Advances in Marine Ecosystem Dynamics from US GLOBEC

The Horizontal-Advection Bottom-up Forcing Paradigm

BY EMANUELE DI LORENZO, DAVID MOUNTAIN, HAROLD P. BATCHELDER, NICHOLAS BOND, AND EILEEN E. HOFMANN

Southern Ocean GLOBEC cruise.
Photo credit: Daniel Costa

ABSTRACT. A primary focus of the US Global Ocean Ecosystem Dynamics (GLOBEC) program was to identify the mechanisms of ecosystem response to large-scale climate forcing under the assumption that bottom-up forcing controls a large fraction of marine ecosystem variability. At the beginning of GLOBEC, the prevailing bottom-up forcing hypothesis was that climate-induced changes in vertical transport modulated nutrient supply and surface primary productivity, which in turn affected the lower trophic levels (e.g., zooplankton) and higher trophic levels (e.g., fish) through the trophic cascade. Although upwelling dynamics were confirmed to be an important driver of ecosystem variability in GLOBEC studies, the use of eddy-resolving regional-scale ocean circulation models combined with field observations revealed that horizontal advection is an equally important driver of marine ecosystem variability. Through a synthesis of studies from the four US GLOBEC regions (Gulf of Alaska, Northern California Current, Northwest Atlantic, and Southern Ocean), a new horizontal-advection bottom-up forcing paradigm emerges in which large-scale climate forcing drives regional changes in alongshore and cross-shelf ocean transport that directly impact ecosystem functions (e.g., productivity, species composition, spatial connectivity). The horizontal advection bottom-up forcing paradigm expands the mechanistic pathways through which climate variability and climate change impact the marine ecosystem. In particular, these results highlight the need for future studies to resolve and understand the role of mesoscale and submesoscale transport processes and their relationship to climate.

LARGE-SCALE CLIMATE VARIABILITY IN GLOBEC REGIONS

Changes in marine ecosystems in regions studied by US GLOBEC have been linked to changes in large-scale atmospheric circulation, which drive important rearrangements in ocean circulation and in regional transport dynamics that impact ecosystem processes. Atmospheric variability is best understood in the context of sea level pressure deviations from the mean atmospheric circulation (Figure 1). In the extratropical latitudes over GLOBEC regions, atmospheric circulation is characterized by dipoles of high and low pressure associated with the mean path of westerly winds (along the pressure gradients). These strong highs and lows are particularly evident in the Northern Hemisphere where the presence of continental boundaries drives standing-wave patterns characterized by dipoles that are

more regionally confined. The Aleutian Low and North Pacific High, and the Iceland Low and Azores High, are the large-scale atmospheric forcing for the Northeast Pacific and Northwest Atlantic GLOBEC regions, respectively (Figure 1). The circumpolar Southern Ocean allows development of meridional dipoles elongated in the zonal direction, which give rise to the strong westerlies that drive the Antarctic Circumpolar Current (ACC).

On seasonal, interannual, and decadal time scales, these atmospheric pressure systems fluctuate substantially in association with three main global modes of atmospheric variability: the El Niño-Southern Oscillation (ENSO); the Southern Annular Mode (SAM); and the Northern Annular Mode (NAM), also referred to as the Arctic Oscillation (AO). See Figure 1 and Box 1 for a more detailed definition of these climate modes. While ENSO involves dynamical coupling between the ocean

and atmosphere, the annular modes are to first order uncoupled from ocean variability and are associated with the strengthening and weakening of the atmospheric polar vortices. Together, these modes explain about one-third of the global atmospheric variation that is responsible for the low-frequency variability in the ocean and ecosystem in each of the GLOBEC regions.

Although the global nature of these climate modes can allow for coherent climate signals across the different GLOBEC study regions, in practice, regional expressions of the modes lead to distinct low-frequency signals in each region. For example, in the Northwest Atlantic, the regional sea level pressure expression of the NAM, which is referred to as the North Atlantic Oscillation (NAO; Figure 1), dominates the forcing of changes in ocean conditions. In the Pacific sector, the surface expression of the NAM is weaker, and regional sea level pressure variability of the Aleutian Low (AL) is more strongly affected by remote response (teleconnection) to ENSO. In the Southern Ocean, the lack of strong continental boundaries makes the SAM the dominant forcing of ocean variability.

OCEAN AND ECOSYSTEM RESPONSE TO CLIMATE FORCING

The large-scale atmospheric modes operate differently in each of the GLOBEC regions. However, they all modify the ocean circulation on multiyear periods, with implications for the marine ecosystem. GLOBEC isolated a common mechanism driving oceanic and ecosystem responses across the GLOBEC regions, a mechanism we refer to as the "horizontal advection bottom-up forcing" paradigm. It can be summarized as follows: changes in atmospheric

forcing → changes in ocean currents and horizontal transport → changes in marine population dynamics and distributions. From a dynamical point of view, each arrow indicates the direction of the forcing and is equivalent to an integration of the forcing function, so that the marine ecosystems have the potential to integrate several times the atmospheric forcing, one by the ocean and a second one by the ecosystem (e.g., the double integration hypothesis; Di Lorenzo and Ohman, 2013). Statistically, each integration can act as a low-pass filter of the input function, which allows marine ecosystems to amplify the low-frequency fluctuations contained in the large-scale atmospheric modes.

The horizontal advection bottom-up forcing paradigm was found to be important in all GLOBEC regions. In the Northeast Pacific, observed long-term changes in zooplankton were linked to changes in ocean transport driven by changes in the Aleutian Low winds. In the Northwest Atlantic, changes in the AO, and in its regional expression, the NAO, forced similar changes in Arctic Ocean circulation, with strong downstream (Arctic outflow) impacts on the Northwest Atlantic ecosystems. In the Southern Ocean, changes in the SAM produced changes of sea ice distribution and ocean circulation that affect connectivity patterns and food web linkages. Here, we report on selected findings in each region that show the importance of the horizontal advection bottom-up forcing paradigm.

THE NORTHEAST PACIFIC

In the Northeast Pacific, GLOBEC focused on two oceanographically distinct regions, the California Current System (CCS) eastern boundary upwelling system and the Gulf of Alaska (GOA)

subpolar gyre, which is characterized by coastal downwelling and upwelling mean conditions in the gyre. On interannual and decadal time scales, changes in the strength and position of the AL strongly impact the physical and biological conditions of the shelf environment in the CCS and the GOA. Changes in AL winds (Figure 2a) drive an oceanic response that is captured in the Pacific Decadal Oscillation (PDO) pattern (Chhak et al., 2009). In the positive phase of the PDO when the AL is stronger, the Northeast Pacific is characterized by downwelling wind anomalies, which drive positive sea level height anomalies (SSHa) along the entire eastern boundary (Figure 2b). The adjustment to higher SSHa anomalies leads to poleward geostrophic flow anomalies in coastal regions. In the GOA, the higher freshwater runoff during stronger AL provides an additional contribution to the stronger alongshore flow

Northern Annular Mode Index (NAM)
Also known as the Arctic Oscillation, the NAM tracks changes in the strength of the polar vortex.

Aleutian Low Index (AL)
Defined as the dominant mode of North Pacific SLPa, the AL is associated in its positive phase with a strengthening and southward shift of the *Aleutian Low* pressure system.

The Mean Atmospheric Circulation

Iceland Low
Aleutian Low
Northeast Pacific
North Pacific High
Northeast Atlantic
Azores High
Southern Ocean

SLP mbar

North Atlantic Oscillation Index (NAO)
Defined as the dominant mode of North Atlantic SLPa, the NAO is the surface expression of the NAM. In its positive phase the NAO is associated with a strengthening of the gradient between the *Iceland Low* and *Azores High*.

Southern Annular Mode Index (SAM)
Also known as the Antarctic Oscillation, the SAM tracks changes in the strength of the low pressure polar vortex over Antarctica.
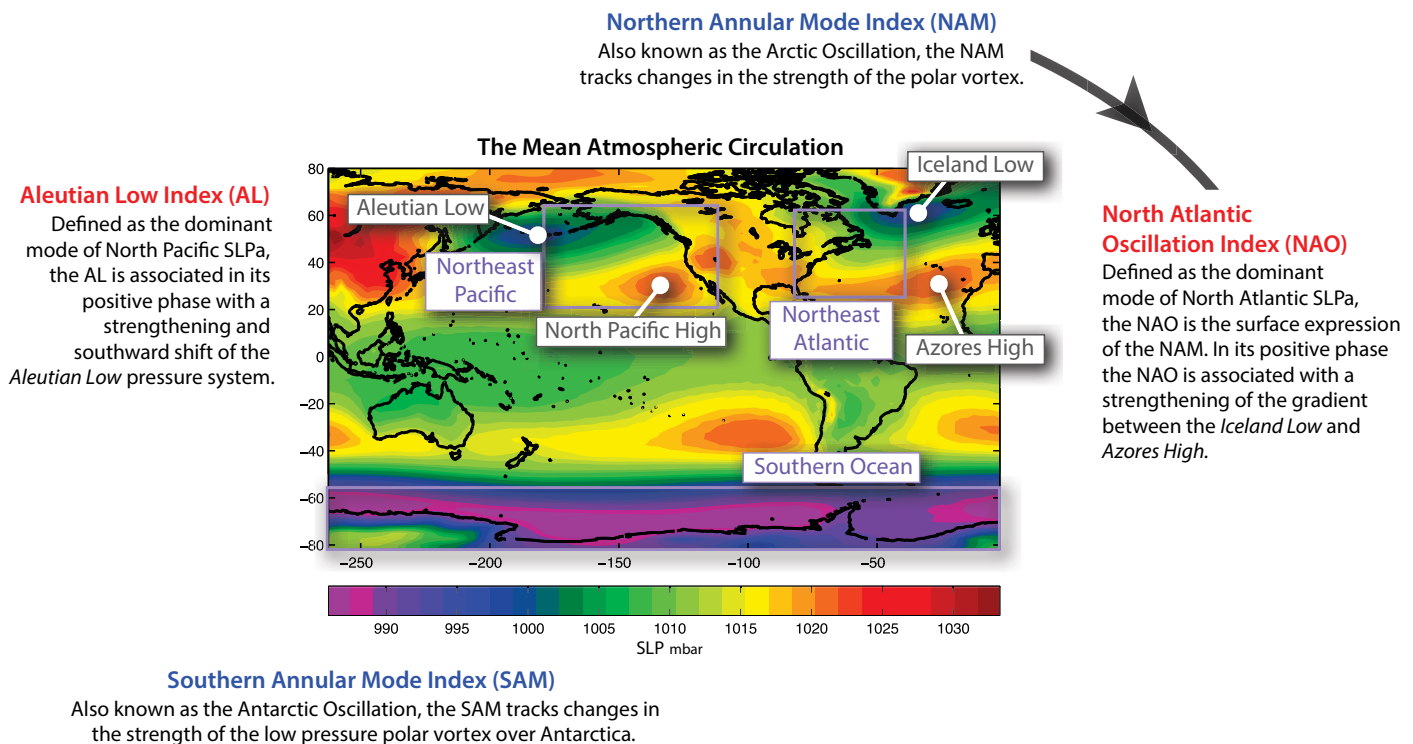
Figure 1. Climate modes in the atmosphere and their relationship to the mean circulation. The graphic shows the mean sea level atmospheric pressure for December–January–February (DJF). High-pressure regions (in both hemispheres) have anticyclonic flow, and low-pressure regions have cyclonic flow. SLPa = sea level pressure anomaly. *SLP data are from the National Center for Environmental Prediction, Kistler et al. (2001)*

by increasing the cross-shelf baroclinicity (e.g., Weingartner et al., 2005). Stronger downwelling winds and coastal currents tend to be accompanied by enhanced mesoscale eddy activity in the GOA (Combes and Di Lorenzo, 2007; Henson and Thomas, 2008); episodes of relaxation in downwelling winds can result in fluxes of nutrient-rich water being driven onto the shelf by these eddies (Ladd et al., 2007). The changes in circulation associated with a stronger Aleutian Low, and resulting positive phase of the PDO, have been identified as an important bottom-up forcing of marine ecosystems in the Northern California Current and Gulf of Alaska.

The Northern California Current System

In the Northern California Current System (NCCS), high productivity along the coast is associated with seasonal upwelling that supplies surface nutrients. Although interannual changes in upwelling and primary production have been linked to changes in the AL alongshore winds and the PDO, the mechanistic link between the AL/PDO and higher trophic levels is still being explored. Several GLOBEC publications (Hooff and Peterson, 2006; Peterson, 2009) suggest that PDO-related changes in along-shelf transport exert a more important control on higher trophic levels. For example, during positive (negative) phases of the PDO, the anomalous transport of

waters from the south (north) bring zooplankton species residing in those waters into the NCCS region, fundamentally and profoundly altering the shelf ecosystem. Poleward-flowing subtropical waters (+PDO) typically have many species of small bodied, lipid-poor copepods, each of relatively low abundance and biomass. Conversely, boreal waters advected from the north (–PDO) have fewer copepod species, but the dominant species have relatively large body size and are often lipid-rich (Hooff and Peterson, 2006). The dependence of zooplankton community composition on changes in transport has been successfully tested both with eddy-resolving ocean model simulations (Keister et al., 2011) and observational studies that use satellite data to infer currents (Bi et al., 2011; Figure 3). The supply of boreal neritic copepods to the Oregon shelf serves as an energy-rich prey base for a food web that supports rapid growth and high survival of juvenile salmon during –PDO periods (Bi et al., 2011; Figure 3c).

The PDO has been mechanistically linked to changes in the alongshore transport that control zooplankton species composition along the entire CCS (Bi et al., 2011; Keister et al., 2011; Di Lorenzo and Ohman, 2013). However, vertical transport and upwelling dynamics show different signals in the NCCS and Southern California Current System. While PDO forcing controls the low-frequency modulations

Emanuele Di Lorenzo (edl@gatech.edu) is Professor of Ocean Sciences, School of Earth and Atmospheric Sciences, Georgia Institute of Technology, Atlanta, GA, USA. **David Mountain** is an independent oceanographer in Tucson, AZ, USA. **Harold P. Batchelder** is Professor, College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA. **Nicholas Bond** is Research Scientist, Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA, USA. **Eileen E. Hofmann** is Professor, Department of Ocean, Earth and Atmospheric Sciences, Old Dominion University, Norfolk, VA, USA.

BOX 1: CLIMATE MODES

AL: The Aleutian Low index, defined as the dominant mode of North Pacific SLPa, is associated in its positive phase with a strengthening and southward shift of the Aleutian Low pressure system.

ENSO: El Niño-Southern Oscillation index is used to track changes in tropical Pacific ocean/atmosphere climate.

NAM or AO: Northern Annular Mode, also known as the Arctic Oscillation, tracks changes in the strength of the polar vortex.

NAO: North Atlantic Oscillation is the dominant mode of North Atlantic SLPa and is the surface expression of the NAM. In its positive phase, the NAO is associated with a strengthening of the gradient between the Iceland Low and the Azores High.

NPGO: The North Pacific Gyre Oscillation is a climate mode of variability in the North Pacific that tracks changes in strength of the North Pacific Current.

PDO: The Pacific Decadal Oscillation is the dominant mode of SSTa variability in the North Pacific.

SAM: Southern Annular Mode, also known as the Antarctic Oscillation, SAM tracks changes in the strength of the low pressure polar vortex over Antarctica.

Daniel Costa

of upwelling in the NCCS (north of 38°N), decadal changes in upwelling in the SCCS are more closely related to the North Pacific Gyre Oscillation (NPGO; Figure 2d,e,f), a second mode of North Pacific climate variability (Di Lorenzo et al., 2008). The NPGO is strongly correlated with long-term changes in surface salinity, nitrate, and chlorophyll in the CCS and in the Gulf of Alaska (Di Lorenzo et al., 2009).

Although more studies are needed to identify the mechanisms of interaction among the PDO, NPGO, and ecosystem responses, it is clear that regional circulation changes associated with these climate modes control water mass transports and upwelling dynamics that alter copepod community structure and abundance, including mean body size, biomass, and lipid (e.g., energy) content. These processes in turn affect the trophic transfer of energy to higher consumers, such as forage fish and salmon (Peterson, 2009; Bi et al., 2011), and can have major implications for the productivity of the shelf ecosystem and for regional economies dependent on that productivity.

The Gulf of Alaska

The GOA subpolar gyre is a high-nutrient, low-chlorophyll region where iron is the limiting factor to primary productivity (Martin et al., 1989). In contrast, coastal GOA biological productivity is high, despite the mostly downwelling-favorable winds there. High phytoplankton production on the shelf is attributed to cross-shelf mixing of nearshore waters rich in iron concentrations, with waters near the shelf break high in nitrate concentrations. The two water masses tend to contain different lower trophic level communities, with the coastal region dominated by large-celled diatoms and dinoflagellates and the oceanic waters by smaller-celled phytoflagellates and pennate diatoms (Strom et al., 2006). The shifting boundary between these waters, and the degree of cross-shelf exchange, is determined by mechanisms related to freshwater runoff, Ekman transports, and eddies and meanders (Stabeno et al., 2004). Strong cyclonic storm systems associated with variability in the AL are frequent during the cool season (e.g., Weingartner et al., 2005) and induce Ekman upwelling in the basin of the Gulf of Alaska, downwelling in the coastal zone due to onshore-directed Ekman transports, and vigorous wind mixing in both regions.

The response of the GOA ecosystem to the AL is evident in the results from a combined empirical orthogonal function (CEOF) analysis of satellite-based SSHa and Chl-*a* distributions (see Brown and Fiechter, 2012, for a GOA application and a description of methods). For example, the 1st CEOF shows that
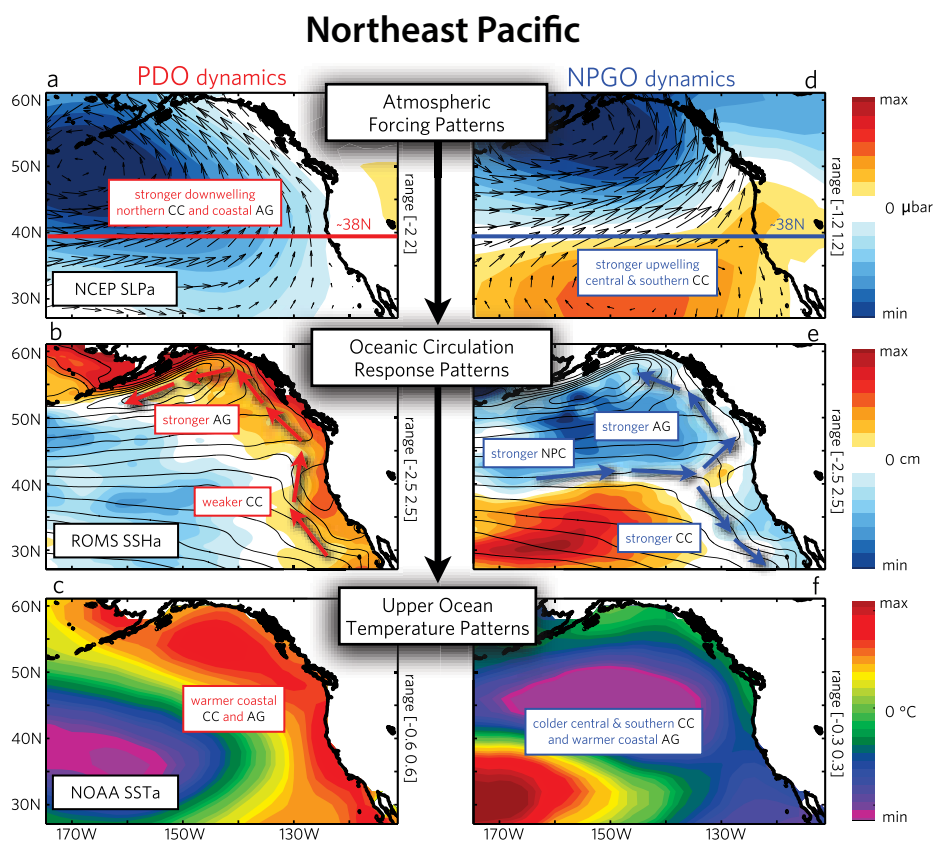

Figure 2. Atmospheric forcing and oceanic response of the Northeast Pacific during positive phases of the Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO). The patterns are obtained by regressing the PDO (left column) and NPGO (right column) indices with the (a, d) sea level pressure anomaly (SLPa) and wind stresses (black vectors), the (b, e) Regional Ocean Modeling System (ROMS) sea surface height anomaly (SSHa), and (c, f) sea surface temperature anomaly (SSTa). In the SSHa panels (b, e), the black contours correspond to the long-term mean SSH (1950–2008), so that it is possible to visualize how the PDO and NPGO SSHa project on the mean circulation—the bold vectors in the SSHa panels indicate the direction of PDO (red vectors) and NPGO (blue vectors) contributions to the circulation. *Figure reproduced from King et al. (2011). SLP data from Kistler et al. (2001), SSTa from the reanalyses of Smith and Reynolds (2004), ROMS SSHa from Di Lorenzo et al. (2009), and mean SSH from Niiler et al. (2003)*
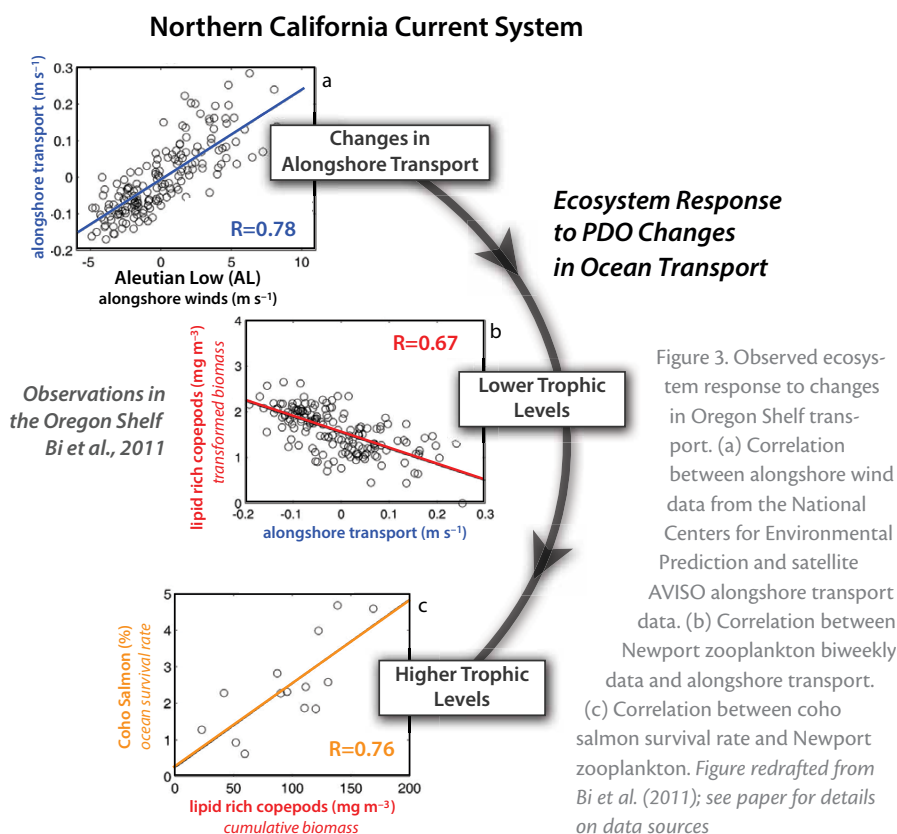
during periods of stronger Aleutian Low, enhanced downwelling in the GOA (positive SSHa in Figure 4a) serves to inhibit productivity in the subpolar gyre interior (negative Chl-*a* in Figure 4b). This mode of variability explains about 50% of the variance in the GOA subpolar gyre (Figure 4b) and is characterized by strong decadal fluctuations that track the PDO (Figure 4c, R = 0.66), which in this region is the oceanic response to AL forcing (Chhak et al., 2009).

In addition to the immediate response of the GOA to AL forcing, the adjustment to stronger downwelling in the coastal region energizes mesoscale eddies along the coastal GOA (Combes and Di Lorenzo, 2007; Henson and Thomas, 2008). These eddies enhance cross-shelf transport of shelf waters (Okkonen et al., 2003; Stabeno et al., 2004; Combes et al., 2009; Janout et al., 2009) and have been linked to cross-shelf export of coastal iron and Chl-*a* into the gyre (Crawford et al., 2005; Ladd et al., 2007; Ueno et al., 2010; Fietcher and Moore, 2012), which increases overall open ocean Chl-*a* concentrations. This delayed response of eddy-induced cross-shelf transport to AL forcing is evident in the 2nd CEOF of SSHa/Chl-*a* (Figure 4d), which shows clear signatures of the three large anticyclonic eddies in the Haida, Sitka, and Yakutat regions (Okkonen et al., 2001; Ladd et al., 2007). This second mode explains ~ 15% of the Chl-*a* variance in the gyre (Figure 4e) and has a weaker time lag (~ 6 months) correlation with the PDO (Figure 4f, R = 0.47) compared to the 1st CEOF. The weak correlation with the AL/PDO reflects the chaotic nature of eddy dynamics in the GOA, especially along the Alaskan Stream (Combes and Di Lorenzo, 2007; Ueno et al., 2010), and it also reflects the important role

that iron from freshwater runoff plays in offshore productivity (e.g., Fiechter et al., 2009; Fiechter and Moore, 2012; Coyle et al., 2012, and references therein). Freshwater runoff in the coastal GOA is weakly correlated with the PDO (< 25%) and more strongly controlled by regional-scale variability associated with the Ketchikan-Seward atmospheric sea level pressure gradient (Weingartner et al., 2005). Here, the freshwater runoff not only controls iron supply but also exerts an important control on mesoscale eddies in the coastal region by determining the baroclinicity of the Alaska Coastal Current.

The complex set of dynamical controls on mesoscale eddy variability, freshwater runoff, and iron supply makes it more challenging to establish in the GOA a clear deterministic link between large-scale climate forcing and ecosystem responses in the lower and higher

trophic levels. Moreover, the responses of higher-trophic level species to variations in lower trophic level community composition require further investigation. For example, juvenile pink salmon (*Oncohynchus gorbuscha*) are generalist feeders, consuming the biomass dominant plankton prey of appropriate size, although prey composition seems to impact juvenile survival (e.g., Armstrong et al., 2008). Other species may have stricter prey preferences and/or habitat requirements and be more sensitive to variations in transport, especially at the larval stage (Doyle et al., 2009). Finally, while cross-shelf exchanges of nutrients and organisms were the focus of GLOBEC, along-shore transport dynamics and mesoscale eddy entrainment of larvae are likely to exert important controls on GOA ecosystem function (e.g., Stabeno et al., 2004; Bailey and Picquelle, 2002; Atwood et al., 2010). The

Figure 3. Observed ecosystem response to changes in Oregon Shelf transport. (a) Correlation between alongshore wind data from the National Centers for Environmental Prediction and satellite AVISO alongshore transport data. (b) Correlation between Newport zooplankton biweekly data and alongshore transport. (c) Correlation between coho salmon survival rate and Newport zooplankton. *Figure redrafted from Bi et al. (2011); see paper for details on data sources*

role of mesoscale entrainment of larvae on higher trophic ecosystem dynamics is only beginning to be explored and requires new, targeted field observations.

A comparison of the CCS and the GOA with other Pacific Ocean boundary current systems was conducted during the GLOBEC Pacific Ocean Boundary Ecosystem and Climate Study (POBEX; http://www.pobex.org; Di Lorenzo et al., 2013, in this issue). POBEX found that changes in horizontal transport dynamics were important drivers of low-frequency variability also in the Kuroshio-Oyashio Extension (Chiba et al., 2013) and the Humboldt or Peru-Chile Current System.

THE NORTHWEST ATLANTIC

The Georges Bank/Gulf of Maine region (GB/GoM) in the Northwest Atlantic is a highly productive area that supports many important commercial fisheries. The local circulation is part of a southwestward flowing,

continental-scale coastal current system that extends from the subarctic to Cape Hatteras (Chapman and Beardsley, 1989; Figure 5). An increase in NAM (see definition in Figure 1) in the late 1980s to mid-1990s led to increased export of low-salinity waters from the Arctic into the North Atlantic, which enhanced the transport of the coastal current system at least as far south as the GB/GoM (Greene and Pershing, 2007). Direct current measurements by GLOBEC (Smith et al., 2001) indicate that during the mid-1990s, the influx to the GB/GoM from the shelf current system was twice that measured in the late 1970s to early 1980s. The measurements also showed that, concurrently, the influx to the region of high-salinity offshore oceanic waters was reduced by half. This change in the proportion of the inflows resulted in reduced salinity throughout the GB/GoM compared to the historical record (Figure 5a), with the transition to persistently negative

salinity anomalies around 1990. Time series formed by combining data collected by GLOBEC with earlier observations indicate that various biological indices changed concurrently with the changes in salinity between the 1980s and the 1990s (Figure 5b–e). Specifically, phytoplankton production in the Gulf of Maine increased, zooplankton community structure in the Gulf of Maine and Georges Bank shifted to a dominance of smaller copepod species, and first-year survival rate for haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank increased threefold, while Atlantic cod (*Gadus morhua*) larval survival decreased threefold (not shown). These findings indicate that a major, decadal-scale shift in the regional ecosystem fundamentally altered its physical properties and transports; transformed the size structure, composition, and ecology of the lower trophic levels; and altered the survival of two commercially important fish stocks.
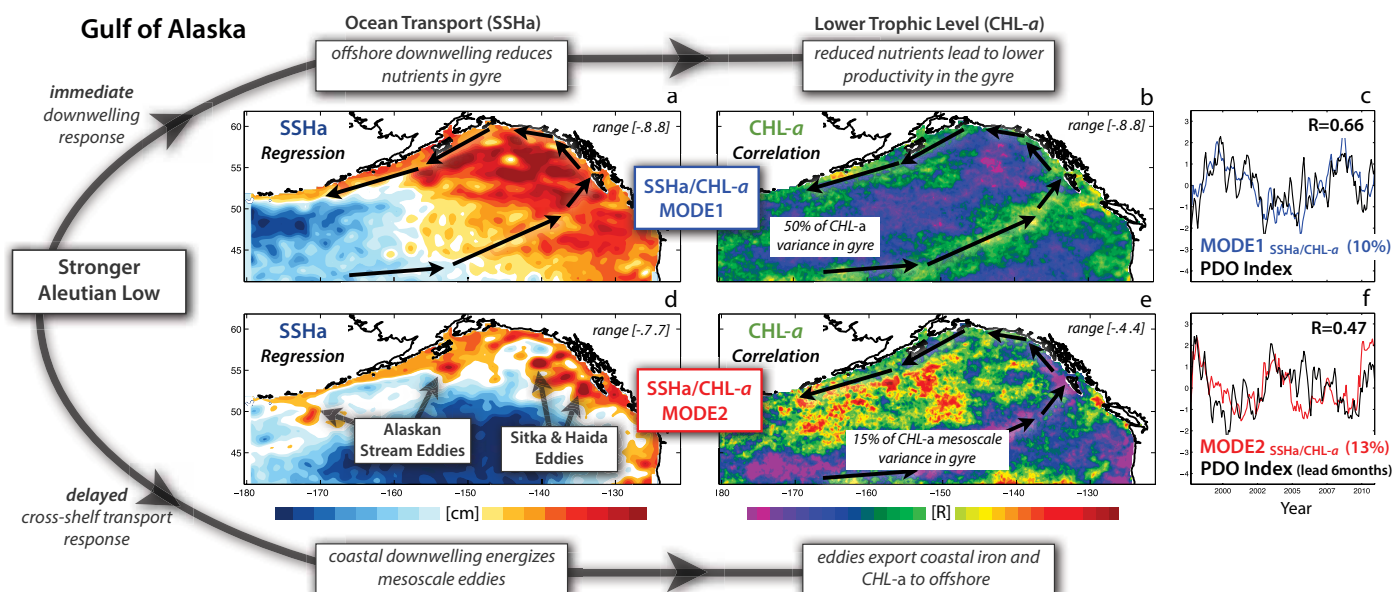

Figure 4. Covariability between AVISO SSHa and SeaWiFS chlorophyll-*a* (Chl-*a*) data from a combined empirical orthogonal function (EOF) analysis from 1998 to 2012. (a,d) SSHa regression maps with time series of MODE1 and MODE2. (b,e) Chl-*a* correlation maps with time series of MODE1 and MODE2. (c,f) Comparison of PDO index with time series of MODE1 and MODE2. The PDO leads MODE2 by six months. The two combined EOF modes are not independent and explain similar amounts of variance (10% MODE1 and 13% MODE2). The order of the modes in the figures is based on the amount of Chl-*a* variance explained in the gyre interior (~ 50% MODE1 in panel b and ~ 15 MODE2 in panel e). The black arrows in (a,b,e) indicate the circulation of the mean Alaskan subarctic gyre.

Coupled models of circulation and ecosystem dynamics (Ji et al., 2008) showed that changes in stratification associated with the increased shelf water inflow and reduced surface layer salinity resulted in changes in the seasonal timing and magnitude of primary production consistent with the observed changes. Bio-physical modeling of large- and small-sized zooplankton species (Ji et al., 2012) captured the spatial and seasonal patterns observed in those species and demonstrated that the patterns were controlled largely through bottom-up trophic processes. Year-to-year changes in zooplankton abundance were difficult to replicate in models, probably because overall abundance is sensitive to top-down processes, particularly predation mortality, which is difficult to measure accurately from field observations. The model could not replicate the shift in zooplankton community structure toward smaller species (Figure 5). The mechanisms responsible for the change in cod and haddock survival are not completely understood. They may be related to prey preferences of the two species. Because larval and juvenile haddock prefer smaller-sized prey than do the early life stages of cod, the increased abundance of smaller zooplankton species such as occurred during the later, lower-salinity period might have conferred a feeding advantage to young haddock compared to young cod. The changes in haddock and cod survival were reflected in the subsequent abundance of the adult stocks, with haddock exhibiting strong stock recovery in the 1990s while the cod stock continued to decline. Strong management measures limiting haddock catches probably also contributed to the increase of the haddock stock. However, the changes in the adult stocks likely were part of

the broad, bottom-up, ecosystem-level changes that GLOBEC documented and that are believed to be the local response to atmospherically driven oceanic variations at high latitude that were advected to the GB/GoM region.

THE WESTERN ANTARCTIC PENINSULA

The US Southern Ocean GLOBEC (SO GLOBEC) program, focused on Marguerite Bay in the southern portion of the western Antarctic Peninsula (sWAP) continental shelf (Figure 6, inset). The program featured an end-to-end food web approach that included predators and competitors of Antarctic krill (*Euphausia superba*), as well as the influence of habitat (Hofmann et al., 2004). Surveys identified biological hotspots, regions of sustained biological production in excess of average conditions (Costa et al., 2007), that had associated enhanced abundance of marine mammals and other top predators

(Burns et al., 2004; Chapman et al., 2004; Širović et al., 2004; Thiele et al., 2004). The hotspot regions were in areas influenced by Circumpolar Deep Water (CDW), a relatively warm (1–1.5°C), salty (34.74) oceanic water mass that moves onto the WAP shelf at depth. This water mass influences heat and salt budgets (Dinniman and Klinck, 2004), sea ice distribution (Dinniman et al., 2012), and food web structure (Prézelin et al., 2004; Ballerini et al., in press).

For the Antarctic Peninsula region, a positive SAM index has been related to warming (Kwok and Comiso, 2002; Thompson and Solomon, 2002; Van den Broeke and van Lipzig, 2004), strengthening of the westerlies (Marshall et al., 2006), and decreases in sea ice extent and seasonal duration (Stammerjohn et al., 2008). Model investigations showed that increased wind strength and ACC transport increased the volume of CDW transported onto the western Antarctic Peninsula continental shelf,
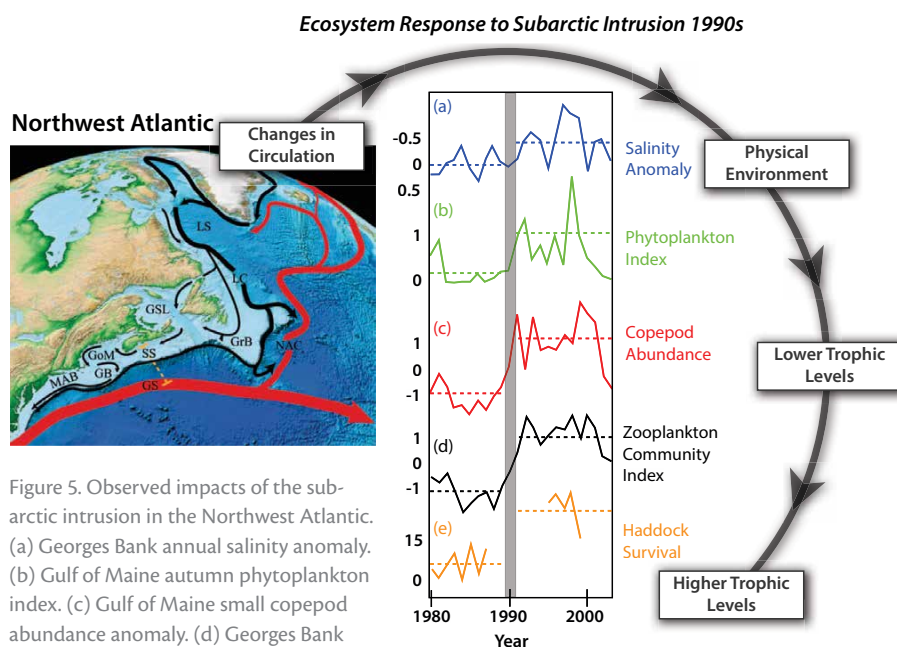

Figure 5. Observed impacts of the subarctic intrusion in the Northwest Atlantic. (a) Georges Bank annual salinity anomaly. (b) Gulf of Maine autumn phytoplankton index. (c) Gulf of Maine small copepod abundance anomaly. (d) Georges Bank zooplankton community structure index. (e) Georges Bank haddock survival (recruits per 104 hatched eggs). The horizontal dashed lines represent the 1980s and 1990s decadal average for each parameter. *Series a, d, and e are redrafted from Mountain and Kane (2010), and series b and c from Greene and Pershing (2007). See paper for description of data sources.*

and the increased heat input reduced sea ice extent and duration, especially in winter (Dinniman et al., 2012).

Simulated transport pathways obtained from Lagrangian particle tracking studies showed that the sWAP shelf receives inputs from upstream regions and local areas (Figure 6), both of which are important in maintaining local shelf Antarctic krill populations and the biological hotspots (Piñones et al., 2011, 2013a). Lagrangian transport simulations using circulation fields produced by increased wind strength and ACC transport showed that the increased volume of CDW on the shelf contributed to the success of larval Antarctic krill, but only for limited areas of the sWAP shelf (Piñones et al., 2013b). The modified circulation also increased advection of Antarctic krill larvae onto the shelf and enhanced retention, but the reduced winter sea ice and shifts in ice cover distribution may compromise overwintering survival of larvae and recruitment to adult stages (Piñones et al., 2013b). On the other hand, in the

SO GLOBEC study region, reproduction and recruitment of Antarctic krill is more closely related to the spring phytoplankton bloom than to sea ice (Daly, 2004; Marrari et al., 2008), so the biological hotspots may not be affected in the short term by climate-induced changes in circulation.

A mass balance food web model developed for the SO GLOBEC region (Ballerini et al., in press) showed that Antarctic krill provide the majority of energy needed to sustain seabird and marine mammal populations. Long-term environmental changes, particularly decreasing sea ice, will possibly alter the distribution and availability of Antarctic krill. The additive effects of bottom-up resource control through changes in phytoplankton assemblages (Antarctic krill prey) and the top-down effects of consumers of Antarctic krill may amplify the effects of climate change on the sWAP food web, thereby adding another dimension to the conceptual model developed for the US GLOBEC regions.

CONCLUSION

Marine ecosystem responses to climate variability in the four regions studied in the US GLOBEC program reflect the different physical characteristics of atmospheric and ocean forcings that influence local biological processes, food web structure, and overall productivity of the ecosystem. Although vertical supply of nutrients remains an important mechanism controlling primary productivity and food web dynamics through the trophic cascade, GLOBEC identified a new set of bottom-up forcing pathways that involve changes in alongshore and cross-shore ocean transport. Specifically, it was shown that changes in atmospheric forcing drive changes in ocean currents and horizontal transport that impact marine population dynamics and distributions. This new horizontal-advection bottom-up forcing paradigm was isolated in each GLOBEC region by combining long-term eddy-resolving ocean models with field observations. This revelation was a direct result of the
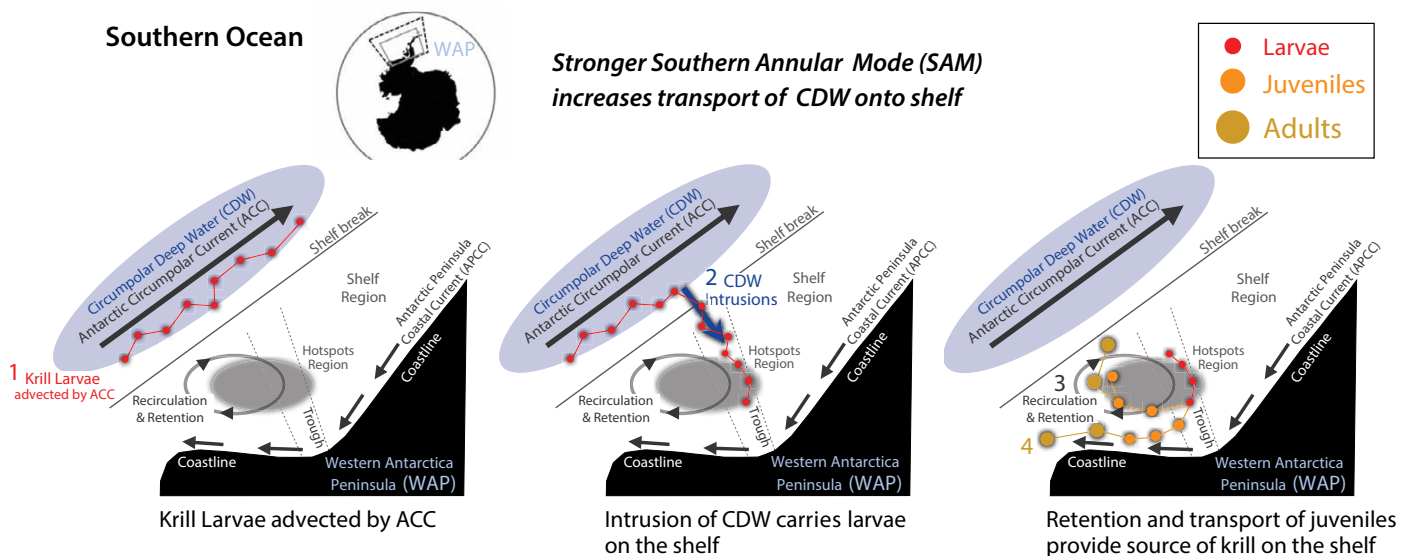

Figure 6. Impact of regional ocean transport on Antarctic krill populations along the western Antarctic Peninsula (WAP) continental shelf. The Antarctic Circumpolar Current (ACC), which flows along the shelf edge, transports Circumpolar Deep Water (CDW) and Antarctic krill larvae (1) that originated in upstream source regions. On-shelf intrusions of CDW (2) occur at specific sites, such as Marguerite Trough, and bring larvae onto the shelf, fueling localized shelf hotspots (3). Local retention regions created by shelf circulation retain larvae and juveniles that are produced on the WAP shelf (4). Transport of larvae to the mid and inner shelf provides a source for the juvenile krill populations in these areas. The Antarctic Peninsula Coastal Current (APCC) potentially provides exchanges along the inner shelf. *Figure redrafted from Piñones et al., 2013b*

three-dimensional regional modeling focus of the GLOBEC program. The modeling studies showed that changes in ocean transport impacted different aspects of ecosystem structure and function (e.g., productivity, species composition, connectivity) in the four regions. In the GOA, the cross-shelf advection of iron-rich coastal waters into the ocean's interior was identified as a mechanism for enhancing productivity in the iron-limited/nutrient-rich subpolar gyre (Figure 7, impact on productivity). In the CCS, changes in the strength of the alongshore southward currents were found to increase the supply of boreal neritic copepod species, which provide energy-rich prey for the local food web and enhance the survival of juvenile salmon (Figure 7, impact on species composition). In the NWA, the southward intrusion of Arctic water masses was linked to an increase in productivity. These effects propagated through the entire food web to higher trophic levels (Figure 7, impact on species composition and fish). In the SO, regional transport dynamics on the shelf were shown to play an important role in the retention of Antarctic krill larvae and the distribution of juvenile krill (Figure 7, impact on connectivity patterns).

The GLOBEC recognition that climate-induced changes in horizontal transport processes exert a dominant control on ecosystem function has important implications for understanding the impact of climate change on marine populations. Future studies will need to develop modeling and observational strategies that account for the nonlocal nature of ecosystem variability associated with basin-scale changes in ocean circulation. Advanced modeling frameworks that resolve regional-scale circulation (e.g., regional alongshore

dynamics) and mesoscale transport processes (e.g. cross-shelf exchanges) are also critical tools for investigating the mechanistic links between changes in basin-scale circulation and coastal marine ecosystems. GLOBEC pioneered the application of eddy-resolving models to understand the impact of regional transport dynamics on lower trophic levels. It is now clear that this approach must be extended in order to fully explore the dynamics of higher trophic levels. For example, ocean entrainment dynamics associated with mesoscale eddies are likely to have strong impacts on fish life cycles via transport of larvae and by altering connectivity patterns. Furthermore, submesoscale transport processes that were not resolved in GLOBEC likely play an equally important role in ecosystem dynamics (e.g., hotspots) and will need to be resolved in future studies. As we advance our modeling framework, it is also critical to develop novel observational strategies that allow constraining the new

processes resolved in the models.

Establishing the link among climate forcing, regional mesoscale, and sub-mesoscale transport processes and marine ecosystem dynamics raises important scientific questions and poses new technical challenges. For example, it is well known that mesoscale and submesoscale dynamics have an important nondeterministic component. This implies that a fraction of ocean and ecosystem variability cannot be predicted or linked to climate forcing. However, climate may have predictable impacts on the statistics of mesoscale and submesoscale features. To this end, applying ensemble approaches with eddy-resolving ocean models may provide a way to separate and quantify the amount of intrinsic and deterministic variance in ocean and ecosystem processes in relation to climate forcing. Finally, it is essential to continue integrating state-of-the-art regional ocean models with Intergovernmental Panel on Climate Change (IPCC) class models
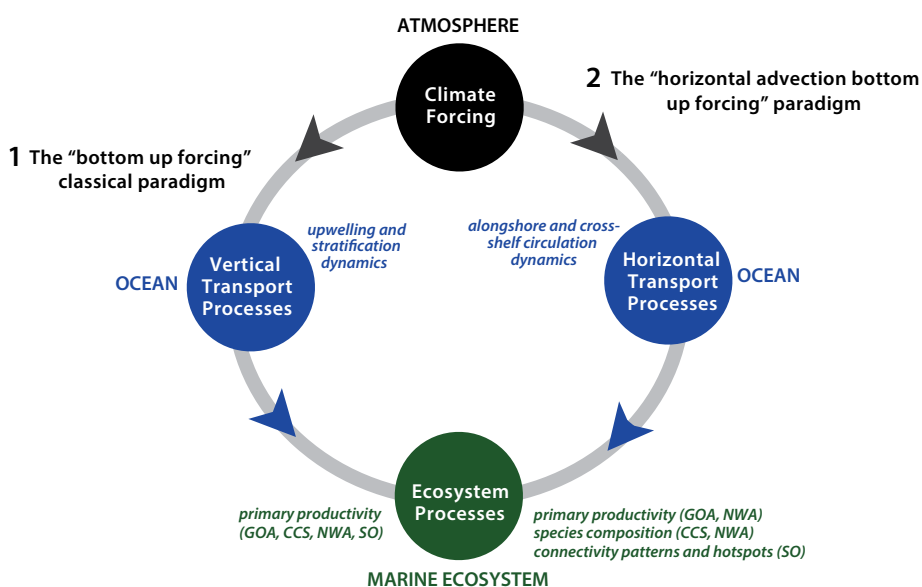

Figure 7. Conceptual advances of GLOBEC. GLOBEC expanded the classical bottom-up forcing paradigm (1) by recognizing that horizontal advection bottom-up forcing paradigm (2) is an equally important mechanism by which marine ecosystems respond to climate forcing. GLOBEC studies identified ocean horizontal transport processes as an equally important driver of marine ecosystem dynamics.

(Curchitser et al., 2013, in this issue) to develop robust strategies for down-scaling large-scale climate forcing to regional and coastal-scale ecosystem dynamics. This process also requires fostering and maintaining a robust dialogue among climate modelers, coastal physical oceanographers, marine ecosystem scientists, and social scientists. This type of interdisciplinary exchange will improve the quality of ecosystem-integrated assessments, with benefits for policy decisions. ◫

This is US GLOBEC contribution 739.

REFERENCES

Armstrong, J.L., K.W. Myers, N.D. Davis, R.V. Walker, D.A. Beauchamp, J.L. Boldt, J. Piccolo, and L.J. Haldorson. 2008. Interannual and spatial feeding patterns of juvenile pink salmon in the Gulf of Alaska in years of low and high survival. *Transactions of the American Fisheries Society* 137:1,299–1,316, http://dx.doi.org/10.1577/T07-196.1.

Atwood, E., J.T. Duffy-Anderson, J.K. Horne, and C. Ladd. 2010. Influence of mesoscale eddies on ichthyoplankton assemblages in the Gulf of Alaska. *Fisheries Oceanography* 19:493–507, http://dx.doi.org/10.1111/j.1365-2419.2010.00559.x.

Bailey, K.M., and S.J. Picquelle. 2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: Potential transport pathways and enhanced onshore transport during ENSO events. *Marine Ecology Progress Series* 236:205–217, http://dx.doi.org/10.3354/meps236205.

Ballerini, T., E.E. Hofmann, D.G. Ainley, K. Daly, M. Marrari, C. Ribic, W.O. Smith, and J.H. Steele. In press. Productivity and linkages of the food web of the southern region of the western Antarctic Peninsula continental shelf. *Progress in Oceanography,* http://dx.doi.org/10.1016/j.pocean.2013.11.007.

Bi, H., W.T. Peterson, and P.T. Strub. 2011. Transport and coastal zooplankton communities in the northern California Current system. *Geophysical Research Letters* 38, L12607, http://dx.doi.org/10.1029/2011GL047927.

Brown, J., and J. Fiechter. 2012. Quantifying eddy-chlorophyll covariability in the coastal Gulf of Alaska. *Dynamics of Atmospheres and Oceans* 55–56:1–21, http://dx.doi.org/10.1016/j.dynatmoce.2012.04.001.

Burns, J.M., D.P. Costa, M.A. Fedak, M.A. Hindell, C.J. Bradshaw, N.J. Gales, and D.E. Crocker. 2004. Winter habitat use and foraging behavior of crabeater seals along the western Antarctic Peninsula. *Deep Sea Research Part II* 51:2,279–2,303, http://dx.doi.org/10.1016/j.dsr2.2004.07.021.

Chapman, D.C., and R.C. Beardsley. 1989. On the origin of shelf water in the Middle Atlantic Bight. *Journal of Physical Oceanography* 19:389–391, http://dx.doi.org/10.1175/1520-0485(1989)019<0384:OTOOSW>2.0.CO;2.

Chapman, E.W., C.A. Ribic, and W.R. Fraser. 2004. The distribution of seabirds and pinnipeds in Marguerite Bay and their relationship to physical features during austral winter 2001. *Deep Sea Research Part II* 51:2,261–2,278, http://dx.doi.org/10.1016/j.dsr2.2004.07.005.

Chhak, K.C., E. Di Lorenzo, N. Schneider, and P.F. Cummins. 2009. Forcing of low-frequency ocean variability in the Northeast Pacific. *Journal of Climate* 22:1,255–1,276, http://dx.doi.org/10.1175/2008JCLI2639.1.

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. *Geophysical Research Letters* 40:5,182–5,187, http://dx.doi.org/10.1002/grl.50999.

Combes, V., and E. Di Lorenzo. 2007. Intrinsic and forced interannual variability of the Gulf of Alaska mesoscale circulation. *Progress in Oceanography* 75:266–286, http://dx.doi.org/10.1016/j.pocean.2007.08.011.

Combes, V., E. Di Lorenzo, and E. Curchitser. 2009. Interannual and decadal variations in cross-shelf transport in the Gulf of Alaska. *Journal of Physical Oceanography* 39:1,050–1,059, http://dx.doi.org/10.1175/2008JPO4014.1.

Costa, D.P., J.M. Burns, E. Chapman, J. Hildebrand, J.J. Torres, W. Fraser, A. Friedlander, C. Ribic, and P. Halpin. 2007. US SO GLOBEC predator programme. *GLOBEC International Newsletter* 13(1):62–66.

Coyle, K.O., W. Cheng, S.L. Hinckley, E.J. Lessard, T. Whitledge, A.J. Hermann, and K. Hedstrom. 2012. Model and field observations of effects of circulation on the timing and magnitude of nitrate utilization and production on the northern Gulf of Alaska shelf. *Progress in Oceanography* 103:16–41, http://dx.doi.org/10.1016/j.pocean.2012.03.002.

Crawford, W.R., P.J. Brickley, T.D. Peterson, and A.C. Thomas. 2005. Impact of Haida Eddies on chlorophyll distribution in the Eastern Gulf of Alaska. *Deep Sea Research Part II* 52:975–989, http://dx.doi.org/10.1016/j.dsr2.2005.02.011.

Curchitser, E.N., H.P. Batchelder, D.B. Haidvogel, J. Fiechter, and J. Runge. 2013. Advances in physical, biological, and coupled ocean models during the US GLOBEC program. *Oceanography* 26(4):52–67, http://dx.doi.org/10.5670/oceanog.2013.75.

Daly, K.L. 2004. Overwintering growth and development of larval *Euphausia superba*: An interannual comparison under varying environmental conditions west of the Antarctic Peninsula. *Deep Sea Research Part II* 51:2,139–2,168, http://dx.doi.org/10.1016/j.dsr2.2004.07.010.

Di Lorenzo, E., V. Combes, J.E. Keister, P.T. Strub, A.C. Thomas, P.J.S. Franks, M.D. Ohman, J.C. Furtado, A. Bracco, S.J. Bograd, and others. 2013. Synthesis of Pacific Ocean climate and ecosystem dynamics. *Oceanography* 26(4):68–81, http://dx.doi.org/10.5670/oceanog.2013.76.

Di Lorenzo, E., and M.D. Ohman. 2013. A double-integration hypothesis to explain ocean ecosystem response to climate forcing. *Proceedings of the National Academy of Sciences of the United States of America* 110:2,496–2,499, http://dx.doi.org/10.1073/pnas.1218022110.

Di Lorenzo, E., J. Fiechter, N. Schneider, A. Bracco, A.J. Miller, P.J.S. Franks, S.J. Bograd, A.M. Moore, A.C. Thomas, W. Crawford, and others. 2009. Nutrient and salinity decadal variations in the central and eastern North Pacific. *Geophysical Research Letters* 36, L14601, http://dx.doi.org/10.1029/2009GL038261.

Di Lorenzo, E., N. Schneider, K.M. Cobb, P.J.S. Franks, K. Chhak, A.J. Miller, J.C. McWilliams, S.J. Bograd, H. Arango, E. Curchitser, and others. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35, L08607, http://dx.doi.org/10.1029/2007gl032838.

Dinniman, M.S., and J.M. Klinck. 2004. A model study of circulation and cross-shelf exchange on the west Antarctic Peninsula continental shelf. *Deep Sea Research Part II* 51:2,003–2,022, http://dx.doi.org/10.1016/j.dsr2.2004.07.030.

Dinniman, M.S., J.M. Klinck, and E.E. Hofmann. 2012. Sensitivity of Circumpolar Deep Water transport and ice shelf basal melt along the west Antarctic Peninsula to changes in the winds. *Journal of Climate* 25:4,799–4,816, http://dx.doi.org/10.1175/JCLI-D-11-00307.1.

Doyle, M.J., S.J. Picquelle, K.L. Mier, M.C. Spillane, and N.A. Bond. 2009. Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003. *Progress in Oceanography* 80:163–187, http://dx.doi.org/10.1016/j.pocean.2009.03.002.

Fiechter, J., and A.M. Moore. 2012. Iron limitation impact on eddy-induced ecosystem variability in the coastal Gulf of Alaska. *Journal of Marine Systems* 92:1–15, http://dx.doi.org/10.1016/j.jmarsys.2011.09.012.

Fiechter, J., A.M. Moore, C.A. Edwards, K.W. Bruland, E. Di Lorenzo, C.V.W. Lewis, T.M. Powell, E.N. Curchitser, and K. Hedstrom. 2009. Modeling iron limitation of primary production in the coastal Gulf of Alaska. *Deep-Sea Research Part II* 56:2,503–2,519, http://dx.doi.org/10.1016/j.dsr2.2009.02.010

Greene, C.H., and A.J. Pershing. 2007. Climate drives sea change. *Science* 315:1,084–1,085, http://dx.doi.org/10.1126/science.1136495.

Henson, S.A., and A.C. Thomas. 2008. A census of oceanic anticyclonic eddies in the Gulf of Alaska. *Deep Sea Research Part I* 55:163–176, http://dx.doi.org/10.1016/j.dsr.2007.11.005.

Hofmann, E.E., P.H. Wiebe, D.P. Costa, and J.J. Torres. 2004. An overview of the Southern Ocean Global Ocean Ecosystems Dynamics Program. *Deep Sea Research Part II* 51:1,921–1,924, http://dx.doi.org/10.1016/j.dsr2.2004.08.007.

Hooff, R.C., and W.T. Peterson. 2006. Copepod biodiversity as an indicator of changes in ocean and climate conditions of the Northern

California Current ecosystem. *Limnology & Oceanography* 51:2,607–2,620, http://dx.doi.org/10.4319/lo.2006.51.6.2607.

Janout, M.A., T.J. Weingartner, S.R. Okkonen, T.E. Whitledge, and D.L. Musgrave. 2009. Some characteristics of Yakutat Eddies propagating along the continental slope of the northern Gulf of Alaska. *Deep Sea Research Part II* 56:2,444–2,459, http://dx.doi.org/10.1016/j.dsr2.2009.02.006.

Ji, R., C.S. Davis, C. Chen, D.W. Townsend, D.G. Mountain, and R.C. Beardsley. 2008. Modeling the influence of low-salinity water inflow on winter-spring phytoplankton dynamics in the Nova Scotian Shelf–Gulf of Maine region. *Journal of Plankton Research* 30:1,399–1,416, http://dx.doi.org/10.1093/plankt/fbn091.

Ji, R., C. Stegert, and C. Davis. 2012. Sensitivity of copepod populations to bottom-up and top-down forcing: A modeling study in the Gulf of Maine region. *Journal of Plankton Research* 35:66–79, http://dx.doi.org/10.1093/plankt/fbs070.

Keister, J.E., E. Di Lorenzo, C.A. Morgan, V. Combes, and W.T. Peterson. 2011. Zooplankton species composition is linked to ocean transport in the Northern California Current. *Global Change Biology* 17:2,498–2,511, http://dx.doi.org/10.1111/j.1365-2486.2010.02383.x.

King, J.R., V.N. Agostini, C.J. Harvey, G.A. McFarlane, M.G.G. Foreman, J.E. Overland, E. Di Lorenzo, N.A. Bond, and K.Y. Aydin. 2011. Climate forcing and the California Current ecosystem. *ICES Journal of Marine Science* 68:1,199–1,216, http://dx.doi.org/10.1093/icesjms/fsr009.

Kistler, R., E. Kalnay, W. Collins, S. Saha, G. White, J. Woollen, M. Chelliah, W. Ebisuzaki, M. Kanamitsu, V. Kousky, and others. 2001. The NCEP-NCAR 50-year reanalysis: Monthly means CD-ROM and documentation. *Bulletin of the American Meteorological Society* 82:247–268, http://dx.doi.org/10.1175/1520-0477(2001)082<0247:TNNYRM>2.3.CO;2.

Kwok, R., and J.C. Comiso. 2002. Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. *Journal of Climate* 15:487–501, http://dx.doi.org/10.1175/1520-0442(2002)015<0487:SOCASI>2.0.CO;2.

Ladd, C., C.W. Mordy, N.B. Kachel, and P.J. Stabeno. 2007. Northern Gulf of Alaska eddies and associated anomalies. *Deep Sea Research Part I* 54:487–509, http://dx.doi.org/10.1016/j.dsr.2007.01.006.

Marrari, M., K.L. Daly, and C. Hu. 2008. Spatial and temporal variability of SeaWiFS derived chlorophyll distributions west of the Antarctic Peninsula: Implications for krill production. *Deep Sea Research Part II* 55:377–392, http://dx.doi.org/10.1016/j.dsr2.2007.11.011.

Marshall, G.J., A. Orr, N.P. van Lipzig, and J.C. King. 2006. The impact of a changing Southern Hemisphere Annular Mode on Antarctic Peninsula summer temperatures. *Journal of Climate* 19:5,388–5,404, http://dx.doi.org/10.1175/JCLI3844.1.

Martin, J.H., R.M. Gordon, S. Fitzwater, and W.W. Broenkow. 1989. Vertex: Phytoplankton/iron studies in the Gulf of Alaska. *Deep Sea Research Part A* 36:649–680, http://dx.doi.org/10.1016/0198-0149(89)90144-1.

Mountain, D.G., and J. Kane. 2010. Major changes in the Georges Bank ecosystem, 1980s to the 1990s. *Marine Ecology Progress Series* 398:81–91, http://dx.doi.org/10.3354/meps08323.

Niiler, P.P., N.A. Maximenko, and J.C. McWilliams. 2003. Dynamically balanced absolute sea level of the global ocean derived from near-surface velocity observations. *Geophysical Research Letters* 30, 2164, http://dx.doi.org/10.1029/2003GL018628.

Okkonen, S.R., G.A. Jacobs, J.E. Metzger, H.E. Hurlburt, and J.F. Shriver. 2001. Mesoscale variability in the boundary currents of the Alaska Gyre. *Continental Shelf Research* 21:1,219–1,236, http://dx.doi.org/10.1016/S0278-4343(00)00085-6.

Okkonen, S.R., T.J. Weingartner, S.L. Danielson, D.L. Musgrave, and G.M. Schmidt. 2003. Satellite and hydrographic observations of eddy-induced shelf-slope exchange in the northwestern Gulf of Alaska. *Journal of Geophysical Research* 108, 3033, http://dx.doi.org/10.1029/2002JC001342.

Peterson, W.T. 2009. Copepod species richness as an indicator of long-term changes in the coastal ecosystem of the Northern California Current. *CalCOFI Report* 50:73–81. Available online at: http://calcofi.org/publications/calcofireports/v50/73-81_Peterson.pdf (accessed December 21, 2013).

Piñones, A., E.E. Hofmann, K.L. Daly, M.S. Dinniman, and J.M. Klinck. 2013a. Modeling environmental controls on the transport and fate of early life stages of Antarctic krill (*Euphausia superba*) on the western Antarctic Peninsula continental shelf. *Deep Sea Research Part I* 82:17–31, http://dx.doi.org/10.1016/j.dsr.2013.08.001.

Piñones, A., E.E. Hofmann, K.L. Daly, M.S. Dinniman, and J.M. Klinck. 2013b. Modeling the remote and local connectivity of Antarctic krill populations along the western Antarctic Peninsula. *Marine Ecology Progress Series* 481:69–92, http://dx.doi.org/10.3354/meps10256.

Piñones, A., E.E. Hofmann, M.S. Dinniman, and J.M. Klinck. 2011. Lagrangian simulation of transport pathways and residence times along the western Antarctic Peninsula. *Deep Sea Research Part II* 58:1,524–1,539, http://dx.doi.org/10.1016/j.dsr2.2010.07.001.

Prézelin, B.B., E.E. Hofmann, M. Moline, and J.M. Klinck. 2004. Physical forcing of phytoplankton community structure and primary production in continental shelf waters of the western Antarctic Peninsula. *Journal of Marine Research* 62:419–460, http://dx.doi.org/10.1357/0022240041446173.

Smith, P.C., R.W. Houghton, R.G. Fairbanks, and D.G. Mountain. 2001. Interannual variability of boundary fluxes and water mass properties in the Gulf of Maine and on Georges Bank: 1993–1997. *Deep Sea Research Part II* 48:37–70, http://dx.doi.org/10.1016/S0967-0645(00)00081-3.

Smith, T.M., and R.W. Reynolds. 2004. Improved extended reconstruction of SST (1854–1997). *Journal of Climate* 17:2,466–2,477, http://dx.doi.org/10.1175/1520-0442(2004)017<2466:IEROS>2.0.CO;2.

Širović, A., J.A. Hildebrand, S.M. Wiggins, M.A. McDonald, S.E. Moore, and D. Thiele. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the western Antarctic Peninsula. *Deep Sea Research Part II* 51:2,327–2,344, http://dx.doi.org/10.1016/j.dsr2.2004.08.005.

Stabeno, P.J., N.A. Bond, A.J. Hermann, N.B. Kachel, C.W. Mordy, and J.E. Overland. 2004. Meteorology and oceanography of the Northern Gulf of Alaska. *Continental Shelf Research* 24:859–897, http://dx.doi.org/10.1016/j.csr.2004.02.007.

Stammerjohn, S.E., D.G. Martinson, R.C. Smith, and R.A. Iannuzzi. 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II* 55:2,041–2,058, http://dx.doi.org/10.1016/j.dsr2.2008.04.026.

Strom, S.L., M.B. Olson, E.L. Macri, and C.W. Mordy. 2006. Cross-shelf gradients in phytoplankton community structure, nutrient utilization, and growth rate in the northern coastal Gulf of Alaska. *Marine Ecology Progress Series* 328:75–92, http://dx.doi.org/10.3354/meps328075.

Thiele, D., E.T. Chester, S.E. Moore, A. Širović, J.A. Hildebrand, and A.S. Friedlaender. 2004. Seasonal variability in whale encounters in the western Antarctic Peninsula. *Deep Sea Research Part II* 51:2,311–2,325, http://dx.doi.org/10.1016/j.dsr2.2004.07.007.

Thompson, D.W., and S. Solomon. 2002. Interpretation of recent Southern Hemisphere climate change. *Science* 296:895–899, http://dx.doi.org/10.1126/science.1069270.

Ueno, H., W.R. Crawford, and H. Onishi. 2010. Impact of Alaskan stream eddies on chlorophyll distribution in the North Pacific. *Journal of Oceanography* 66:319–328, http://dx.doi.org/10.1007/s10872-010-0028-6.

van den Broeke, M.R., and N.P. van Lipzig. 2004. Changes in Antarctic temperature, wind and precipitation in response to the Antarctic Oscillation. *Annals of Glaciology* 39:119–126, http://dx.doi.org/10.3189/172756404781814654.

Weingartner, T.J., S.L. Danielson, and T.C. Royer. 2005. Freshwater variability and predictability in the Alaska Coastal Current. *Deep Sea Research Part II* 52:169–191, http://dx.doi.org/10.1016/j.dsr2.2004.09.030.