Understanding Climate Control of Fisheries Recruitment in the Eastern Bering Sea

Long-Term Measurements and Process Studies

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ABSTRACT. Alaska's Bering Sea ecosystem is changing rapidly, and the people and animals living in this area must quickly adapt. The US National Oceanic and Atmospheric Administration's Ecosystems and Fisheries-Oceanography Coordinated Investigations program has been monitoring the Bering Sea ecosystem for more than 20 years with a multidisciplinary toolbox of biophysical moorings, ship-based operations, and satellite-tracked drifters. Physical and biological time-series data collected from a series of three-to-seven-year programs have supported foundational ecosystem science and provided great insight into how climate can influence fisheries recruitment. In this article, we highlight the major discoveries made during nearly two decades of observations in the Bering Sea.

INTRODUCTION

The availability of reliable baseline ecosystem data against which to measure change is requisite for understanding the impact of climate on ecosystems. Collection and analysis of long-term time series data are arguably the best available method for detecting ecosystem change. Multidecadal time series reveal the natural variability of marine ecosystems, allowing detection of anomalous events or trends outside the normal range (Sukhotin and Berger, 2013); however, programs designed to collect data over multiple decades in the marine environment are rare, especially programs that focus on high-latitude ecosystems (Wassmann et al., 2011). A variety of recent studies and reviews have advocated greater support for, and expansion of, long-term monitoring programs in the marine environment (e.g., Ducklow et al., 2009; Lindenmayer et al., 2012; McClatchie et al., 2014, in this issue).

The Bering Sea is a dynamic and extraordinarily productive ecosystem that has great economic and cultural value. Commercial fisheries in the Bering Sea supply approximately 40% of the US catch (Wiese et al., 2012). Alaska's coastal communities depend upon its resources for cultural and nutritional subsistence. Major changes hypothesized to be related to climate variability have been observed in the system, including changes in the timing and extent of seasonal sea ice (Stabeno et al., 2012b), unprecedented occurrence of coccolithophore blooms (Vance et al., 1998), shifts in recruitment of groundfish and salmon species (Walther et al., 2002; Grebmeier et al., 2006), massive seabird die-offs (Baduini et al., 2001), and shifts in distribution and abundance of marine mammal species (Kovacs et al., 2011).

The southeastern Bering Sea is an ecotone (a transition area between two biomes, having some characteristics of each) between the sub-Arctic and Arctic biogeographic provinces, where temperature and seasonal sea ice conditions have changed dramatically in recent decades. Climate models predict the Arctic (including the Bering Sea) will become warmer with nearly sea-ice-free summers by 2050 (Wang and Overland, 2009). A simple northward shift in the distribution of Bering Sea species with changing climate is unlikely (Stabeno et al., 2012a); instead, a cascading series of complex, interlinked mechanisms is probable, including disruptions in trophic linkages; changes in community structure; shifts in population demographics mediated by changes in mortality, growth, and reproduction; and shifts in physiology and behavioral responses (Rjinsdorp et al., 2009). Ecosystem effects from regional warming are likely to be exacerbated by decreases in ocean pH, which will make the ocean more acidic and will affect Alaska's coastal communities and our national economy (Mathis et al., 2014). Long-term ecosystem monitoring to enable detection of changes and inform predictions of future change is of paramount importance to sustainable fisheries and resilient communities.

In this paper, we describe data collected and advancements made during a series of three-to-seven-year programs in the Bering Sea that focused on recruitment processes and environmental conditions that influenced recruitment. These multidisciplinary programs have provided baseline ecosystem understanding. Based on this knowledge, a variety of interdisciplinary research efforts are continuing to develop more focused, hypothesis-based investigations and process studies.

Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) is a joint research program between the US National Oceanic and Atmospheric Administration/Pacific Marine Environmental Laboratory (NOAA/PMEL) and the NOAA/Alaska Fisheries Science Center (http://www.pmel.noaa.gov/foci). Its mission is to understand the dynamic relationships among climate, fisheries, and the marine environment to ensure sustainability of Alaskan living marine resources and healthy ecosystems. Acting as an umbrella program, EcoFOCI encompasses the original Fisheries-Oceanography Coordinated Investigations (FOCI) program, initiated in 1984, that concentrated research effort on the walleye pollock (*Gadus chalcogrammus*[1]) fishery in Shelikof Strait, Gulf of Alaska, and the more recent, complementary North Pacific Climate Regimes and Ecosystem Productivity (NPCREP; http://www.pmel.noaa.gov/foci/NPCREP) program, initiated in 2004 (see Box 1). NPCREP investigates the impacts of climate on ecosystem dynamics in both the Bering Sea and the Gulf of Alaska. An integral part of both of these programs has been the commitment to, and persistence of, collecting long-term abiotic and biotic

[1] The Latin name for walleye pollock was formerly *Theragra chalcogramma*.

Box 1. EcoFOCI Timeline

EcoFOCI (Ecosystems and Fisheries-Oceanography Coordinated Investigations) has a long history of overlapping research initiatives that have helped guide research in the Bering Sea. The program (originally called FOCI) began its work in the Bering Sea with a seven-year effort funded by NOAA's Coastal Ocean Program: Bering Sea FOCI (1991–1997). The project goals were to: (1) determine stock structure in the Bering Sea and its relationship to physical oceanography, and (2) examine recruitment processes in the eastern Bering Sea (Macklin, 1998). To accomplish these goals, 20 research cruises were completed; three long-term biophysical mooring sites were established, of which two are still maintained; over 40 satellite-tracked drifters were deployed; and aircraft measurements were made of ocean surface color and temperature.

From 1996–2002, EcoFOCI participated in another coastal ocean program, the Southeast Bering Sea Carrying Capacity (SEBSCC) study, which investigated the marine ecosystem of the middle and outer shelves of the southeastern Bering Sea. The goals of this program were to: (1) understand the changing physical environment and its relationship to the biota of the region, (2) relate that understanding to natural variations in year-class strength of walleye pollock, and (3) improve the flow of ecosystem information to fishery managers. Specifically, the study focused on four questions: (1) how does climate variability influence the marine ecosystem of the Bering Sea, (2) what determines the timing, amount, and fate of primary and secondary production, (3) how do oceanographic conditions on the shelf influence distributions of fish and other species, and (4) what limits the growth of fish populations on the eastern Bering Sea shelf? A complementary program, the Inner Front Study supported by the National Science Foundation and conducted with participation by several EcoFOCI scientists, asked similar questions on the inner and middle shelves (1997–2000).

In 2004, NOAA's North Pacific Climate Regimes and Ecosystem Productivity (NPCREP) program, part of the National Marine Fisheries Service Climate and Ecosystems Initiative, began supporting EcoFOCI research in the Bering Sea. NPCREP has two long-term goals: (1) observe, understand, and predict relationships between climate and ecosystems, and (2) help society plan for and mitigate potential impacts of climate change on our marine resources. More specifically, NPCREP helped to support our Bering Sea observation system of moorings and ship-based observations as well as dissemination of the data collected to our stakeholders. In addition, there were studies to develop tools for synthesizing a large number of indices or metrics into a few that could be reported annually (http://www.pmel.noaa.gov/foci/NPCREP/pdfDocs/EBSsynthesisMtgRpt08032010.pdf), and there were specific process-oriented studies such as ice-edge ecosystem investigations.

The Bering Sea Project was a six-year (2007–2012) multidisciplinary effort to understand the impacts of climate change and dynamic sea ice cover on the eastern Bering Sea ecosystem. The leading programs within this project were the National Science Foundation's Bering Ecosystem Study (BEST) and the North Pacific Research Board's Bering Sea Integrated Ecosystem Research Program (BSIERP). The project included more than 100 collaborating scientists from federal and state government and academia. This extremely successful program resulted in over 120 journal articles, including four special issues, leading to major new understanding of the Bering Sea ecosystem. Its success can be partly attributed to the availability of historical measurements previously taken by FOCI and NPCREP, which placed short-term BEST-BSIERP observations in decadal context and permitted crucial comparisons between warm (2001–2005) and cold year dynamics (2007–2012).

Recent efforts (2013–present) focus on a cross-program, multidisciplinary endeavor, the Recruitment Processes Alliance, that integrates biennial fisheries oceanographic surveys of the Southeast Bering Sea shelf with laboratory studies and trophic and biophysical modeling to determine the impact of climate and ecosystem function on recruitment of walleye pollock, Pacific cod, arrowtooth flounder, and selected salmonid species by focusing on factors influencing the first year of life. The Alliance incorporates the expertise and talents of members of the Alaska Fisheries Science Center's Ecosystem Monitoring and Assessment, Resource Ecology and Ecosystem Modeling, and Marine Acoustics and Conservation Engineering groups. The Alliance takes a bottom-up approach, designing studies based on the hypothesis that climate change and variability have predictable effects on mechanisms that regulate fisheries recruitment in Alaska through conditions and events that occur during the early life histories of the target species. The Alliance continues the time series of field observations begun by EcoFOCI and brings continued inquiry, investigation, monitoring, and research to the highly dynamic and, in the face of climate change, mutable Bering Sea ecosystem.

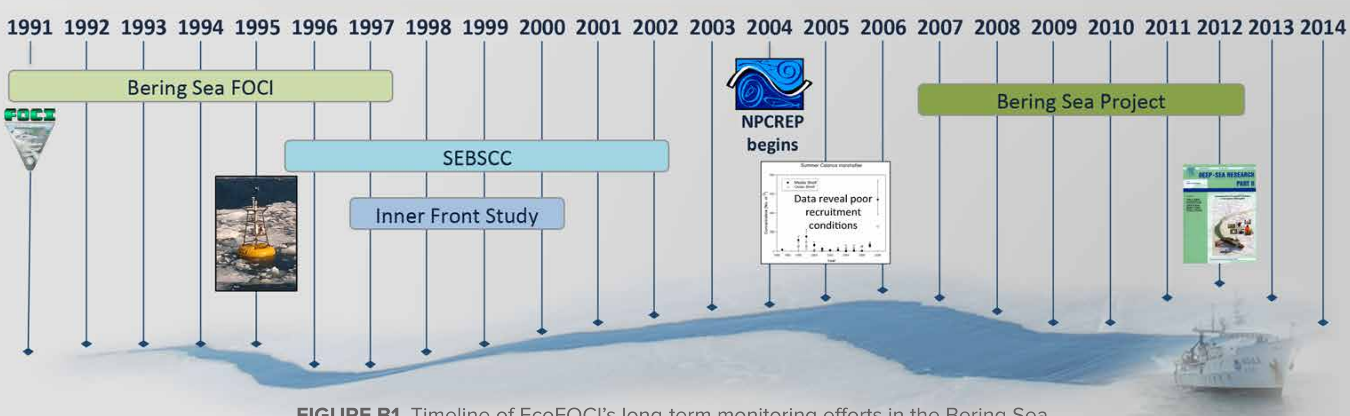

FIGURE B1. Timeline of EcoFOCI's long-term monitoring efforts in the Bering Sea.

observations using an intricate network of year-round surface and subsurface moorings as well as multiple research cruises each year.

During the past two decades, EcoFOCI has participated in a succession of multidisciplinary and highly productive shorter-term programs that have built upon its historical time-series measurements (see Box 1). These NOAA-sponsored, short-term programs were essential to placing recent observations into historical context.

Long-Term Measurement Tools

EcoFOCI scientists monitor the status of and trends in the eastern Bering Sea by collecting physical and biological data using several different methods: continuous measurements from moorings at fixed locations over the middle shelf; occupation of transect stations along latitudinal (70 m isobath) and longitudinal (cross-shelf) survey lines; satellite-tracked drifters; and dedicated fisheries surveys using a fixed station grid. Other opportunistic sampling approaches supplement these four methods, including use of depth-discrete measurements, remotely operated vehicles, satellites, underwater cameras, benthic samplers, and acoustics.

An EcoFOCI array of four long-term biophysical moorings (M2, M4, M5, and M8) is positioned along the 70 m isobath of the eastern Bering Sea shelf (Figure 1). These moorings provide year-round measurements of temperature, salinity, chlorophyll (fluorescence), and currents (Figure 2). In addition, the M2 mooring, which was deployed for the twentieth consecutive year in 2014, has intermittently hosted acoustic instruments (Tracor Acoustic Profiling System, or TAPS) that record zooplankton size, abundance, and marine mammal vocalizations; nitrate sensors; and pCO_2 instruments to examine ocean acidification. At M2, a surface mooring deployed during spring supports instruments to measure atmospheric variables. This mooring is recovered and replaced with a subsurface mooring each fall to prevent winter sea-ice-related damage to or loss of surface instruments.

EcoFOCI makes seasonal, oceanographic, and plankton ship-based measurements over the Bering Sea shelf and at repeat hydrographic stations along the 70 m isobath. Data collection is most often accomplished during servicing of the moorings in spring (April or May) and fall (September or October). Both the cross-shelf transect lines and the 70 m isobath line are associated with each of the four biophysical moorings (Figure 1; Stabeno et al., 2012a). Water-column measurements of temperature, salinity, oxygen, photosynthetically active radiation, nutrients, and chlorophyll fluorescence are collected by hydrographic (CTD) casts. Zooplankton and ichthyoplankton samples are collected from double-oblique and depth-discrete plankton tows (Napp et al., 2002; Matarese et al., 2003).

EcoFOCI has deployed hundreds of satellite-tracked drifters in the Bering Sea since 1986. Positions of drifters fitted with "holey sock" drogues at 40 m depth are transmitted via satellite using the Argos system. Animations of drifter tracks from all years and all EcoFOCI study areas, including drifters actively transmitting, are available online at http://www.ecofoci.

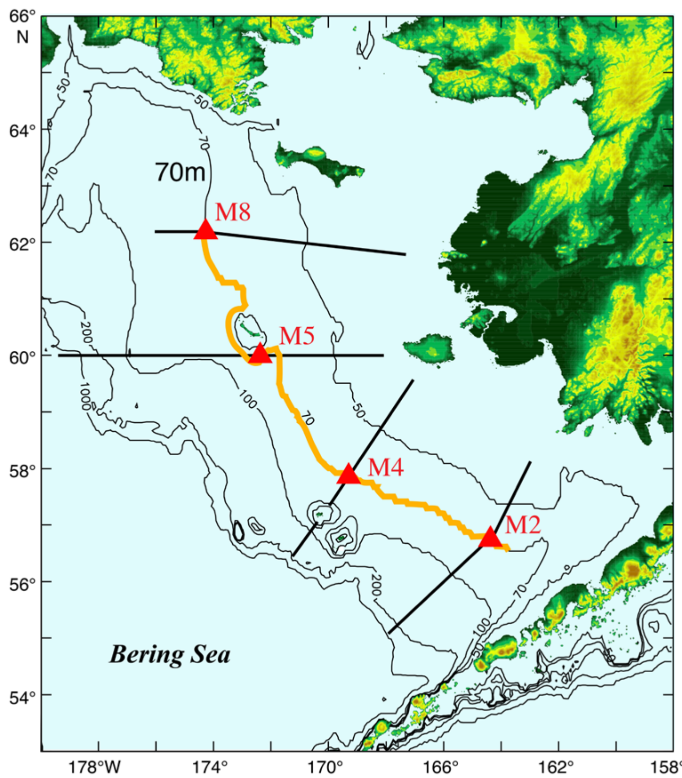

FIGURE 1. Locations of EcoFOCI (Ecosystems & Fisheries-Oceanography Coordinated Investigations; http://www.ecofoci.noaa.gov) moorings (▲) and Bering Sea transects along the 70 m isobath and across the shelf.

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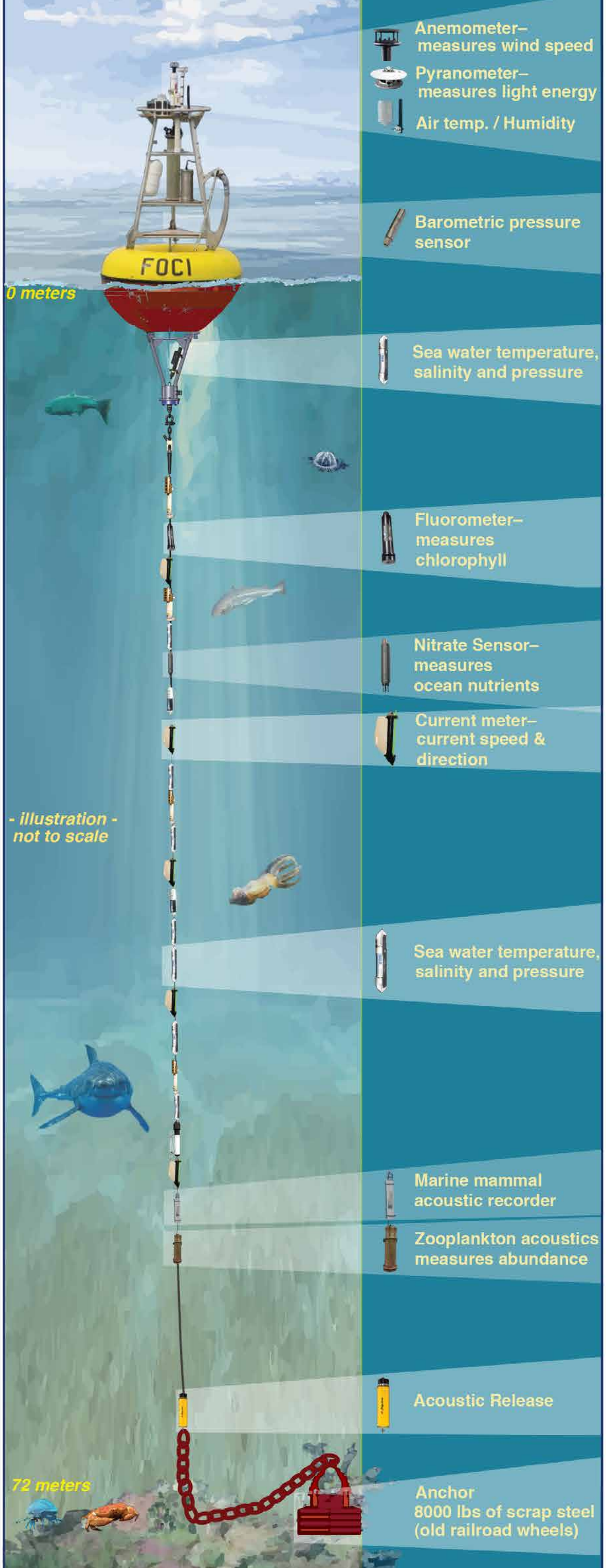

noaa.gov/efoci_drifters.shtml.

EcoFOCI program-led ichthyoplankton and juvenile fish surveys (Figure 3A) and associated physical measurements date from the 1970s (Figure 3B). Sampling methods for biological surveys include plankton tows for ichthyoplankton (fish eggs and larvae) and associated zooplankton in the spring (May), small-mesh trawl net tows for juvenile forage and demersal fishes in the fall (August, September), CTDs, nutrient and chlorophyll sampling, and underway acoustic Doppler current profiler, acoustic, and thermosalinograph measurements (both seasons). Punctuated, ancillary sampling throughout the time series includes depth-discrete MOCNESS (multiple sampling net) collections of fish larvae and zooplankton, satellite-tracked drifter deployments to examine current speed and direction, oxygen and carbon dioxide measurements, and sediment and infaunal prey collections. Surveys now occur biennially (in even years); annual historical data are available on open-access websites (http://access.afsc.noaa.gov/ichthyo/index.php) and upon request (see McClatchie et al., 2014, in this issue).

ADVANCES IN EASTERN BERING SEA SHELF UNDERSTANDING

Climate of the Bering Sea—Invariably Variable

The Bering Sea lies in a transitional area between the cold, dry Arctic and the warmer, high precipitation North Pacific. Historically, the climate of the southeastern Bering Sea shelf was more characteristic of the Arctic, but it shifted in the mid-1970s to a more sub-Arctic climate (Overland and Stabeno, 2004; Wang et al., 2006). Though the long-term trend is toward a warmer climate in the Bering Sea, large interannual variability in temperature is common there. Climate is

FIGURE 2. Biophysical mooring illustrating placement of instruments for measuring temperature, salinity, nitrate, chlorophyll (fluorescence), currents, sea ice, and marine mammal vocalizations.

influenced by both longer-scale decadal patterns such as the Pacific Decadal and Arctic Oscillations and shorter-scale shifts such as the El Niño–Southern Oscillation (Stabeno and Overland, 2001; Overland and Stabeno, 2004; Stabeno et al., 2007).

During nearly 20 years of EcoFOCI observations in this area, Bering Sea climate has shifted from being dominated by high-frequency interannual variability to protracted periods of relatively warm (2000–2005) or cold (2006–2013) conditions defined by ice extent in the southern Bering Sea (Figure 1 in Stabeno et al., 2012b). Predictions indicate that sea ice extent and sea surface temperature in the Bering Sea will continue to be highly variable, though with an overall reduction in spring sea ice extent and delayed development of fall ice over the next 40 years superimposed (Wang et al., 2012). Long-term EcoFOCI observations, including those covering the five-year period of relatively warm conditions in the Bering Sea from 2001–2005, provide key knowledge about how the ecosystem will likely respond to longer periods of reduced sea ice extent and warmer ocean temperatures (e.g., Hunt et al., 2011; Stabeno et al., 2012a; Sigler et al., 2014).

Climate forcing varies between the northern and southern shelves. In the south, reductions in seasonal sea ice are predicted to result in warmer sea temperatures. We have observed that the northern Bering Sea shelf is more resistant to changes than the southern shelf. Winters at ice-covered higher latitudes are invariably dark and consistently cold, while land surrounding the northern shelf results in a more continental climate. Thus, north of ~ 60°N, sea ice is expected to persist into May even with warming, resulting in cold bottom water temperatures (Stabeno et al., 2012a).

Upper Ocean and Sea Ice

During the past 20 years, EcoFOCI scientists have learned much about how physical forcing varies between the northern and southern shelves. The transition zone between these areas occurs at approximately 59–60°N (Stabeno et al., 2012a). This zone is not a static feature, but rather shifts in strength and position with changes in seasonal sea ice, currents, and temperature. The southern shelf is sharply stratified by temperature between a cool/cold bottom layer and a warm upper layer. Stratification on the northern shelf is more gradual and is controlled equally by temperature and salinity. Weaker tides on the northern shelf create a stable layer between the bottom and surface mixed layers, which often supports a subsurface phytoplankton bloom during summer.

In years when sea ice is more extensive in March and April, ocean temperatures stay cooler throughout the summer and fall (Stabeno et al., 2012b). The southern shelf is much warmer in years with reduced ice cover or early (before mid-March) ice retreat. The speed of ice advance in fall/winter is determined primarily by winds and, to a lesser extent, by ocean heat content of the previous summer. Northerly spring winds help maintain sea ice on the southern shelf in cold years, while in warm years, northerly winds are weaker (Stabeno et al., 2012b). In addition, currents on the middle shelf are weaker during summer, and there is stronger offshore flow during winters with extensive ice.

EcoFOCI's biophysical mooring array and ship-based observations provided important foundational data on the hydrography of the southeastern shelf. Initial observations in the Bering Sea helped define hydrographic

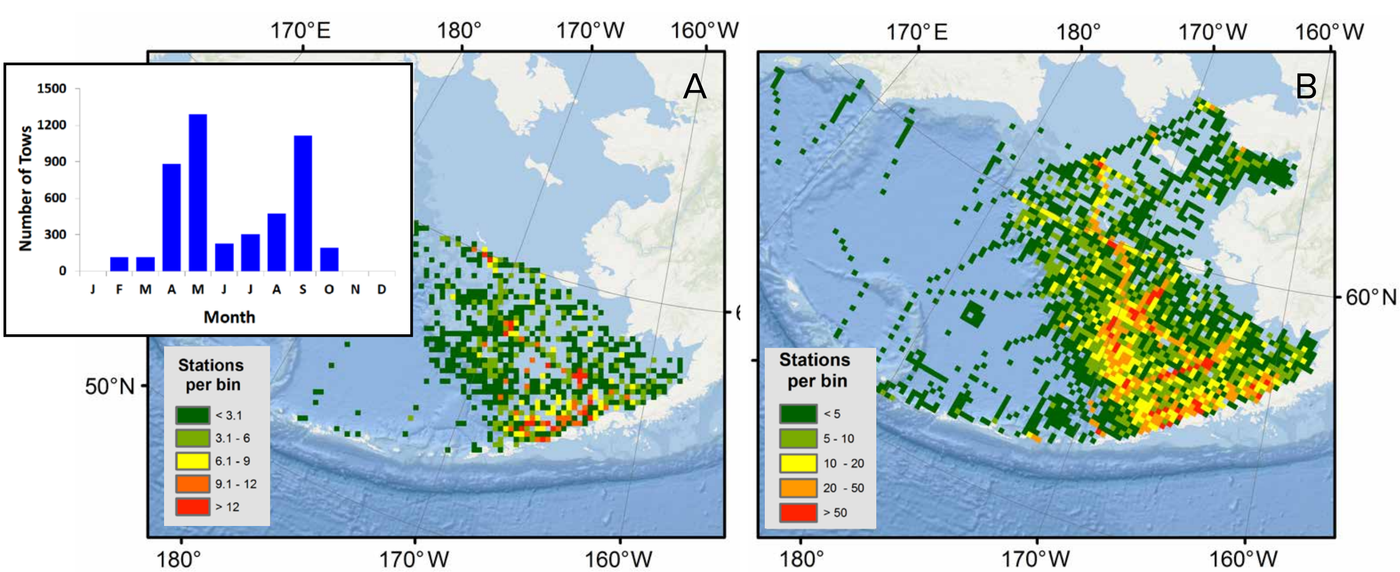

FIGURE 3. (A) Locations of historical (1979–2013) ichthyoplankton sampling conducted by EcoFOCI. Samples are gridded into 20 km^2 areas, and the total number of tows in each bin for 1979–2013 is calculated. Bin values range from three or fewer samples (dark green) to over 12 samples (red). Inset: Temporal distribution and number of combined bongo and Tucker tows (number of tows scaled to 1,500) conducted by the EcoFOCI program in the Bering Sea for the years 1979–2013 by month. (B) Spatial distribution of physical oceanographic sampling for 1975–2014 in the Bering Sea. Stations are binned to 20 km^2 bins. Values range from fewer than five stations per bin (dark green) to bins with more than 50 stations (red).

characteristics and circulation patterns on the shelf, including descriptions of the varying conditions of the coastal (0–50 m depth), middle (50–100 m depth), and outer (100–180 m depth) domains (Coachman, 1986; Stabeno et al., 2001; Kachel et al., 2002).

Variability in seasonal sea ice cover is a major driver of the southeastern Bering Sea ecosystem. The maximum southern extent of sea ice in winter varies annually by more than 100 km (Stabeno et al., 2012b). Sea ice is typically present on the southern shelf from January through March. EcoFOCI's early work during the Inner Front and Southeast Bering Sea Carrying Capacity programs (then, just called FOCI) explored how aerial extent and duration of ice cover affected the timing of the spring bloom and determined extent of the cold pool (Stabeno and Hunt, 2002). In years with extensive sea ice, spring sea surface temperatures were colder, with an early ice-associated phytoplankton bloom, a less saline water column, and summer "cold pool" bottom temperatures of less than 2°C.

During the Inner Front project, FOCI effort focused along the 50 m isobath inner front area, which separates the coastal and middle domains (Kachel et al., 2002). The inner front was associated with a "cold belt" area of low sea surface temperature (< 6.5°C) and near-surface nutrient enrichment facilitated by the interface between these hydrographically disparate domains. This work explained the occurrence of and variability in "cold belts" and described the mechanism by which nutrients could be pumped from the bottom layer of the middle shelf into the euphotic zone.

In the mid-1990s, Bering Sea FOCI moorings provided the first time series from moored instruments during winter and spring, when rapidly advancing spring ice advanced over the surface mooring. These data revealed the importance of advection of warmer, lower-salinity water to establishing vertical structure and replenishing the nutrients needed to fuel spring phytoplankton blooms on the middle shelf, and revealed the occurrence of an under-ice phytoplankton bloom (Stabeno et al., 1998). Also, data collected from the Bering Sea FOCI project led to better understanding of the physical drivers, characteristics, and ecosystem implications of the cold pool—an area where bottom temperatures remain below 2°C throughout the summer. The extent of the cold pool was discovered to be highly variable year to year and positively associated with extent of sea ice in March and April (Stabeno et al., 2001). The cold pool creates a thermal barrier and/or refugia for temperature-sensitive species (e.g., Ciannelli and Bailey, 2005; Hollowed et al., 2012; Stabeno et al., 2012a).

Building on 10 years of nearly continuous observations, the oscillating control hypothesis (Hunt et al., 2002) proposed that walleye pollock recruitment in the Bering Sea ecosystem alternates between bottom-up control during cold regimes, when energy flows into benthic communities, and top-down control during warm regimes, when more energy flows into pelagic communities. This hypothesis was adapted a decade later to incorporate continued long-term observations gained from the Bering Sea Project and new insight into how bottom-up effects of prolonged warm periods weaken pollock recruitment (Coyle et al., 2011; Hunt et al., 2011).

Nutrients and Primary Production—Timing Is Everything

Spring blooms are a major driver of ecosystem productivity in the Bering Sea, setting the stage for energy flow throughout the food web. The broad expanse (~ 500 km wide) of the Bering Sea shelf has raised the question: how are nutrients replenished across this shelf to support high levels of primary production? To address this question, EcoFOCI work continues to explore the effects of eddies, canyons, and irregular bathymetry on shelf-slope exchange of salts and nutrients (Stabeno et al., 1999). We found that these processes influence nutrient levels mainly on the outer shelf and on parts of the middle shelf, but do not extend over the inner shelf (Mordy et al., 2010; Granger et al., 2013). Even in winter, when storm energy mixes the water column, injects deep nutrients into surface waters, and increases the transport of nutrients and salt over the shelf, nutrient replenishment over the shelf remains incomplete. During winter, ~ 50% of nutrients at M2 are replenished from slope waters (recent work of author Stabeno and colleagues), and on the inner shelf, only ~ 5% of nutrients are derived from the slope (Granger et al., 2013). So as winter turns to spring, the following conditions generally prevail as shelf waters prepare to bloom: ice covers the northern shelf while ice extent in the south varies from year to year, the water column inshore of ~ 90 m is well mixed, there are strong cross-shelf gradients in salt and nutrients, and nutrient concentrations are especially low on the inner shelf (Figure 4). Prior to ice retreat, algal production is evident within the sea ice, and these organisms may seed production within the water column.

The decades-long M2 time series has allowed us to unravel links between physical forcing (ice and winds) and spring water column primary production. On the southern shelf, timing of the spring phytoplankton bloom (algae not associated with the sea ice) is highly variable and depends largely upon the presence or absence of sea ice after mid-March (Sigler et al., 2014). The presence of ice after mid-March results in a bloom that is associated with ice melt and retreat (April–May). Otherwise, if ice is absent or there is an early ice retreat, the bloom is delayed until the water column begins to thermally stratify (late May to early June). During the spring bloom, depletion of nutrients in the upper water column can be abrupt, occurring in some years within ~ 5–10 days (Stabeno et al., 2010).

In summer, strong vertical gradients in temperature, salinity, and nutrients combine with persistent horizontal gradients in the deeper water to increase the oceanographic complexity on the shelf (Figure 4). Along the slope, nutrients are continually supplied to the upper water column and support the highest production rates observed in the Bering Sea—the "Green Belt" (Springer et al., 1996). On the shelf, nutrients beneath the euphotic zone may also be injected and sustain production along the inner front (Kachel et al., 2002).

Over the middle shelf in summer, nutrients are depleted in the upper mixed layer, and the strong two-layer system greatly impedes mixing of nutrients into the upper water column. In addition, ammonium accumulates in the bottom layer of the middle shelf upon decay of organic biomass and is evident in intermediate waters on the outer shelf and slope (Mordy et al., 2008). On the northern middle shelf, the 1% light level often resides below the pycnocline (Stabeno et al., 2012a), and in these deeper waters, we have observed oxygen supersaturation coincident with high phytoplankton biomass, suggesting active photosynthesis in the deeper water column (Mordy et al., 2012). Strong wind mixing events inject pulses of nutrients into the euphotic zone, resulting in short periods of production (Stabeno et al., 2010; Mordy et al., 2012; Eisner et al., 2014). Some wind events result in blooms that can upset the entire ecosystem. One such example occurred in 1997, when strong May storms gave way to light winds and a very shallow mixed layer (Bond and Overland, 2005). This resulted in nutrient depletion through most of the water column (including the bottom layer) and a bloom of *coccolithophores*, small unicellular plants that are not usually abundant in the Bering Sea (Stockwell et al., 2001). In this instance, the coccolithophore bloom altered water column visibility and food availability to the short-tailed shearwater, resulting in a major die-off (Napp and Hunt, 2001; Hunt et al., 2002).

Bering Sea FOCI efforts built upon work accomplished in the Processes and Resources of the Bering Sea Shelf (PROBES) study (Sambrotto et al., 1986) to link phytoplankton dynamics over the shelf and slope to pollock prey densities (Napp et al., 2000). This FOCI work highlighted the importance of advection and eddies to phytoplankton blooms in the oceanic region as well as to under-ice phytoplankton blooms and in situ processes on the shelf (Stabeno et al., 1998; Napp et al., 2000).

Zooplankton—Changes in Biomass and Community Structure

Zooplankton biomass and community structure are very sensitive to warm and cold oscillation cycles in the eastern Bering Sea. Previous work focused on cross-shelf patterns in community structure and biomass (e.g., Cooney and Coyle, 1982; Napp et al., 2002); continued EcoFOCI observations in the 1990s and 2000s revealed north-south and warm-cold patterns in the distribution, abundance, and community composition of zooplankton over the middle shelf (Stabeno et al., 2012a,b). One "large" crustacean zooplankter *Calanus* spp. was found to be more abundant in the southeast during cold years with greater southerly ice extent (Baier and Napp, 2003). Work along the 70 m isobath helped to demonstrate lower biomass of large crustacean zooplankton and strong north-south differences in community structure in warm years (Stabeno et al., 2010). Expansion to other domains sampled during the 2000s by the Bering-Aleutian Salmon International Survey (BASIS) program (http://www.afsc.noaa.gov/ABL/MESA/mesa_basis.php) helped to develop the picture of fluctuations in biomass and community composition in warm and cold years (Coyle et al., 2008; Eisner et al., 2014) and to refine the oscillating control hypothesis (Hunt et al., 2011).

Sea ice extent in the southeastern Bering Sea has a large influence on zooplankton biomass and community structure. Multiyear periods of cold or warm conditions are important factors controlling the persistence of certain zooplankton species distributions in the Bering Sea. In recent years, cold conditions have resulted in higher middle-shelf biomass of large crustacean species,

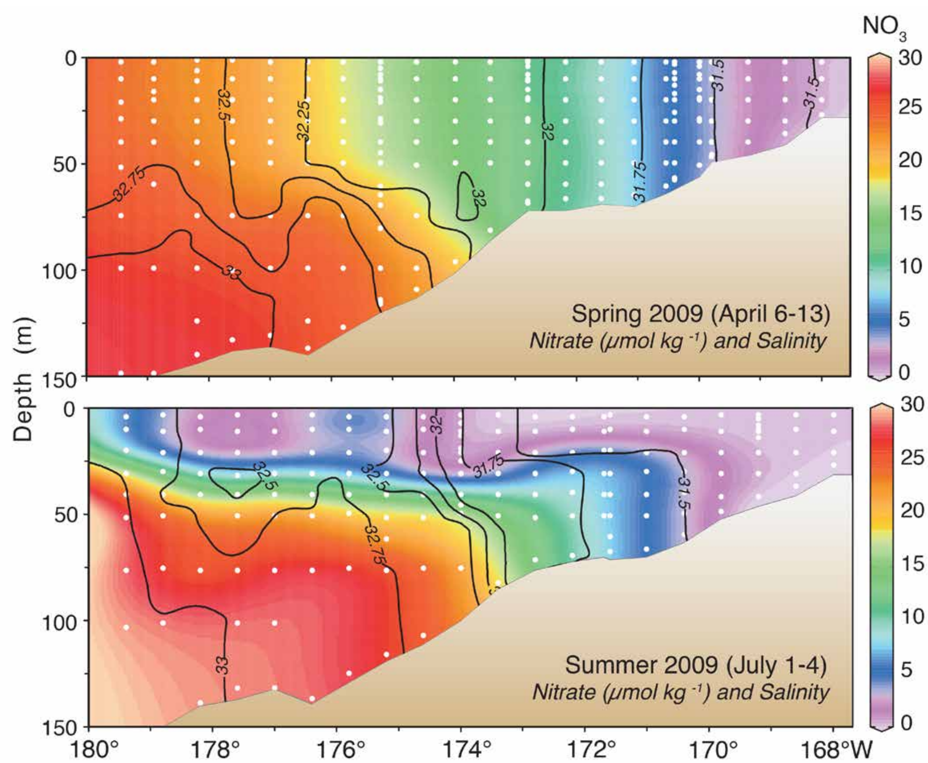

FIGURE 4. Hydrographic sections (white dots indicate sampling stations) of nitrate and salinity along the 60°N hydrographic line during spring (top) and summer (bottom). Data were used to extrapolate nitrate (color bar in µmol kg^{-1}) and salinity (contours).

such as *Calanus* spp. and the euphausiid *Thysanoessa raschii*, than occurs in warm years. The chaetognath *Parasagitta elegans* also increased in abundance from warm to cold periods, while the abundance of small jellyfish decreased from warm to cold periods. The biomass of small crustacean copepods is similar in warm and cold years, but there are changes in species dominance from *Oithona* spp. in warm years to *Acartia* spp. and *Pseudocalanus* in cold years. The changes in zooplankton community structure were strongest over the middle shelf, but were evident in all shelf domains and in both the north and the south (Eisner et al., 2014). There were no detectable changes in the species composition of *Pseudocalanus* spp. between warm and cold periods in the southeastern Bering Sea (Lisa De Forest, NOAA Fisheries, *pers. comm.*, 2014).

> "Given their degree of environmental sensitivity, coupled with the rapid response times, multidecadal time series of fish larvae abundances may be key harbingers of environmental change, forewarning of effects of broad-scale perturbations more quickly than animals at higher trophic levels."

Larval Fish Are Timely Indicators of Environmental Change

EcoFOCI has conducted routine, seasonal larval and juvenile fish surveys over the southeastern Bering Sea shelf since the mid 1980s, though opportunistic sampling efforts date from the 1970s (Figure 3A). The two foci of these surveys have been to conduct process-oriented research and to examine changes in the distributions of young walleye pollock. The nearly four decades of observations that span climatological Bering Sea warm and cold regimes (Stabeno et al., 2012b) have contributed to the understanding of how meteorological and oceanographic variability affect the early life ecology and recruitment dynamics of walleye pollock (Napp et al., 2000; Duffy-Anderson et al., in press). The success of this ongoing research is due to overlapping, shorter-term funding initiatives that have made it possible to mount sustained effort over multiple decades; in turn, the long-term observations made possible by those initiatives serve to place short-term results into decadal ecological context.

Most recently, funding through the North Pacific Research Board and the National Science Foundation's Bering Sea Project, a five-year effort to examine the impacts of climate change on the Bering Sea ecosystem with an emphasis on walleye pollock, Pacific cod (*Gadus macrocephalus*), and arrowtooth flounder (*Atheresthes stomias*) enabled an intensive, short-term field project executed during a prolonged cool climate phase. One project objective was to compare ecosystem conditions between warm and cold climate phases, a goal that could not be realized within the short time frame of fieldwork executed solely within a cold ocean phase. As a result of the accumulation of NOAA-supported long-term observations over the eastern Bering Sea slope and shelf that spanned warm and cold phases, including the EcoFOCI survey time series data, critical observations of walleye pollock early life ecology during cold periods could be placed in historical context. These data showed how water temperature contributes to the fishery's variability in distribution, abundance, and recruitment. For example, climate-mediated shifts in spawning locations of adults (Petrik et al., in press) between warm and cold years was hypothesized after exploring spawning data collected from Bering Sea Integrated Ecosystem Research Program (BSIERP) funded studies during cold years and from NOAA-led data collections over earlier warm years. Likewise, research to highlight how differential wind forcing (Danielson et al., 2012) and ocean currents (Stabeno et al., 2012b) act synergistically to affect an eastward shift in the distribution and abundance of eggs, larvae, and juveniles during warm ocean phases (Smart et al., 2012a; Figure 5) relied on extensive time series data stretching back over three decades. Finally, evidence of temperature-dependent shifts in timing of spawning was realized after integrating BSIERP-funded data with EcoFOCI historical data across climate regimes (Smart et al., 2012a).

During the Bering Sea Project, there was a focused investigation of the spatial overlap of larval walleye pollock and their zooplankton prey in one of several major spawning areas (Unimak Bight). Again, it was only through using data collected by previous studies that a comparison between warm and cold years was possible. In this comparison, using six years of data, differences were found in the community structure and abundance of small zooplankton between warm and cold periods. However, the spatial overlap between the centers of distribution of larvae and of potential prey were remarkably similar between warm and cold periods, even though the locations of the centroids varied (Lisa De Forest. NOAA Fisheries, *pers. comm.*, 2014).

Not only are EcoFOCI time series data

invaluable for single-species investigations, they also help to shape our understanding of the interactions between climate and multispecies assemblages. EcoFOCI research shows that fish larvae are sensitive to broad-scale environmental perturbations such as El Niño (Duffy-Anderson et al., 2006), fluctuations in ocean temperature and currents (Siddon et al., 2011), and presence and extent of sea ice (Busby et al., 2014). Moreover, these studies demonstrate that response times are rapid, with changes in community structure evident in as little as one to two years (Boeing and Duffy-Anderson, 2008; Siddon et al., 2011).

Given their degree of environmental sensitivity, coupled with the rapid response times, multidecadal time series of fish larvae abundances may be key harbingers of environmental change, forewarning of effects of broad-scale perturbations more quickly than animals at higher trophic levels. Thus, continued ichthyoplankton monitoring is essential to identifying future changes in the Bering Sea ecosystem.

Juvenile Fish—Factors Affecting Recruitment

Ongoing EcoFOCI research in the Bering Sea has proven valuable in the study of long-term effects of climate on juvenile

Box 2. Walleye Pollock Life History and Importance

Walleye pollock are a sub-Arctic gadid that inhabit the Bering Sea year-round and support one of the largest commercial fisheries in the world (Bailey, 2013). Economic value of the fishery is nearly $350 million, and market value of walleye pollock products is $1 billion. Walleye pollock are not only of significant economic value; they also occupy a key trophic position in the Bering Sea ecosystem, connecting upper and lower trophic levels by serving as predators that consume small forage fishes and zooplankton and as prey for larger piscivorous fishes, seabirds, and marine mammals. Effort to understand recruitment variability in this critical economic and ecologically important species has been a long-standing focus of the EcoFOCI program, resulting in a significant body of work spanning several decades that describes the ecology of this species in the Bering Sea, examining and describing its relationship to the broader ecosystem.

Long-term EcoFOCI observations have contributed to the resolution of at least three major spawning areas for walleye pollock over the Southeast Bering Sea shelf and basin (Hinckley, 1987; Bacheler et al., 2010): Bogoslof Island (spawning February–April), north of Unimak Island and along the Alaska Peninsula (spawning March–April), and around the Pribilof Islands (spawning April–August). Evidence also exists for spawning activity north of the Pribilof Islands (Sandra Neidetcher, NOAA Fisheries, *pers. comm.*, 2014), as well as for a historical spawning aggregation over the Bering Sea basin (Bailey, 2013). Walleye pollock show fidelity to generalized spawning regions. EcoFOCI time series data have been used to resolve temperature-induced spatial shifts within generalized regions as well as phenological shifts in spawning activity as a function of thermal regime (Smart et al., 2012a; Petrik et al., in press). Indeed, temperature significantly influences early life ecology of walleye pollock and is a major force driving interannual variability in abundance of early life stages, explaining more of the variability in egg and larval abundance than zooplankton biomass, adult spawning biomass, winds, currents, or salinity (Smart et al., 2012b).

Bottom-up fluctuations in zooplankton community structure spurred by ocean thermal variability (Eisner et al., 2014) influence young walleye pollock feeding, condition, and growth (Napp et al., 2000). In spring, larvae allocate food energy to morphological development, which improves sensory perception and swimming ability, but by summer energy allocation changes to somatic growth, which maximizes much-needed energy reserves prior to winter onset (Siddon et al., 2013). Evidence of larvae being in poor physiological condition in spring is equivocal (Porter and Bailey, 2011), but the condition of juveniles in autumn is critical to overwinter survival and recruitment to age-1 (Heintz et al., 2013). This new understanding of the importance of feeding and energetics to pre-winter conditioning provides the framework for present and future Recruitment Processes Alliance walleye pollock research. The Recruitment Processes Alliance effort will continue long time series observations and monitoring and will expand focus to include observations and study during winter, a critical time of age-0 mortality that is hypothesized to be a recruitment bottleneck.

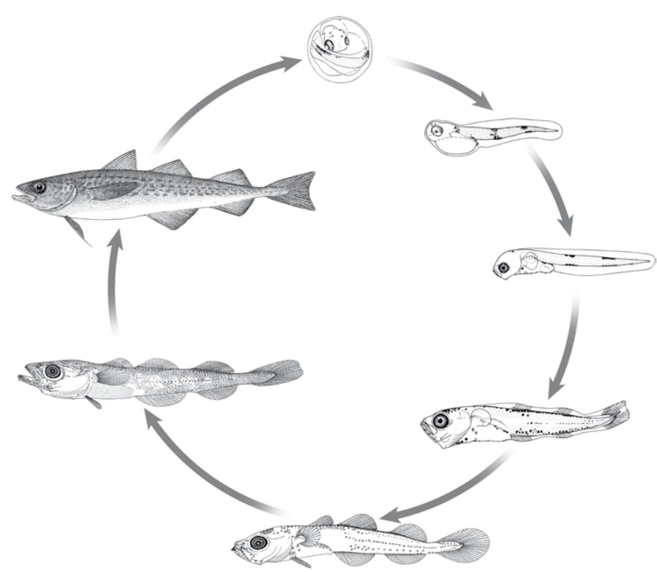

FIGURE B2. Life cycle of walleye pollock (*Gadus chalcogrammus*). Stages shown (starting at top, moving clockwise) are egg (1.5 mm; unpublished data), yolk-sac larva (3.5–5.0 mm SL; Matarese et al., 1989), preflexion larva (5.0–12.0 mm SL), flexion larva (12.0–25.0 mm SL; Dunn and Vinter, 1984), postflexion larvae (26.0–40.0 mm SL), juvenile (40.0–100.0 mm SL; unpublished data), and adult (Mecklenburg et al., 2002). Time for completion of the life cycle is three years. Spawning occurs in early spring (March–April), larvae are present in the water column spring–early summer (April–June), juveniles are present in summer through autumn (July–October), and late juveniles overwinter (November–March) until the following spring when they become age-1 individuals.

fishes. Research on walleye pollock juveniles shows that prey quality and availability relative to juvenile energetic condition influences recruitment as a function of environmental conditions. Climate effects on zooplankton prey field composition (Baier and Napp, 2003; Coyle et al., 2011; Eisner et al., 2014) are correlated with the consumption of high lipid diets among juvenile walleye pollock in cold years (Heintz et al., 2013), and total energy content of age-0 fish is higher during oceanographic cold phases than during warm phases. Further, the energetic status of juvenile walleye pollock in the autumn prior to first winter is a successful predictor of post-winter recruitment (Heintz et al., 2013), suggesting that energy storage in juveniles, and subsequent energy levels, is critical to overwinter survival and recruitment success.

EcoFOCI research has played a role in the development of additional juvenile-centric recruitment hypotheses advanced for other large marine ecosystems that ultimately carried over to Bering Sea research. Bailey (2000) predicted that control of walleye pollock recruitment in the Gulf of Alaska shifted from bottom-up control of abiotic parameters acting on feeding and survival of larvae in spring to top-down control by large piscivorous predators, most notably arrowtooth flounder and Pacific cod feeding on age-0 walleye pollock in summer and autumn. EcoFOCI multidecadal time series data describing the relationship between spring larval survivorship and age-1 recruitment allowed the change in bottleneck to be realized. Ciannelli et al. (2005) took this idea further by recognizing the dynamic interplay of physical and biological forcing factors on walleye pollock, advocating that recruitment variability and abundance would be below average during ecosystem phases characterized by elevated sea surface temperatures and intense predation on juveniles. Though EcoFOCI investigators studying the Gulf of Alaska developed these ideas, they have carried over to understanding the dynamics of the Bering Sea ecosystem. In particular, linked trophic models suggest that predation, both in the form of cannibalism of age-0s and interspecific predation of age-0 walleye pollock by large piscivorous groundfishes, accounted for nearly half of the total mortality of juveniles in the eastern Bering Sea in the 1990s (Aydin et al., 2007).

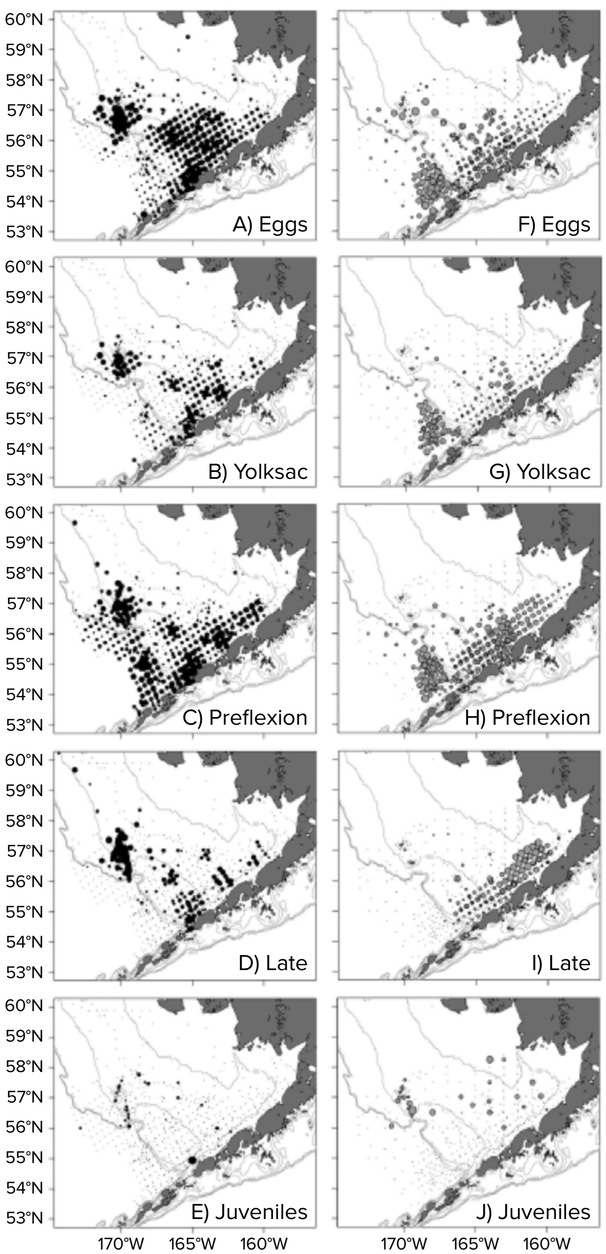

FIGURE 5. Walleye pollock early life stages in the southeastern Bering Sea showing relative abundances of eggs (A,F), yolk-sac larvae (B,G), preflexion larvae (C,H), late larvae with SL of 13.0–25.0 mm (D,I), and juveniles with SL of 26.0–100.0 mm SL (E,J) within cold (A–E) and warm (F–J) temperatures categories. Bubble size is proportional to the largest catch within each stage. SL = standard length, which is measured from the tip of the snout to the posterior end of the fish, but not including the tail fin. See http://access.afsc.noaa.gov/ichthyo/StageDefPage.php for definitions of early life stage terminology. *Figure reprinted from Smart et al. (2012a)*

Work on juveniles of other fish species has benefited from extended observations in the Bering Sea. Collaborative work between EcoFOCI and faculty at the University of Alaska demonstrates that climate variability and the extent of the cold pool limit the availability of inshore nursery areas for settled juvenile northern rock sole (*Lepidopsetta polyxystra*) (Cooper et al., 2014) during cold-year climate periods. This habitat limitation for the earliest settled sizes is significant because habitat availability during the first year of life affects spatial distribution of older juveniles (ages 2 and 3), which is correlated with recruitment to the adult population (Daniel Cooper, NOAA Fisheries, *pers. comm.*, 2014). Work to develop an index of habitat size and availability as a performance indicator, and incorporation of that indicator into the stock assessment for northern rock sole in the Bering Sea, is ongoing (http://www.afsc.noaa.gov/REFM/Docs/2013/BSAIrocksole.pdf).

EcoFOCI-assisted work also shows that recruitment of groundfishes in the eastern Bering Sea is correlated to variations in along-shelf and cross-shelf transport (Vestfals et al., 2014). Specifically, the Bering Slope Current has strong seasonal and interannual variability (Stabeno et al., 2012b; Vestfals et al., 2014), with greatest transport in winter (Ladd, 2014), coinciding with spawning times of several key groundfish species, including arrowtooth flounder, Pacific halibut (*Hippoglossus stenolepis*), Greenland halibut (*Reinhardtius hippoglossoides*), Pacific cod, and walleye pollock. Improved Pacific cod recruitment was correlated with decreased along- and cross-shelf flow, while Pacific halibut recruitment was positively associated with on-shelf transport through submarine canyons.

Finally, recurring EcoFOCI field sampling in the southeastern Bering Sea, conducted synoptically and in collaboration with other programs at the Alaska Fisheries Science Center, helped to determine that coastal nursery habitats along the Alaska Peninsula were essential to the southeastern Bering Sea Pacific cod population, supporting a significant fraction of the age-0 Pacific cod in that system (Hurst et al., in press).

APPLICATIONS AND WAYS FORWARD

Long-term ecosystem research is difficult to accomplish given the short time scales (two to seven years) of many interdisciplinary programs. This hampers an ecosystem-based approach to management of living marine resources (e.g., Livingston et al., 2011). As seen during the recent highly successful Bering Sea project, the timing of individual programs may not allow sampling in more than one ecosystem state (e.g., the Bering Sea project sampled only during a cold period). In the eastern Bering Sea, the EcoFOCI program has had a lead role in building understanding from a decadal perspective using multiple, process-oriented programs. This approach resulted in greatly increased knowledge of the operative mechanisms controlling important ecosystem processes. We are now at the point where we can begin to forecast how different ecosystem states may affect major fisheries (Ianelli et al., 2011; Mueter et al., 2011), which will soon enable us to perform management strategy evaluations for single species and for multiple species complexes (Kirstin Holsmann, University of Washington, *pers. comm.*, 2014).

Our new understanding greatly increases our chances of anticipating and mitigating the potential effects of climate change. Ecosystems, however, are known to have multiple states. Phase transitions in recruitment processes for living marine resources are evident (Duffy-Anderson et al., 2005). The current operative mechanisms for the Bering Sea ecosystem that were revealed only after many years of observation may not be the mechanisms that control the structure and function of the eastern Bering Sea in the future. Thus, continual observation, as proposed in an integrated ecosystem assessment (e.g., Levin et al., 2009), is necessary to ensure that future evaluations have both the current ecosystem (environmental) state and the correct operative mechanisms to make their predictions.

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