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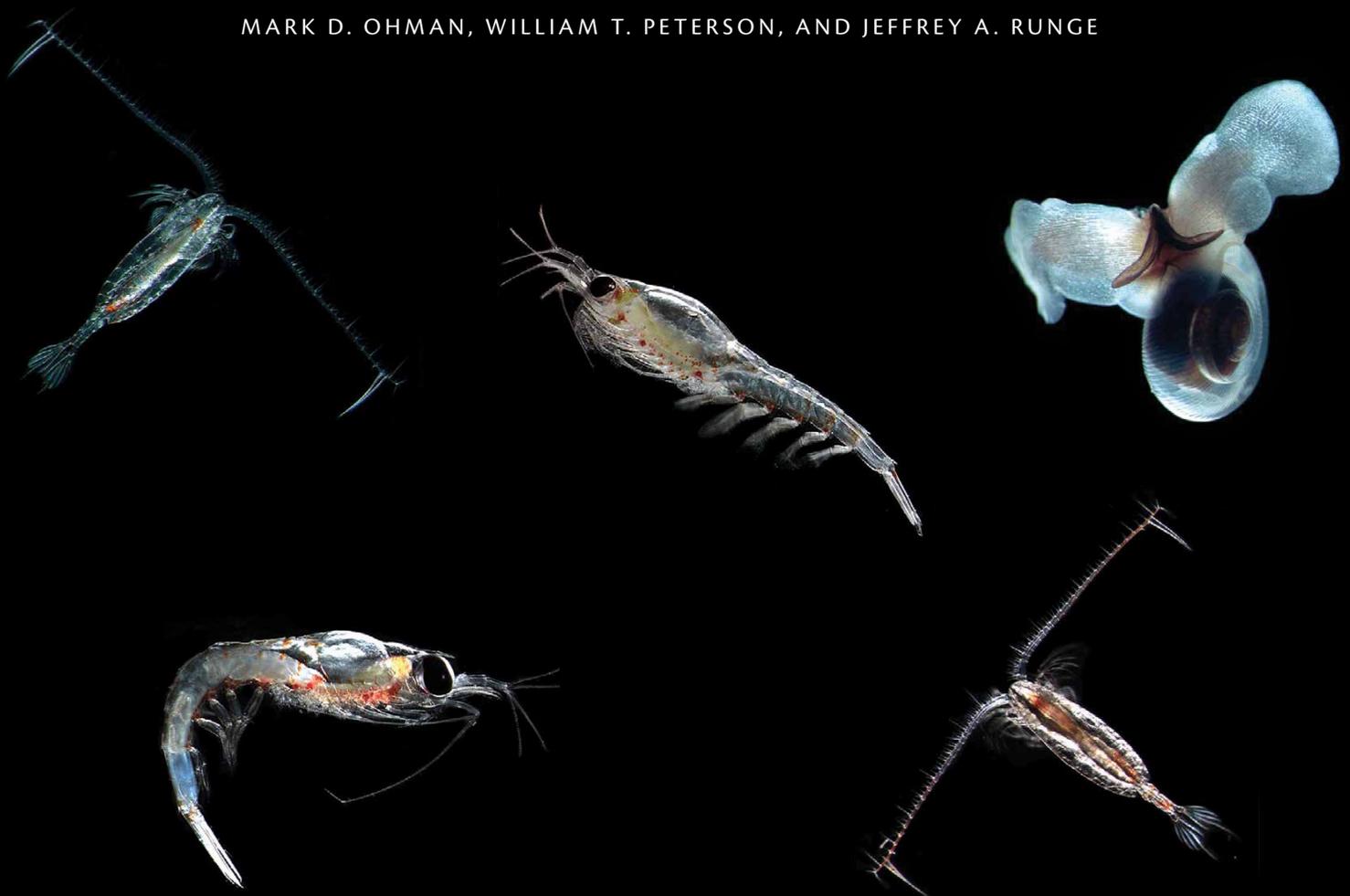
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SPECIAL ISSUE ON US GLOBEC:
UNDERSTANDING CLIMATE IMPACTS ON MARINE ECOSYSTEMS



Climate Impacts on Zooplankton Population Dynamics in Coastal Marine Ecosystems

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The GLOBEC approach is to develop fundamental information about the basic mechanisms that determine the abundance and distribution of marine animal populations and, most importantly, the variability of these populations about their average values.

(GLOBEC, 1991a, p. 1)



Moreover, the characteristics of a region that determine its suitability for any given organism depend not only on the availability of food and the abundance of predators but also upon the dynamic physical features of the local environment that influence the success of recruitment, the efficiency of feeding, and the susceptibility to predation.

(GLOBEC, 1991b, p. 5)

ABSTRACT. The 20-year US GLOBEC (Global Ocean Ecosystem Dynamics) program examined zooplankton populations and their predators in four coastal marine ecosystems. Program scientists learned that environmental controls on zooplankton vital rates, especially the timing and magnitude of reproduction, growth, life-cycle progression, and mortality, determine species population dynamics, seasonal and spatial distributions, and abundances. Improved knowledge of spatial-temporal abundance and distribution of individual zooplankton taxa coupled with new information linking higher trophic level predators (salmon, cod, haddock, penguins, seals) to their prey yielded mechanistic descriptions of how climate variation impacts regionally important marine resources. Coupled ecological models driven by improved regional-scale climate scenario models developed during GLOBEC enable forecasts of plausible future conditions in coastal ecosystems, and will aid and inform decision makers and communities as they assess, respond, and adapt to the effects of environmental change. Multi-region synthesis revealed that conditions in winter, before upwelling, or seasonal stratification, or ice melt (depending on region) had significant and important effects that primed the systems for greater zooplankton population abundance and productivity the following spring-summer, with effects that propagated to higher trophic levels.

INTRODUCTION

US GLOBEC (Global Ocean Ecosystem Dynamics) scientists examined zooplankton populations and their predators in four coastal marine ecosystems: Georges Bank/Gulf of Maine, Northern California Current, coastal Gulf of Alaska, and western Antarctic Peninsula (Turner et al., 2013, in this issue). In each, understanding the spatial and temporal abundances of zooplankton species required understanding of the species population dynamics (vital rates) and the physical processes affecting the habitat. In continental shelf ecosystems, environmental conditions, such as temperature, stratification, and current velocity, vary over both small and large spatial ranges and temporal scales, from daily to interdecadal. Species life histories interact with temporal-spatial environmental variability, often in a nonlinear manner. For example, short-term temporal variability in ocean conditions may be important for some species but not

PHOTOS | (top left) *Neocalanus flemingeri* adult female, showing development of eggs, from the Gulf of Alaska. (top right) *Euphausia pacifica*. (middle left) *Calanus finmarchicus*, a biomass dominant copepod in the North Atlantic. (middle center) The euphausiid, *Thysanoessa inermis*, important in the Gulf of Alaska. (middle right) A pelagic mollusk, *Limacina helicina*. (bottom left) Another euphausiid, *Thysanoessa longipes*, from the Gulf of Alaska. (bottom right) *Calanus marshallae*, an important copepod in the Northeast Pacific. Top right photo of *Euphausia pacifica* by Mark D. Ohman, Scripps Institution of Oceanography. All other photos by Russ Hopcroft, University of Alaska Fairbanks.

for others, and a species with a diverse repertoire of behaviors may respond differently to climate change than species with less flexible life-history strategies. These differences among zooplankton may have dramatic effects on marine ecosystem structure (Peterson, 2009; Johnson et al., 2011).

Population ecology focuses on population abundance, how it varies temporally, and the biotic and physical processes that determine it. Fundamental to zooplankton population dynamics are the vital rates of birth, development, growth, and mortality that lead to changes of body size and numbers (or biomass), as well as the environmental factors that influence individual vital rates (Figure 1). Key zooplankton and fish or other higher trophic level species

were targeted for detailed study based on their importance to the ecological dynamics or fisheries of a region (Turner et al., 2013, in this issue). We begin with a brief discussion of the efforts to link physics and biology on similar time-space scales. We then focus on new approaches used to examine mortality, the least well-known vital rate in zooplankton. We present selected examples of environmental forcing of zooplankton population dynamics in four US GLOBEC regional ecosystems, and we put forward an emerging multi-regional synthesis that reveals the hitherto unsuspected importance of winter conditions. Finally, we describe advances in understanding the connection between zooplankton and the early life-history stages of targeted fish taxa.

PROVIDING A SPATIAL AND TEMPORAL CONTEXT FOR EXAMINING POPULATION DYNAMICS

Temperature, food concentration, predators, turbulence, and light, which may vary over multiple spatial and temporal scales, strongly influence the vital rates of zooplankton. GLOBEC sampled organisms and their environments at multiple scales in order to better link individuals and groups of individuals (subpopulations) to variable physical, chemical, and biotic conditions (Figure 2). Standard net tow and pump sampling methods were used to collect zooplankton in the Northwest Atlantic (Durbin and Casas, 2006), Northeast Pacific (Coyle and Pinchuk, 2003, 2005; Peterson and Keister, 2003; Lavaniegas and Ohman, 2007), and Southern Ocean (Marrari et al., 2011a,b; Wiebe et al., 2011). These regions provided the samples needed to characterize the detailed species and life stage information critical for population and life-history studies (Daly, 2004; Reese et al., 2005; Marrari et al., 2011a,b), such as recruitment into krill and copepod populations (Feinberg and Peterson, 2003; Runge et al., 2006; Feinberg et al., 2010), stage-specific rates of mortality (Ohman et al., 2002), and timing of dormancy (Johnson et al., 2008; Maps et al., 2012). Bioacoustic and optical technologies were developed and employed to describe finer-scale distributions over broad areas. The Video Plankton Recorder enabled specific identification of species and stage (or size) of zooplankton that could be directly related to concurrent physical measurements at similar spatial-temporal scales (Benfield et al., 1996; Norrbin et al., 1996; Davis et al., 2005). Localized aggregations of krill (euphausiids) at spatial scales spanning a few centimeters

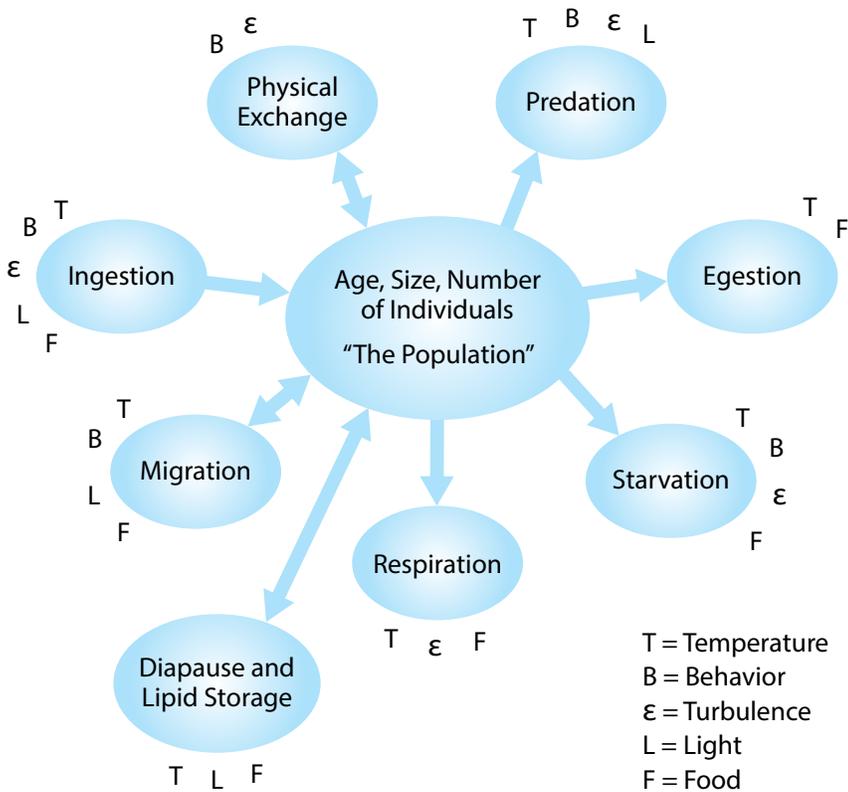


Figure 1. Processes that influence vital rates of individuals and abundance and distribution of zooplankton populations. Environmental (temperature, turbulence, light, food) and individual (behavior) factors that control these processes are shown. Modified from Figure 3 in GLOBEC (1992) to include diapause and lipid storage impacts on individuals

(Jaffe et al., 1999) up to 50 m or even coast-wide were characterized using a variety of bioacoustic or optical instruments (Ressler et al., 2005; Swartzman et al., 2005; Wiebe et al., 1996; Lawson et al., 2004, 2008). Such data are necessary for assessing the spatial patchiness of prey composition and evaluating its impact on the feeding dynamics of zooplankton predators (Young et al., 2009).

GLOBEC observations and understanding of population dynamics provide insight into the mechanisms of bottom-up physical forcing that determine biological production at lower trophic levels (phytoplankton and zooplankton), which in turn influence production of upper trophic level species subject to resource management (Fogarty et al., 2013, in this issue). Coupled bio-physical population models provided predictions of spatio-temporal distribution and abundance of key zooplankton species in the North Atlantic (e.g., Ji et al., 2009; Stegert et al., 2012), Northeast Pacific (Dorman et al., 2011; Lindsey, 2014), and Southern Ocean (Piñones et al., 2013). These models allow a dynamic description of interactions among life history strategies and the physical environment at many scales simultaneously (Figure 2). Examples of these models are described in greater detail in a review of the advancements in coupled modeling achieved by GLOBEC (Curchitser et al., 2013, in this issue).

MORTALITY CAUSES AND UNCERTAINTIES

Zooplankton and larval fish mortalities are the vital rates for which responses to environmental conditions and climate variability are least well understood and most difficult to forecast for future climate scenarios. Mortality is a complex function of factors, including physical

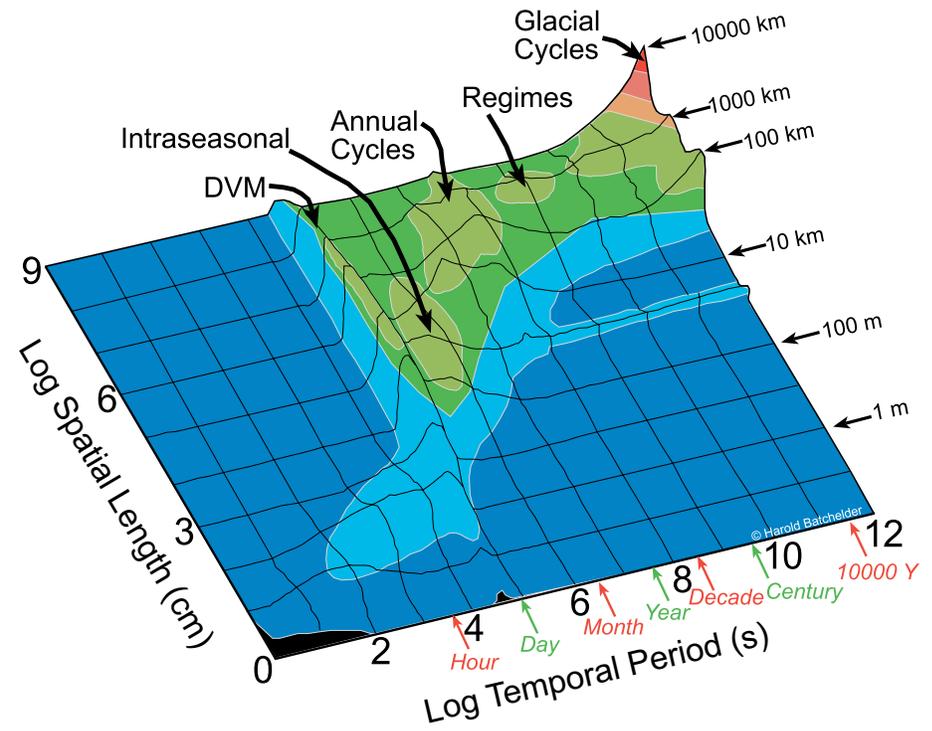


Figure 2. Schematic plot of zooplankton abundance or biomass variability (peaks are greater variability) in space and time (both log scaled). Note the general tendency for the correlation to be positive when there is higher variability between spatial and temporal scales, with the greatest variability at daily (DVM = diel vertical migration; all scales > 1 m), intraseasonal (mesoscale), annual (basin), multidecadal (basin-global), and glacial-interglacial (global) time (space) scales. Modified and redrafted with inspiration from an original graphic in Haury et al. (1978)

circulation (through advective losses) and hydrography (temperature effects), and the number, distribution, and types of both prey (starvation and condition effects) and predators. Among the key vital rates influencing zooplankton population dynamics, mortality is the most challenging to estimate. While modeling studies have repeatedly demonstrated high sensitivity to the formulation of

zooplankton mortality, few empirical studies have provided useful mortality estimates applicable to natural populations. During the GLOBEC era, four numerical approaches were applied, some for the first time, to estimate species-specific mortality: matrix projection (Caswell, 2001), population surface (Wood, 1994), vertical life table (Aksnes and Ohman, 1996), and an

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advection-differencing method (Li et al., 2006). A fifth approach for estimating mortality of the total plankton community using biomass spectrum theory (Zhou and Huntley, 1997; Edvardsen et al., 2002) was applied in the California

the California Current System (Ohman and Hsieh, 2008) and the Georges Bank region (Li et al., 2006; Ohman et al., 2008). Notably, regions of elevated food availability to zooplankton in the coastal upwelling region were also associated

salmon (*Oncorhynchus gorbuscha*) in the Gulf of Alaska. Seasonally averaged instantaneous mortality estimates of eggs derived from decreases in the abundance of developing cohorts of cod and haddock between successive seasonal surveys from 1995–1999 ranged from 0.10–0.28 d⁻¹ for cod and 0.08–0.14 d⁻¹ for haddock, with interannual variability attributed largely to wind-driven transport of eggs that resulted in their loss from the bank (Mountain et al., 2008). Seasonally averaged mortality of early larvae was 0.07 d⁻¹ for cod and 0.11 d⁻¹ for haddock in 1995 and 1996, but 0.04 d⁻¹ and 0.06 d⁻¹, respectively, in 1998 and 1999 (Mountain et al., 2008). The reduced (by 40–45%) mortality of the late 1990s was attributed to higher larval prey abundances in the Gulf of Maine associated with a change in stratification due to increased presence of low-salinity surface water from the Arctic (Buckley and Durbin, 2006).

Pink salmon survival in the Gulf of Alaska was variable, by a factor of three, among the four years of most intensive sampling (2001–2004). Pink salmon were persistently larger throughout summer to early fall in 2002 and 2004, the years of higher survival (Moss et al., 2005; Cross et al., 2008). High growth and survival appear linked to earlier horizontal migrations to continental shelf habitats having higher quality (i.e., energy-rich) prey, such as pteropods (Armstrong et al., 2008). Salmon in high survival years, and salmon that survived the first marine winter, had faster May to October growth during their first marine year, determined from scale circuli growth, than salmon that did not survive the first winter (Cross et al., 2008, 2009), suggesting size-selective mortality (e.g., death of the slowest growing individuals occurred after the first growing season).

“ GLOBEC SAMPLED ORGANISMS AND THEIR ENVIRONMENTS AT MULTIPLE SCALES IN ORDER TO BETTER LINK INDIVIDUALS AND GROUPS OF INDIVIDUALS (SUBPOPULATIONS) TO VARIABLE PHYSICAL, CHEMICAL, AND BIOTIC CONDITIONS. ”

Current System (Wu, 2008) and the Southern Ocean (Zhou et al., 2004). While the biomass spectrum approach may be considered for examining growth and survival of the plankton community in total, it is not usually applicable to the study of population dynamics of individual species.

While each method incorporates key assumptions that must be examined carefully (Aksnes et al., 1997), the species-specific and stage-resolved population data generated during GLOBEC field studies afforded an excellent opportunity to apply these methods in a systematic manner to target species. GLOBEC results demonstrated that the high fecundity, high mortality life history of broadcast-spawning *Calanus* may co-exist with the low fecundity, low mortality life history of egg-brooding *Pseudocalanus*, with approximately equal fitness in the same study site (Ohman et al., 2002). Mortality rates, which vary not only in time, but also in space, were found to covary with predators in both

with elevated predation mortality, confirming Bakun's (2006, p. 117) assertion that “for planktonic organisms... food heaven almost invariably equates to predation hell.” A comparison of mortality rates of *Calanus finmarchicus* in five locations across the North Atlantic revealed regional differences in stage-specific patterns of mortality (Ohman et al., 2004), together with evidence for density-dependent egg mortality related to cannibalism in both the open ocean (Ohman and Hirche, 2001) and on the Northwest Atlantic continental shelf (Ohman et al., 2004). The findings of density-dependent mortality in GLOBEC field studies corroborated the inference of the importance of this process deduced from pelagic ecosystem models (Steele and Henderson, 1992; Fasham, 1995).

In addition to zooplankton mortality, GLOBEC investigated mortality of early life stages of targeted fish species Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the Northwest Atlantic, and juvenile pink

While GLOBEC and other research programs have in the past few decades greatly advanced knowledge of age- or stage-based patterns of mortality rates, it remains difficult in most cases to assign causation to mortality. Mortality may occur through advection of organisms to unfavorable habitats, starvation, or predation (Peck and Hufnagl, 2012). Often, these processes are intertwined. For example, advection of zooplankton to warmer, low-food environments offshore may lead to starvation, reduced growth, delayed development, smaller size, and increased probability of predation. Despite these interactions, Ohman et al. (2008) provide strong arguments that the source of *Calanus finmarchicus* early life stage mortality on Georges Bank is invertebrate predation. Coupled bio-physical models that include advection, starvation, and mortality (Dorman et al., 2011; Figure 3) provide insight into these interacting processes, contributing to understanding of not only population dynamics but also biological fluxes (sinking versus trophic transfer; see Curchitser et al., 2013, in this issue).

REGIONAL ZOOPLANKTON POPULATION DYNAMICS

Southern Ocean

The Southern Ocean was chosen as a GLOBEC site because of the strong linkages between climate variability/change and ecosystem dynamics (Hofmann et al., 2004). A feature of the food webs of the Southern Ocean is that many regions are characterized by a short trophic chain dominated by fewer than six species, with Antarctic krill (*Euphausia superba*) serving as a key intermediary. *E. superba* essentially occupies the trophic niche that is filled by forage fish, such as sardines and anchovies, in eastern boundary

current upwelling systems. Many predators are dependent on Antarctic krill, or on a small group of species, such as other euphausiids and a few fish. Thus, bottom-up environmental perturbations or top-down pressure, such as fishing, on Antarctic krill or Patagonian toothfish can potentially cascade to all components of the Antarctic marine ecosystem (Ballerini et al., in press). The primary objective of the Southern Ocean GLOBEC (SO GLOBEC) program was to understand the physical and biological factors that contribute to enhanced Antarctic krill growth, reproduction, recruitment, and survivorship throughout the year; the effort also included

research on predators and competitors of Antarctic krill, such as penguins, seals, cetaceans, fish, and other zooplankton. SO GLOBEC was an international interdisciplinary investigation of ecosystems in many sectors of the Antarctic. The US contribution to SO GLOBEC field studies focused on the Marguerite Bay shelf region of the western Antarctic Peninsula, which has large concentrations of krill during summer and is thought to be a site of successful krill overwintering. The Antarctic Peninsula is one of the most productive regions of the Southern Ocean (Deibel and Daly, 2007). It is also a region of rapid warming (Vaughan and Doake, 1996) and sea

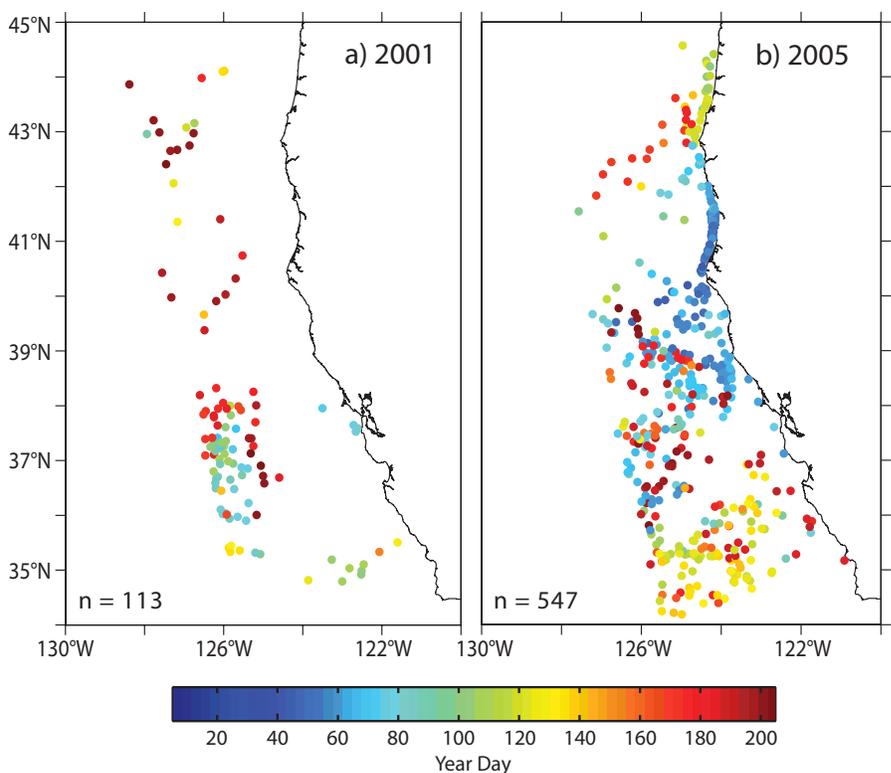


Figure 3. Starvation location of modeled furcilia IV–VII (intermediate larval stages), juvenile, and adult *Euphausia pacifica* during (a) 2001, and (b) 2005. Color axis shows year-day of starvation. Results are from an individual-based bioenergetics model of krill growth, development with life stage-dependent diel vertical migration forced by physical fields from a regional ocean model for 2001 and 2005. Krill were initiated over the continental shelf from Cape Mendocino (40°N) to the southern model boundary on January 2. The later spring transition of 2005 resulted in more northward transport early in the year, lower shelf and offshore food concentrations, lower krill growth, and higher starvation mortality. Figure modified from Dorman et al. (2011)

ice decline (Stammerjohn et al., 2012), both of which are hypothesized to significantly impact ocean productivity and the growth, survival, and population dynamics of Antarctic krill that overwinter there. US GLOBEC studies in the Southern Ocean focused on austral winters in 2001 and 2002. Sea ice was more extensive and appeared earlier in Marguerite Bay during 2002 than in 2001, consistent with the 1–2°C cooler sea surface temperatures (SSTs) during the preceding austral summer (Marrari et al., 2008, 2011a).

The dominant members of the zooplankton community in Marguerite Bay included three species of euphausiids (Antarctic krill, *Euphausia superba*; a neritic euphausiid, *Euphausia crystallorophias*; and *Thysanoessa macrura*), several copepod species, ostracods, and pteropods (Marrari et al., 2011a,b). Total zooplankton abundance and biomass from net collections diminished by 60% between fall (April to June) and winter (July to August) (Ashjian et al., 2004). A winter-specific mortality rate for mesozooplankton, determined from an Optical Plankton Counter mounted on a MOCNESS (Multiple Opening and Closing Net, with an Environmental Sensing System), was about 0.07 d⁻¹, resulting in disappearance of 90% of the biomass between fall and winter (Zhou et al., 2004).

Environmental conditions along the Antarctic Peninsula in winter are cold, dark, and relatively food poor. Measurement of vital rates of overwintering larval and adult krill was a focus for SO GLOBEC field investigations. Interannual differences in the stage composition and abundances of zooplankton were related to the unusually high summer chlorophyll concentrations during 2000/2001 (Marrari et al., 2008,

2011a). Copepod abundances were highest during 2001 (Marrari et al., 2011a) and larval Antarctic krill abundances were among the highest ever recorded (Daly, 2004). Larval *Euphausia superba* feeding and growth during fall 2001 were similar to summer rates (Pakhomov et al., 2004). *Thysanoessa macrura*, which develops relatively rapidly from larval to juvenile stages between spring and fall, was the most abundant euphausiid during 2001 (Marrari et al., 2011a). In contrast, *Euphausia crystallorophias* and *Euphausia superba* juvenile and adult populations increased in 2002, owing to slower development in which larval stages recruit to juveniles during the following spring/summer.

Despite the presence of sea ice, overwintering larval *Euphausia superba* were food-limited during 2001 and 2002, based on observed decrease in growth and development rates (Daly, 2004). At this high latitude, the late formation of sea ice and declining irradiance did not allow sea ice biota to accumulate sufficiently to support larval feeding throughout the winter. Instead, larval krill fed opportunistically on microzooplankton, sea ice biota, benthic larvae, scarce phytoplankton, and detritus (Daly, 2004). Opportunistic feeding, coupled with delayed development, flexible physiology (increased intermolt period, reduced growth), some lipid storage, and the ability to combust body carbon and nitrogen to support metabolism, enabled survival of krill larvae through winter (Daly, 2004).

Northwest Atlantic

The planktonic copepod *Calanus finmarchicus* dominates the biomass of net zooplankton and is important prey in pelagic food webs across the northern North Atlantic; hence, its

designation as a target species in the US Northwest Atlantic/Georges Bank program. Its significance in the Gulf of Maine food web has been recognized since the earliest surveys conducted by Henry Bigelow (1926), who wrote that “the importance of *C. finmarchicus* in the general economy of the Gulf of Maine...can hardly be overestimated.” Nevertheless, evidence for a direct relationship between production of *Calanus* early life stages and recruitment of cod and haddock populations, hypothesized for cod populations in the Norwegian and North Seas (Ellertsen et al., 1987; Beaugrand et al., 2003), was not found on Georges Bank (Heath and Lough, 2007). While more than 95% of identifiable prey consumed by larval cod and haddock (3–13 mm length) on Georges Bank in late spring are copepods, most of the diet consisted of various life stages of *Pseudocalanus* spp. and *Oithona* spp., which were positively selected based on concurrent net sampling of prey fields (Broughton and Lough, 2010). Buckley and Durbin (2006) found strong correlations between the growth rates of larval cod and haddock and the contemporaneous biomass of *Pseudocalanus* in the sea. Their results indicate that prey abundance has a strong effect on larval growth, especially in the early stages, and that prey levels in nature are often below what is needed for larvae to grow at a maximum rate.

The significance of *C. finmarchicus* in the coastal Northwest Atlantic ecosystem derives from the older, lipid-rich copepodite stages, which are abundant on the ledges and banks of the coastal Gulf of Maine in spring and summer. These stages constitute the principal prey for forage fishes (herring, sand lance, and mackerel), which are in turn fed upon by other fish, including cod

and the migratory bluefin tuna. The high abundance of *C. finmarchicus* also sustains the endangered northern right whale population that resides in the Gulf of Maine in summer to feed on aggregations of lipid-rich, late-stage *Calanus* (Beardsley et al., 1996).

The abundance of the lipid-rich stages of *Calanus* in this region is subject to environmental forcing. Atmospheric climate patterns in the North Atlantic are influenced by the North Atlantic Oscillation (NAO), which is hypothesized to have ecosystem impacts in the Northeast and Northwest Atlantic (Beaugrand et al., 2003; Drinkwater et al., 2003; MERCINA, 2012). GLOBEC sampling activities revealed that *C. finmarchicus* population abundance in the Gulf of Maine was extremely low in 1998, two years after an intensely negative NAO (Greene et al., 2003). Physical processes associated with very negative NAOs are hypothesized to force (with a two-year lag) colder, fresher, and *Calanus*-poor Labrador Subarctic Slope Water into the Gulf of Maine (Greene et al., 2003). In addition to shifts in circulation pattern, temperatures in the Gulf of Maine have been increasing recently at a rate (0.1–0.3°C yr⁻¹; Mills et al., 2013) 10 times faster than the regional 100-year trend (Shearman and Lentz, 2010). The northward migration of the 10°C surface isotherm in the North Atlantic predicted from atmosphere-ocean climate models may result in disappearance of *C. finmarchicus* from the Gulf of Maine in the next several decades (Reygondeau and Beaugrand, 2011). This certainly would, unless replaced, alter the entire regional food web, including a possible shift away from a lipid-based trophic structure (Johnson et al., 2011). While

the impacts of these physical changes on dynamics of the local abundance of *C. finmarchicus* are not yet fully understood, the life history knowledge and bio-physical modeling capacity acquired during the GLOBEC program provide the foundation for understanding mechanisms sustaining *C. finmarchicus* regionally (Curchitser et al., 2013, in this issue).

GLOBEC research also advanced understanding of the population dynamics of other copepods, including *Pseudocalanus* spp., and their contributions to zooplankton community structure and trophic interactions in relation to climate variability. Strong decadal-scale shifts of copepod community structure in the Gulf of Maine/Georges Bank region have been observed from long-term surveys such as NEFSC MARMAP/EcoMon¹ (1977 to present) and the Continuous Plankton Recorder (1961 to present for Gulf of Maine). Small copepods were more abundant in the 1990s than in the 1980s or 2000s (Kane, 2007; Greene and Pershing, 2007). This appears associated with increased haddock recruitment and with a substantial change in the fishery ecosystem of the Northwest Atlantic shelf in the 1990s (Link et al., 2002; Mountain and Kane, 2010).

Bottom-up and top-down controls likely contribute to decadal variability. The bottom-up view suggests that changes in surface salinity and water-column stability and the resulting changes in fall-winter phytoplankton blooms can influence zooplankton populations (e.g., Durbin et al., 2003; Durbin and Casas, 2006; Greene and Pershing, 2007; MERCINA, 2012; see also Di Lorenzo et al., 2013, in this issue). However, lower salinity is not

always associated with higher abundance of small zooplankton, as shown by data from the first decade of this century (Hare and Kane, 2012) suggesting that top-down control (Frank et al., 2005, 2011; Ji et al., 2012) may also contribute to decadal variability.

Coastal Gulf of Alaska

The coastal Gulf of Alaska (CGOA) exhibits unusually high production of upper trophic levels, especially fish and birds (Sambrotto and Lorenzen, 1986), despite persistent downwelling winds that do not enhance the nutrient supply that sustains lower trophic productivity (Royer, 1998; Stabeno et al., 2004). Sufficient exchange of deep, nutrient-rich waters must occur to provide the macronutrients to the surface (Okkonen et al., 2003; Ladd et al., 2005; Hermann et al., 2009). GLOBEC characterized the spatial-temporal composition of the zooplankton secondary producers that are the base of the consumer food web and important prey for juvenile pink salmon and other fish. Feeding, reproduction, development, and growth rates were measured for many of the copepods and euphausiids that dominate secondary production and the prey biomass for fish (Liu et al., 2005; Napp et al., 2005; Liu and Hopcroft, 2007, 2008).

GLOBEC research revealed strong cross-shelf gradients in phytoplankton community structure, nutrient limitation, growth rate, zooplankton species composition, and grazing rates (Coyle and Pinchuk, 2005; Strom et al., 2006). During spring (April to May), chlorophyll-*a* concentrations on the inner and sometimes the middle CGOA shelf are five to 20 times higher than during summer (July to August) and

¹ NOAA Northeast Fisheries Service Center (NEFSC) survey that includes MARMAP (Marine Monitoring Assessment and Prediction, 1977–1987) and the subsequent EcoMon (Ecosystem Monitoring, 1988–present) programs.

are dominated by large diatom cells (Strom et al., 2007). Small phytoplankton (< 5 µm) dominate outer shelf stations during most of the spring-summer. The cross-shelf gradients in phytoplankton cell size and concentration are believed to be due to limited availability of iron offshore and limited nitrogen nearshore (except for the spring phytoplankton bloom in April to May). Nitrogen may become limiting on much of the inner shelf as early as April, shortly after development of stratification. Inner shelf chlorophyll concentrations are low and phytoplankton are small (< 5 µm) in summer, except where spatially limited diatom blooms are present, perhaps due to localized upwelling (Strom et al., 2007; Hermann et al., 2009). Microzooplankton consumed most of the production by small (< 20 µm) cells and roughly half of the production by larger diatoms.

The large *Neocalanus* spp. copepods that dominate the plankton biomass in Prince William Sound (PWS) and shelf regions in spring are important consumers of diatoms and microzooplankton (Liu et al., 2005; Dagg et al., 2009), but are important prey to juvenile pink salmon only in PWS, because few salmon outmigrate to the shelf in spring (Armstrong et al., 2005). Juvenile pink salmon arrive to feed on the open shelf in late June to July after most *Neocalanus* spp. have departed surface waters into seasonal diapause. Therefore, the principal shelf prey of pink salmon are smaller copepods, larvaceans, pteropods, and euphausiids (Coyle and Pinchuk, 2003; Armstrong et al., 2005, 2008). The dominant prey of juvenile pink salmon varied with geographic region (PWS, shelf, offshore), with season, and interannually (Boldt and Haldorson, 2003; Armstrong et al., 2005, 2008), likely reflecting local

zooplankton abundance and composition, and perhaps patchiness of aggregations. GLOBEC research in the Gulf of Alaska focused on the production of euphausiids and copepods. Growth rate of the copepods *Metridia lucens*, *Calanus marshallae*, *C. pacificus*, and *Pseudocalanus* spp. that dominate late summer-fall biomass on the shelf (Coyle and Pinchuk, 2003) was measured (Liu and Hopcroft, 2007, 2008), as were growth rates of multiple euphausiid species (Pinchuk and Hopcroft, 2007). Other investigations examined egg production of copepods (Napp et al., 2005) and euphausiids (Pinchuk and Hopcroft, 2006). Growth, development, and reproduction rates applied to stage-specific field abundances provided estimates of seasonal production of prey for larval fishes in the northern Gulf of Alaska. These zooplankton vital rate measurements will contribute to future coupled bio-physical models directed at understanding climate impacts on population dynamics (Pinchuk et al., 2008).

California Current System

Euphausiids and copepods are important prey for higher trophic levels in the California Current. Copepods are indicators of transport processes and the bioenergetic content of the food chain. The California Current program included biweekly monitoring of physical and biological properties along a cross-shelf transect (Newport Hydrographic Line) that had been intensively sampled in the 1960s and early 1970s (Huyer, 1977; Peterson and Miller, 1977). The 17+-year record of observations (still continuing) is of sufficient length to characterize the response of the coastal upwelling ecosystem to basin-scale forcing associated with the Pacific Decadal Oscillation (PDO). The PDO signal has varied

strongly and frequently since 1998, providing a natural experiment for examining how PDO signals are transmitted and expressed locally in the Oregon shelf ecosystem. Changes in the sign of the PDO, related to sea surface temperature anomalies, are followed closely by changes in copepod community structure: during negative (“cool”) phases of the PDO, a “cold water community” dominates, whereas during positive (“warm”) phases, a “warm water community” dominates (<http://www.nwfsc.noaa.gov/oceanconditions>; Keister et al., 2011; Francis et al., 2012). The biomass dominant copepods during the cool phase are *Calanus marshallae* and *Pseudocalanus mimus*, large, lipid-rich species that anchor a food chain having higher bioenergetic content than the “warm water community” dominated by small-sized, lipid-poor species such as *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus* spp., and *Calanus pacificus* (Peterson and Keister, 2003).

Horizontal transport was suggested as the process linking the PDO with coastal ecosystem structure in the Northern California Current (Peterson and Hooff, 2005; Hooff and Peterson, 2006). In a modeling study, Keister et al. (2011) showed that northward and onshore transport of warmer waters during the positive phases of the PDO introduced smaller, subtropical copepods to the shelf waters off central Oregon (Figure 4; see also Di Lorenzo et al., 2013, in this issue). Conversely, during negative phases of the PDO, strong equatorward currents led to copepod communities dominated by subarctic species. Consistent with the model results, geostrophic currents estimated from satellite altimeter and coastal sea level (tide gauge) data showed that alongshore currents and the biomass of the cold neritic copepods (*Pseudocalanus*

mimus, *Calanus marshallae*, and *Acartia longiremis*) exhibited a strong seasonal pattern that fluctuated in opposite phase: strong northward currents lead to low biomass of these species in winter and strong southward currents lead to high biomass in summer; moreover, coldwater copepod biomass variation at monthly to annual time scales was related to cumulative alongshore transport patterns forced by the PDO (Bi et al., 2011).

Chelton et al. (1982) examined zooplankton biomass in the California Current prior to recognition of the PDO influence and the availability of sophisticated circulation models, satellite altimeters, and data on zooplankton species composition. Using CalCOFI (California Cooperative Oceanic Fisheries Investigations) data (1950–1979), they showed that increased southward transport (as indexed by sea

level height) led to higher zooplankton biomass, whereas reduced southward transport was accompanied by decreases in zooplankton biomass. Roemmich and McGowan (1995) suggested that the cause of the decline in zooplankton biomass in the southern California Current in the 1980s and early 1990s was a northward shift in the location of the bifurcation of the North Pacific Current, resulting in more subtropical water being imported into the Northern California Current. Subsequent re-examination revealed that the decline in zooplankton biomass reported by Roemmich and McGowan was largely due to the decline in the California Current over time in the biomass of one particular group of zooplankton, the pelagic tunicates (Lavaniegos and Ohman, 2003).

A difference between these historical studies and the recent GLOBEC results is the use of data on copepod species composition, not biomass, to deduce differences in transport. Temporal variations in zooplankton biomass are much stronger and responsible processes more easily understood when examined on species-specific basis. The recent studies

of the California Current system illustrate how patterns based on individual species are explained by local water masses and lead to mechanistic explanations (through transport processes) that may enable skillful predictions about patterns and bioenergetic implications at multiple trophic levels when applied to future climate change scenarios of physical forcing in the California Current.

Euphausia pacifica was also targeted for study in the Northeast Pacific region, research that included laboratory studies of development, growth, and reproduction and field studies of year-to-year variations in distribution, abundance, egg production, and growth. Adult female *E. pacifica* incubated for one to two days following capture produced ~ 150 eggs per brood on average (Gómez-Gutierrez et al., 2006). Adult growth rates averaged 0.02 mm d⁻¹ during summer upwelling season and 0.01 mm d⁻¹ during winter (Shaw et al., 2010). Negative growth occurred in some individuals during winter, most likely related to poor feeding conditions, and during the summer upwelling season, when investment of energy

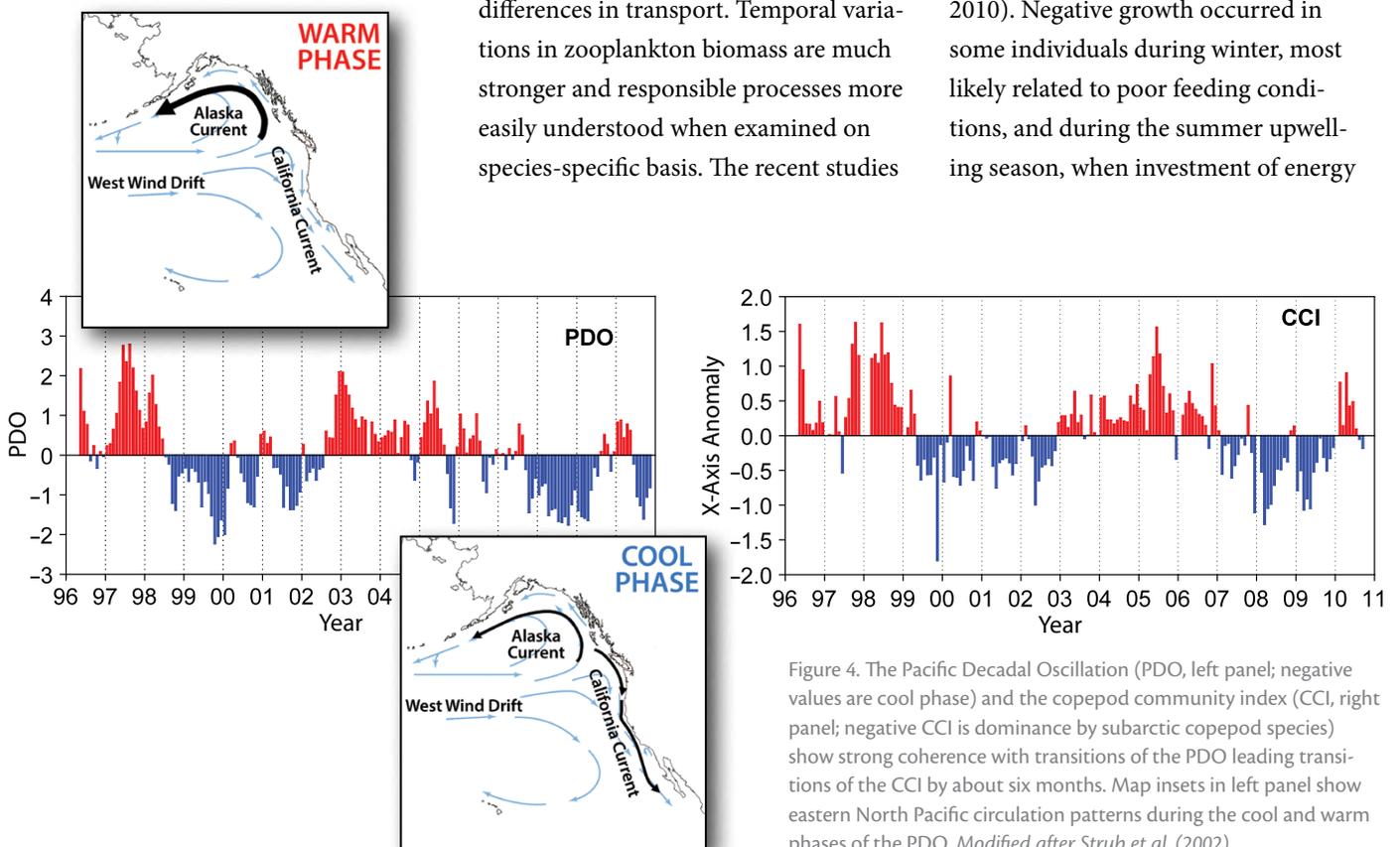


Figure 4. The Pacific Decadal Oscillation (PDO, left panel; negative values are cool phase) and the copepod community index (CCI, right panel; negative CCI is dominance by subarctic copepod species) show strong coherence with transitions of the PDO leading transitions of the CCI by about six months. Map insets in left panel show eastern North Pacific circulation patterns during the cool and warm phases of the PDO. Modified after Strub et al. (2002)

went into reproduction rather than somatic growth. Seasonal growth rates of *E. pacifica* from short-term incubations were similar to cohort analysis estimates from the Oregon shelf (e.g., Smiles and Percy, 1971). These results were complemented by observations of ontogenetic behavioral differences in diel vertical migration, and modeling of cross- and along-shelf transport of eggs, larvae, and adults (Dorman et al., 2011; Lindsey and Batchelder, 2011; Lindsey, 2014).

THE IMPORTANCE OF WINTER CONDITIONS TO ZOOPLANKTON DYNAMICS

The Southern Ocean GLOBEC program, a priori, focused on winter conditions and mechanisms that permitted the dominant zooplankton of the system, *Euphausia superba*, to survive the extended (~ 4 month) period of near-continuous darkness and low food. A new finding was that wintertime conditions in three other regional US GLOBEC studies in the California Current, the coastal Gulf of Alaska, and the Northwest Atlantic had significant and important effects that primed the systems for greater zooplankton population abundance and productivity the following spring-summer. During winter in the higher latitude Gulf of Alaska, wind stress curl-driven Ekman upwelling transported nutrients into surface waters, but because winter phytoplankton production is light limited, the nutrients remained available in the surface layers to enhance phytoplankton (and zooplankton) concentrations only during the ensuing spring bloom when light was not limiting (Fiechter and Moore, 2009). In the California Current and Northwest Atlantic, the wintertime priming occurred due to enhanced off-season phytoplankton and zooplankton

production (Durbin et al., 1997, 2003; Feinberg et al., 2010).

Wind-driven coastal upwelling of nutrients supports primary production in the California Current (Checkley and Barth, 2009). In the Northern California Current (Oregon), production is concentrated in spring and summer when upwelling-favorable winds dominate, and both nutrients and light are favorable for phytoplankton growth. Indeed, the conventional view that production depends almost entirely upon local coastal upwelling processes during the so-called “upwelling season” is reflected in the design of GLOBEC (Batchelder et al., 2002) and other large interdisciplinary studies of ecosystem processes and productivity in the California Current (Barth and Wheeler, 2005; Largier et al., 2006). While the upwelling season is without question important, production events outside of the conventional upwelling season may have disproportionate influence on ecosystem dynamics. One such period occurs on the Oregon shelf during early winter (January), when *Neocalanus* spp. and *Calanus marshallae* awaken from diapause (Liu and Peterson, 2010), resulting in a rapid two- to fivefold increase in copepod biomass in surface waters. Another production window is late winter (anytime between late January and early March), when intermittent calm winds and clear skies allow diatoms to bloom in response to increased stratification, light, and sufficient nutrients. While these ephemeral early bloom events are minor compared to spring-summer coastal upwelling blooms (Legaard and Thomas, 2006), the early diatom production nonetheless fuels elevated egg production by *C. marshallae* and *C. pacificus* and an early burst of egg production by the coastal euphausiid, *Thysanoessa*

spinifera (Feinberg et al., 2010). Years with an early diatom bloom produce a cohort of *T. spinifera* that matures in July when it becomes an important prey for juvenile salmon and other planktivores. If there is no winter bloom, there is no early cohort and reduced biomass of *T. spinifera* in summer.

Other California Current studies have identified statistical relationships between ocean conditions during the winter months and population dynamics, including North Pacific krill *Euphausia pacifica* survival (Dorman et al., 2011), rockfish growth (Black et al., 2010, 2011) and recruitment (Laidig, 2010), and initiation of seabird nesting (Schroeder et al., 2009) in regions south of the Northern California Current. Winter phytoplankton blooms may also affect survival and recruitment of winter spawners of commercially important living marine resources, such as Dungeness crabs, sablefish, and Dover sole. Productivity in winter can set the stage for better than average recruitment of spring spawning fishes by “preconditioning” the ocean, an idea suggested by Logerwell et al. (2003) with respect to ocean conditions experienced by salmon when they first enter the sea in April and May. Preconditioning is also important for several California Current resident fishes, such as Pacific whiting (*Merluccius productus*) and Pacific sardines (*Sardinops sagax*), that spawn in the relatively quiescent waters off southern California during winter, but migrate to the Northern California Current in spring to feed upon krill and juvenile fishes that are part of a food chain supported by lipid-rich boreal copepods. Several highly migratory species, including apex predators, make extensive use of the California Current seasonally for foraging (Block et al., 2011).

Late autumn or early winter blooms of phytoplankton in the Gulf of Maine allow both early reproduction of *Calanus finmarchicus* and higher growth and reproduction of small copepods through the winter, providing a larger seed population that could provide the colonizers for downstream regions, such as Georges Bank, which depend on annual resupply from the Gulf of Maine (Durbin et al., 1997, 2003; Miller et al., 1998). The fall-winter changes in phytoplankton production have also been hypothesized to impact subsequent reproduction by cod and haddock (Friedland et al., 2008).

ZOOPLANKTON AND LARVAL FISH

While this paper's emphasis is on the physical and ecological processes that impact holozooplankton population dynamics, similar processes impact the planktonic eggs and larvae of fish and benthic invertebrates. However, life-history differences between holozooplankton (organisms that are planktonic for their entire life cycles) and meroplankton (organisms that are planktonic for only a part of their life cycles) determine how populations respond to environmental change/variability. Longer adult life spans, larger size, and motility (of fish and some benthos) confer enhanced resilience to shorter-term environmental perturbations and, perhaps, higher probability of eventual reproductive success. Understanding the physical forcing and processes that control the abundance and distribution of zooplankton is fundamental to understanding the growth and survival of larval fish that rely on zooplankton prey (Buckley and Durbin, 2006; Castonguay et al., 2008). There is strong evidence that growth, survival, and transport of larval stages of fish and benthos are important in

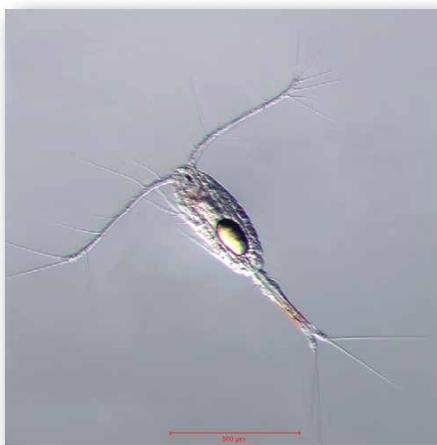
determining interannual and longer-term variations in population growth, with implications for management of these resources. Thus, conclusions derived from zooplankton studies may apply also to the larval stages of fish, such as the cod and haddock that were targeted in the Northwest Atlantic studies.

Survival through the early life-history stages of marine fish is high only when the combination of losses from adverse transport, inadequate prey (abundance or type), and predation are all simultaneously low. Here, we discuss two examples, Atlantic cod and Pacific salmon, where GLOBEC research was able to identify mechanisms linking zooplankton populations directly to fish population responses.

In the Northwest Atlantic GLOBEC program, hydrodynamic and trophodynamic processes were related to growth and survival of larvae of Atlantic cod and haddock using field observations, experiments, and models (Werner et al., 1996, 2001; Mountain et al.,

2003, 2008; Kristiansen et al., 2009). Individual-based modeling, often linked with physical and/or ecosystem models, is a common approach for investigating the importance of advection, starvation, and predation on survival of larval fish (Peck and Hufnagel, 2012). Cod and haddock larvae in the Northwest Atlantic rely extensively on zooplankton (especially copepods) as prey (Broughton and Lough, 2010), and larval survival is positively related to the abundance of suitable zooplankton prey (Buckley and Durbin, 2006; Mountain et al., 2008). Mountain et al. (2008) linked egg mortality to wind-driven Ekman (e.g., transport) losses from Georges Bank, which has also been shown using coupled trophodynamics-transport models (Werner et al., 2001).

In the Northern California Current, salmon survival and climate are linked through zooplankton transport and population dynamics. Francis and Hare (1994) and Mantua et al. (1997) showed that salmon survival was correlated with shifts in the North Pacific Index and the PDO, respectively, but neither suggested a mechanism for this correlation. Peterson and Schwing (2003) correlated salmon survival with the biomass of "cold water copepods," which was later extended to show that salmon survival was highly correlated with both the



(above) *Oithona similis*, an abundant small copepod. (right) *Metridia pacifica* adult female (total length ca. 2.7 mm), common in the Gulf of Alaska, from the Northeast Pacific. Photos by Russ Hopcroft, University of Alaska Fairbanks



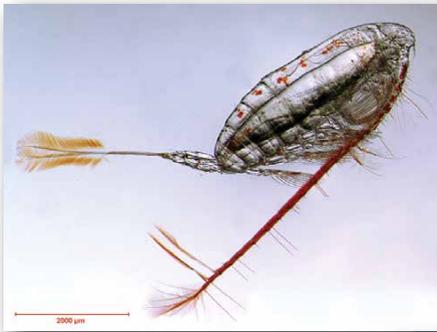
biomass of cold water copepods and alongshore transport (Bi et al., 2011). Thus, the mechanism that links the PDO with salmon survival and productivity operates through transport influences on species composition and the productivity of the zooplankton base that sustains higher trophic levels—for example, the growth of juvenile salmon during their first summer-fall after ocean entry in the Northern California Current. Specifically, when the PDO is in a persistent phase, there is a chain of events that leads to either good (–PDO) or poor (+PDO) ocean conditions. When the PDO is persistently negative, waters that upwell are cold, salty, have higher nutrient content, and exhibit greater influx of subarctic waters, whereas when the PDO is positive, a subtropical water type dominates shelf waters in the Northern California Current (Chhak et al., 2009; Di Lorenzo et al., 2013, in this issue). The result is a food web dominated by large, lipid-rich, subarctic copepods when the PDO is negative and small, lipid-poor,

subtropical copepods when the PDO is positive. The more lipid-rich base of the food web during negative PDO, illustrated by the copepods, provides a better feeding environment for euphausiids and anchovy, which are fed upon by salmon, yielding faster growth, higher survival, and larger-sized fish that are more likely to survive their first winter at sea than salmon during positive PDO (Beamish and Mahnken, 2001).

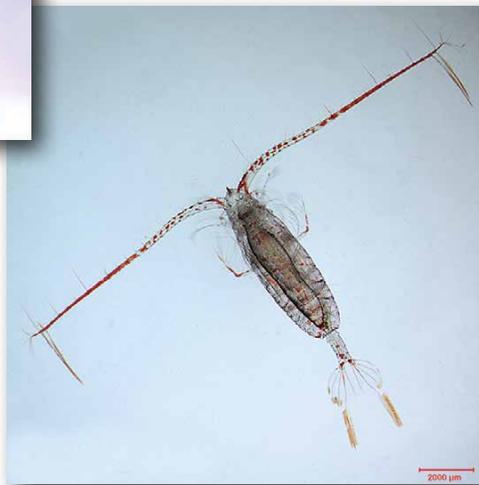
THE GLOBEC LEGACY AND FUTURE NEEDS

US GLOBEC provided new insights about the influence of climate or environmental change and variability on coastal zooplankton species in selected regional ecosystems. Specific species were targeted in each region for intensive study based on a priori knowledge or assumptions about their roles and importance to the marine ecosystem. In the California Current, the zooplankton focus was on two species of krill, *Euphausia pacifica* and *Thysanoessa spinifera*, and a few of the dominant copepod species. In the Northwest Atlantic and Georges Bank system, the focus was on *Calanus finmarchicus* and *Pseudocalanus* spp., with some attention

directed to *Centropages typicus* and other species. In the coastal Gulf of Alaska, both krill and copepods were targeted (*Euphausia pacifica*; *Thysanoessa longipes*, *Metridia* spp., *Neocalanus*, and others). In the Southern Ocean, the emphasis was mostly on the Antarctic krill *Euphausia superba*, with additional studies on other zooplankton species. While the emphasis was on target species in each regional program, other zooplankton taxa, including microzooplankton in some regions, were also investigated. Understanding the environmental controls on zooplankton vital rates—especially the timing and magnitude of reproduction, growth, life-cycle progression, and mortality that determine their population dynamics, seasonal and spatial distributions, and abundances—was fundamental to the US GLOBEC regional studies. US GLOBEC scientists were fortunate that significant, strong, climate-related forcing that was traceable through the marine ecosystems occurred during most of their regional studies; however, they had different degrees of success in identifying mechanisms, depending upon their regions. In the Northern California Current, there was a strong El Niño during 1997 and 1998 as well as significant variations in low frequency climate forcing (PDO) that resulted in dramatic changes in the coastal ecosystem's structure and productivity. The Northern California Current was the region where mechanisms linking climate variability to juvenile salmon growth and survival were most clear, involving changes in horizontal transport and implications for richness and species composition of the lower trophic food web. The Northwest Atlantic study on Georges Bank showed significant changes in timing and size structure of zooplankton



(above) A biomass dominant copepod in spring in the Gulf of Alaska, *Neocalanus plumchrus*. (right) The largest copepod in the Gulf of Alaska, *Neocalanus cristatus*, fifth copepodite stage. Photos by Russ Hopcroft, University of Alaska Fairbanks



populations and survival of cod and haddock related to surface freshening and changed stratification in the Gulf of Maine due to enhanced low-salinity waters from Arctic ice melt related to the Arctic Oscillation (see Di Lorenzo et al., 2013 in this issue); however, details of the mechanisms linking climate to zooplankton and fish populations are not fully understood. In the Southern Ocean, interannual variability in sea ice timing and extent influenced the timing and magnitude of phytoplankton blooms, which appeared important in determining interannual variability in krill recruitment. As in the Northwest Atlantic, mechanisms were not fully elucidated. The least variability in climate forcing was found in the coastal Gulf of Alaska region; though there was a threefold variation in interannual pink salmon survival, the detailed processes responsible for the variation in survival have not been determined.

US GLOBEC provided many new insights into individual zooplankton taxa beyond those described in this paper. An electronic supplement to this paper provides tables and references for more comprehensive identification of zooplankton publications resulting from US GLOBEC. The improved knowledge of the spatial-temporal abundance and distribution of individual zooplankton taxa, coupled with new information linking higher trophic levels (salmon, cod, haddock, penguins, seals) to their prey, yielded mechanistic descriptions of how climate variation operates through ecological interactions to impact regionally important marine resources. The insights have application to coupled ecological models driven by climate scenario models that generate forecasts of plausible future conditions in these or similar ecosystems. The GLOBEC program fostered progress

in ecosystem observation and analysis along many fronts, including identification of key, lower trophic level species, their ecosystem roles, and knowledge of their life histories. More generally, the new process-level understanding linking physical forcing, prey (zooplankton), and predators (fish) developed by GLOBEC, together with improved regional-scale climate scenario projections, will aid and inform decision makers and communities as they assess, respond, and adapt to the effects of future environmental change.

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