However, while the OFES model has been shown to capture the macro-scale properties of mixing and transport in the KOE region, the model cannot resolve the exact structure of the meanders, which is at the scale of the sampling box (Figure 3b). For this reason, we



**Figure 3.** (a) Regression maps of the Kuroshio Extension (KE) Strength Index with sea surface height anomaly (SSHa) (shading) and currents (black arrows). (b) Regression map of the KE Strength Index with the tracer concentration monthly anomalies. (c) Same as Figure 3b but showing the correlation ( $R > 0.15$ ,  $p < 0.05$ ). The sign convention for the KE Strength Index is taken so that the maps are showing the relationships of the field (e.g., SSHA and tracers) during years when the KE is weaker. Patterns for the strong KE years would be reversed from these (not shown). Red and black boxes are as in Figure 1. Thick black line shows the mean position of the KE axis between 1950 and 2008.

cannot expect an exact spatial correspondence between the tracer anomaly and the sampling box.

### 3.2. Influence of NPGO and PDO on the KOE Ecosystem

[15] We revealed that the decadal-scale zooplankton biogeography in the KOE region was influenced by the NPGO. The NPGO is driven by the North Pacific Oscillation (NPO) [Chhak *et al.*, 2009], which is a mode of sea level pressure with a dipole signal centered in the eastern and central North Pacific [Walker and Bliss, 1932]. The NPGO has been reported to explain the interannual variation in strength of oceanic currents and coastal nutrient upwelling and thus influences phytoplankton production in the eastern North Pacific [Di Lorenzo *et al.*, 2008]. Therefore, this study indicates that the NPO/NPGO system exerts basin-scale climate/ocean control on the regional ecosystem throughout the North Pacific.

[16] We did not find any influence of the PDO on warm-water zooplankton abundance. The large-scale atmospheric forcing that triggers the KE Axis Index is associated with changes in the strength of the Aleutian Low (AL), which generate the PDO-related SSHa anomalies (SSHa) [Taguchi *et al.*, 2007]. Observing a roughly synchronized increase in geostrophic flow along 137°E and the abundance of warm-water zooplankton in the Transition region in the KOE after the major phase change of the PDO of the late 1970s [Miller *et al.*,

1994], Chiba *et al.* [2009] hypothesized that more warm-water copepods were transported northward in years with a strong Kuroshio flow and its driver might be the AL/PDO system. Although Kuroshio transport increased in the upstream region around 130°E after the late 1970s [Qiu and Miao, 2000], the local increase of geostrophic flow does not necessarily represent the overall strength of the northward and eastward advection transports of Kuroshio and KE, respectively. In conclusion, the findings of the present study support the idea that advection transport driven by circulation dynamics controls zooplankton biogeography in the KOE region, but revealed a different process than that suggested by Chiba *et al.* [2009]: the key factor is the strength of the KE rather than Kuroshio, and the climatic driver of advection transport was the NPO/NPGO systems rather than the AL/PDO system.

[17] Influence of the AL/PDO-related cool-warm cycle on the lower trophic-level production, phenology, and species composition has been well documented on a decadal-scale in the Oyashio and Transition regions, particularly for cold-water zooplankton species. The AL dynamics alter the extent of wintertime mixing and springtime stratification that control seasonal nutrients and light supply for phytoplankton production within a surface mixed layer and secondarily affect zooplankton ecology [Chiba *et al.*, 2008]. In summary, the AL/PDO system induces temporal variation in the KOE zooplankton through a bottom-up control by dominating

the seasonal mixed-layer process. On the other hand, the present study proposes an additional mechanism whereby the NPO/NPGO system drives the KE dynamics and its advection transport determines the KOE zooplankton biogeography. Our study findings suggest that the variation in zooplankton community structure observed in the KOE region results from a combination of two climate-ocean controls: AL/PDO and PDO/NPGO systems.

### 3.3. Regional Comparison of Long-Term Changes in Zooplankton Biogeography

[18] This study, together with previous studies, demonstrates that climate-driven changes in ocean currents influence zooplankton biogeography both in eastern boundary and western boundary currents system in the North Pacific. However, the observed patterns and mechanisms controlling the biogeography differed between the east and the west.

[19] In the eastern boundary currents, the subtropical California Current and subarctic Alaskan Gyre bifurcate along the coast, where interannual variation in climate alternatively controls the strength of each current and along-shore transport. Its driver is the AL/PDO system [Chhak *et al.*, 2009]. Latitudinal shifts in the copepod community driven by the current dynamics result in the local alternation of the dominance of large cold-water and small warm-water species [Keister *et al.*, 2011]. Reduction of large copepods associated with the biogeography shift of zooplankton possibly impacts regional salmon reproduction [Peterson and Schwing, 2003].

[20] In contrast, in the western boundary system, the subtropical Kuroshio and subarctic Oyashio merge off the Japanese islands, where an increase in warm-water species abundance in the northern region does not mean the replacement of cold-water species as observed by Chiba *et al.* [2009]. Moreover, higher retention within the transition region as opposed to the strength of advection transport indicated by this study results in the regional high concentration of warm-water species. That suggests a considerable increase in total zooplankton prey for fish even if warm-water species are less nutritious than cold-water species of the same biomass. Some warm-water species, such as *Paracalanus* spp., *Oncaea* spp., and *Corycaeus* spp., have been reported to be important food sources of larval and juvenile Japanese sardine (*Sardinops melanostictus*) in the Kuroshio and KE regions [Takagi *et al.*, 2009]. In addition, the interannual variation in cold-water species is likely determined by the PDO-related seasonal mixed-layer bottom-up process rather than advection transport (see section 3.2). For this reason, evaluation of the impact of the observed zooplankton biogeography on the higher trophic levels and local fisheries is more challenging in the KOE region.

[21] An east-west contrast in zooplankton biogeography in response to large-scale climate control has also been reported in the North Atlantic [Greene *et al.*, 2003]. North Atlantic Oscillation-driven decadal variation in oceanic currents induces a warm-cool dipole condition between eastern and western boundary currents, resulting in a latitudinal shift of dominant cold-water copepods (*Calanus finmarchicus*) in the opposite direction in the eastern [Beaugrand *et al.*, 2002] and western [Greene *et al.*, 2003] North Atlantic. Ultimately, these studies in the North Pacific and North Atlantic underline the importance of further investigation of regionally specific climate-ocean control on marine ecosystems.

## 4. Conclusion

[22] This study provides the first evidence that the NPO/NPGO system controls ecosystems not only in the eastern North Pacific but also in the western North Pacific through changes in the advection transport of zooplankton, showing climate control of marine ecosystems throughout the North Pacific. Our results are particularly important for predicting ecosystem responses to future global-scale changes and evaluating its influence on local fisheries and other ecosystems. As we found that the mechanisms of biogeographic variation are regionally specific, integrative approaches for studying ecosystem changes through regional comparisons are highly encouraged.

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