

1                                   **An Introduction and Overview of the Bering Sea Project: Volume IV**

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25 **1. Introduction**

26

27 The seasonal rhythm of sea-ice advance and retreat in the eastern Bering Sea (EBS) moves ice  
28 hundreds of kilometers across the broad continental shelf and exerts a powerful influence on the  
29 ecology of these waters. In winter, the combination of latitude, geology, winds, and ocean currents  
30 produces ice cover extending far into the southern Bering Sea. In the spring and summer, retreating  
31 ice, longer daylight hours, and nutrient-rich ocean water result in exceptionally high marine  
32 production, vital to both sea life and people. The intense burst of spring production, together with  
33 more episodic summer and early fall production, provides the energy that powers the complex food  
34 web and ultimately sustains nearly half of the US annual commercial fish landings, as well as  
35 providing food and cultural value to thousands of Bering Sea coastal and island residents.

36

37 These spatial and temporal changes in seasonal ice cover act as the major organizing feature and  
38 driver of the eastern Bering Sea ecosystem. We know that the timing and extent of the seasonal ice  
39 play essential roles in the productivity and community structure of this ecosystem, that sea-ice  
40 dynamics have been changing over recent decades (e.g. Stabeno et al., 2012), and that major changes  
41 in ice cover are predicted in the near future (e.g. Wang et al., 2012). Past and present changes in  
42 Bering Sea ice have attracted the curiosity of scientists, but it is the potential for future change and its  
43 consequences that are an increasing cause of concern for scientists, resource managers, and a broad  
44 array of Native, local, and regional stakeholders.

45

46 In response, the National Science Foundation (NSF) and the North Pacific Research Board (NPRB)  
47 created a novel partnership in 2007 to support an ecosystem-scale study to examine how a changing  
48 climate and changing sea-ice conditions affect the EBS ecosystem, from physics and chemistry to  
49 lower trophic level organisms (e.g. plankton) to humans. The “Bering Sea Project” (Fig. 1) integrated  
50 two major research programs, the NSF-funded Bering Ecosystem Study (BEST) and the NPRB-funded  
51 Bering Sea Integrated Ecosystem Research Program (BSIERP), and was underpinned by substantial in-  
52 kind contributions from National Oceanic and Atmospheric Administration (NOAA) and additional  
53 contributions from other agencies, universities, and institutions. The Bering Sea Project brought  
54 together nearly 100 principal investigators, leading a sprawling team of several hundred postdocs,  
55 graduate students, technicians, ship officers and crew, and many others. Over its seven-year course  
56 of activity (2007-2014, with primary fieldwork taking place during 2008-2010), the Bering Sea Project  
57 has provided new insights into the functioning of the EBS ecosystem, particularly in the north-central  
58 region ( $\sim 59^{\circ}$  –  $\sim 62^{\circ}$ N) where data sets and temporal coverage previously had been sparse.

59

60 Since the final full-project meeting in early 2014, Bering Sea Project participants have focused on  
61 discussion, collaboration, data analysis, and publications, culminating in nearly 200 peer-reviewed  
62 Bering Sea Project papers to date published across a broad spectrum of journals. This growing  
63 publication library includes 76 papers in the previous three Bering Sea Project special issues in Deep-  
64 Sea Research II— volumes 65-70 published in 2012, volume 94 published in 2013, and volume 109  
65 published in 2014. These special issues provide a home for sharing peer-reviewed results across a

66 broad audience, and facilitate project integration and synthesis. On behalf of all Bering Sea Project  
67 participants and supporters, we are pleased to share this collection of papers in the fourth and final  
68 Bering Sea Project special issue.

69

70 The first two special issues presented papers that described new information about the EBS  
71 ecosystem, focusing on how change will affect individual species and trophic levels (Wiese et al.,  
72 2012, Harvey and Sigler, 2013). Papers in those issues placed new data in historical context and  
73 assessed implications for the future of the Bering Sea ecosystem. They addressed one or more of the  
74 core program hypotheses that guided the entire field program and provide a framework for ongoing  
75 synthesis activities: 1) physical forcing, including climate, affects food availability; 2) ocean conditions  
76 structure trophic relationships through bottom-up processes; 3) ecosystem controls are dynamic; 4)  
77 location matters; and 5) commercial and subsistence fisheries reflect climate.

78

79 The third special issue (Lomas and Stabeno, 2014) continued to address the core hypotheses and had  
80 an increased focus on mid-level synthetic activities, striving to advance our understanding of the  
81 ecosystem as an integrated whole, and how it might respond to changes in climate. The third issue  
82 also featured a suite of papers focused on marine ecosystem connections to regional human  
83 communities and other stakeholders, within the scope of the Bering Sea Project's explicit  
84 consideration of humans as part of the EBS ecosystem

85

86 This fourth and final special issue continues that evolution, with further focus on synthesis of  
87 information across broader ranges of disciplines and inclusion of new collaborative author teams.  
88 This issue also presents information on some of the extensive model-based research directions within  
89 the project. In the following paragraphs, we provide some context and brief summaries of each of  
90 the papers appearing in this fourth and final Bering Sea Project special issue, grouped by broad topic  
91 or trophic level.

92

## 93 **2. Current and future Bering Sea physical conditions**

94 Stabeno and coauthors assembled a suite of physical measures to better understand the complex  
95 pattern of current transport across the EBS shelf (**Stabeno et al.**, this issue). Extensive data sets  
96 were required to capture the multiplicity of sources impacting the northward flow of waters to the  
97 Bering Strait. Their analyses relied on data collected over two decades originating from physical  
98 moorings, satellite-tracked drifters, and shipboard hydrographic transects to develop integrated  
99 maps of flow patterns on the eastern shelf. These estimates were then combined with data sets of  
100 sea ice and wind fields to calculate annual estimates of flow paths and velocity for the region. Results  
101 showed that large horizontal spatial scales and low bathymetric relief contribute to the relatively  
102 weak ( $< 0.1$  Sv), but organized, transport. Winds were an important influence on surface flow fields,  
103 but were variable and complicated by seasonal shifts in direction, ice, and varied bottom topography.  
104 Other dynamics influenced the bottom flow on the southern middle shelf and on the northern shelf  
105 near the M8 mooring. Stabeno and colleagues determined the waters that transit the more shallow  
106 areas (especially along the 50-m and 100-m isobaths) are important contributors to transport through

107 Bering Strait, including the waters from the Gulf of Alaska that flow through Unimak Pass. The  
108 relatively long (8-14 months) residence times estimated for waters flowing north also implies that  
109 most of the heat entering into the Chukchi Sea through Bering Strait originates from air-sea  
110 interactions in the Bering Sea, rather than from the Gulf of Alaska. The impact of sea ice remained  
111 difficult to quantify, but important differences were seen in currents in cold versus warm years.

112

113 **Hermann et al.** (this issue) used three global climate simulations to predict future trends in  
114 temperature over the EBS shelf. Their research used the Intergovernmental Panel on Climate Change  
115 Fourth Assessment (AR4) as physical forcing to drive a regional model that included both physical and  
116 biological elements of the Bering Sea. They found considerable variation among the three  
117 simulations, but each downscaled projection indicated a warming of 1– 2 °C between 2010 and 2040  
118 on the Bering Sea shelf. In a forecast to at least 2040, Hermann et al. found that the magnitude of  
119 presently-observed interannual variability of bottom temperatures and ice cover is expected to be  
120 maintained, but with a steadily increasing probability of warm years with less ice on the southern  
121 shelf. Overall, their modeling work indicates a trend toward warmer ocean temperatures, and  
122 reduced ice in the southeastern Bering Sea, but continued ice cover in the northeastern Bering Sea.  
123 Hermann et al. (this issue) also attempted to determine which factors were responsible for the  
124 modeled increases in temperature. Sensitivity analyses suggest both increasing air temperature and  
125 northward wind as primary drivers of future increases in water-column temperatures.

126

127 **Durski et al.** (this issue) used a high-resolution 2-km model to capture the regional oceanographic  
128 processes and flow patterns. In general, their model simulations compared well to observations,  
129 particularly in the passes in the Aleutian arc, where flow has been difficult to model because of the  
130 narrowness of most of the passes compared to the spatial resolution of the models. The model  
131 simulations replicated both temporal variability, including the fortnightly signal, and the magnitude of  
132 flow. The Aleutian passes play an important role in mixing nutrients into the surface waters via tidal  
133 mixing, and as a pathway for oceanic zooplankton. These nutrients support local production, and are  
134 also advected eastward in the Bering Slope Current and onto the shelf. In addition, the Durski et al.  
135 model provided insight into the decay of the cold pool during the summer, which occurs on multiple  
136 time scales. This model's very high resolution (2 km x 2 km) allowed the examination of processes at  
137 spatial and temporal scales not previously possible.

138

139 The reliability and utility of temperature and salinity data collected by instrumenting research fishing  
140 trawls on the annual NOAA Fisheries bottom trawl surveys in the EBS was explored in **Cokelet** (this  
141 issue). Equipping each trawl made on the regular grid of the annual groundfish survey with  
142 conductivity-temperature-depth (CTD) instruments permits an evaluation of frontal structure,  
143 stratification and temporal variability, using gridded observations from roughly 1000 CTD casts over  
144 three summers on the EBS shelf. These gridded data provide information on both along- and across-  
145 shelf spatial patterns in temperature and salinity.

146

147 **3. Phytoplankton abundance and productivity**

148 The Marginal Ice Zone (MIZ), where ice breakup and melt occurs, has long been known to be an  
149 important Bering Sea physiographic feature for enhanced primary production. This is due to  
150 stabilization of the water column by ice melt and seeding of the water column with ice algae melting  
151 out of the ice. **Sambrotto et al.** (this issue) show that while the contribution of ice algal seed  
152 populations and the shallowing of the mixed layer depth were contributory factors to the  
153 establishment of MIZ blooms, those factors were by themselves not sufficient to explain the spatial  
154 variations in bloom intensity. Rather, in situ observations suggest that ice melt was releasing  
155 additional growth factors (e.g. particulate and dissolved iron and dissolved organics) into the salinity  
156 stratified water column that were leading to enhanced primary production and phytoplankton  
157 growth. On the western regions of the shelf and near the St. Lawrence Island polynya, advection of  
158 MIZ water under the ice, coupled with light transmission through the ice, allowed for continued  
159 primary production that was not readily observed in ocean color data by satellites. This 'hidden'  
160 production may account for nearly one third of the annual production in the non-shelf break regions  
161 of the EBS.

162

163 Physical and chemical control of phytoplankton production and abundance occur year round, and the  
164 Bering Sea Project aimed to encompass studies that examine control mechanisms across all seasons.  
165 **Eisner et al.** (this issue) analyzed a 10-year record (2003-2012) of late summer/early fall  
166 phytoplankton abundance (estimated by chlorophyll-*a*) on the EBS, and observed that warm years in  
167 the early part of the record (2003-2005) were characterized by higher chlorophyll-*a* concentrations  
168 on the southern outer and middle shelf domains than those same regions in cold years (2007-2012).  
169 These elevated chlorophyll-*a* conditions in warm years were also associated with a higher prevalence



170 of larger phytoplankton cells. Eisner et al. observed that the frequency of wind-mixing and sea  
171 surface temperature were positively correlated with both total chlorophyll-*a* and the large size  
172 fraction of phytoplankton chlorophyll-*a*, suggesting that a combination of repetitive nutrient injection  
173 and temperature-enhanced growth supported this accumulation of phytoplankton biomass on the  
174 southern shelf. In a companion study, **Gann et al.** (this issue) examined processes during a single,  
175 cold year (2007) when there was a particularly obvious absence of wind mixing and thus nutrient  
176 entrainment. During that summer of 2007, they observed some of the lowest measured rates of  
177 primary production on the southern shelf. While the differences in chlorophyll-*a* between warm and  
178 cold temperature stanzas were obvious over the southeastern Bering Sea shelf, they were not  
179 observed on the northern shelf— consistent with prior Bering Sea Project studies that showed a  
180 decoupling of change between the northern and southern shelf (e.g. Stabeno et al., 2012). These  
181 patterns in phytoplankton abundance and productivity in the late summer are curiously out of phase  
182 with patterns in large crustacean zooplankton abundance and biomass, which are highest during cold  
183 stanzas, suggesting a trophic connection complicated not only by physics, but by biology as well.

184

185 Previous field observations indicate that spring and fall phytoplankton blooms on the EBS continental  
186 shelf co-vary, so that a year with a strong spring bloom also tends to have a strong fall bloom (Sigler  
187 et al., 2014). Similar co-variability of primary production is also seen in the multi-year (1987–2007)  
188 integration of a coupled physical–biological model described in earlier Bering Sea Project publications  
189 (e.g. Gibson and Spitz, 2011; Gibson et al., 2013; Hermann et al., 2013). **Cheng et al.** (this issue) used  
190 a coupled, physical–biological model simulation to examine the relative contributions to this co-  
191 variability of wind mixing, local nutrient recycling/regeneration, horizontal nutrient advection, and

192 water-column stability. They found no significant correlation between the spring and fall surface wind  
193 mixing, and concluded that although wind mixing is an important mechanism for bringing nutrients in  
194 the lower water column to the surface layers in the EBS, it is not the mechanism tying the two  
195 seasons' productivity together. They highlight the importance of local recycling and regeneration of  
196 nutrients assimilated during spring phytoplankton bloom in linking together the spring and fall  
197 primary productions on EBS shelf region.

198

199 The work by **Liu et al.** (this issue) examined phytoplankton carbon cycling using an analytical model to  
200 estimate daily, mixed-layer gross primary production (GPP) together with 8-day, chlorophyll-*a*  
201 composite satellite images of phytoplankton biomass fields to describe the total phytoplankton loss  
202 from the mixed layer. The model was applied to five regions of the EBS shelf over the major domains  
203 to quantify GPP and total phytoplankton losses, and to compare differences between warm and cold  
204 stanzas of years. Additional information including calculated SST and mixed layer depth were  
205 obtained from database and field archives. The annual shelf-wide mean modeled Chl-*a* concentration  
206 was slightly higher in warm years than in cold years, but the difference was not significant. This is  
207 consistent with findings for August-September by Eisner et al. (this issue), who saw higher Chl-*a*  
208 during warm years, but results were not significant over the majority of the shelf. Although the  
209 dynamic nature of phytoplankton blooms over the water column and their spatial extent complicate  
210 the observations, maximum GPP values were seen during the spring bloom and minimum values in  
211 the summer. Warm years were slightly higher than cold years for annual GPP and carbon loss terms,  
212 but differences between climate regimes were not significant in most instances. Modeled estimates  
213 of losses from microzooplankton grazers were consistent with published field observations that

214 microzooplankton grazing loss is a relatively small fraction of phytoplankton standing biomass  
215 (<10%), but can be a significant impact on daily primary production, with the percent grazed higher in  
216 summer than spring. Overall, respiration dominated total loss, following by the losses due to  
217 zooplankton grazing and sinking. The authors noted that the summation of all loss processes did not  
218 account for phytoplankton total loss, suggesting that additional processes or more detailed  
219 information are needed to fully calibrate chlorophyll estimates determined by satellite.

220

#### 221 **4. Zooplankton**

222 Euphausiids and large copepods are important parts of the EBS marine food web and are essential  
223 components of fish, seabird, and marine mammal diets in the region. In particular, for walleye  
224 pollock (*Gadus chalcogrammus*— a commercially and ecologically important species and a focal fish  
225 species in the Bering Sea Project—hereafter referred to as 'pollock'), large copepod and euphausiid  
226 populations have been shown to be an important predictor of recruitment (Heintz et al., 2013, Siddon  
227 et al., 2013). Several manuscripts in this special issue address the ecology of these important  
228 zooplankton taxa and their role in the ecosystem. **Campbell et al.** (this issue) documented spring  
229 grazing rates and diet of major crustacean zooplankton taxa during three sequential cold years for the  
230 middle and outer EBS shelf. The proportion of microzooplankton in crustacean zooplankton diets was  
231 higher than that found in the prey field for six of the eight taxa examined, indicating selection for  
232 microzooplankton. However, phytoplankton and ice algae were the most important component of  
233 the diet because they accounted for a much greater fraction of the prey biomass. The grazing impact  
234 of zooplankton as a whole (comprising both micro- and mesozooplankton) was a small fraction of the  
235 total standing stock of chlorophyll, and was generally 50% or less of primary production during spring

236 phytoplankton blooms. This leaves a large fraction of primary production available for direct  
237 transport to the benthos to support high biomasses of infauna and epifauna, including many  
238 flatfishes.

239

240 **Bailey et al.** (this issue) applied molecular bar coding techniques to understand the distribution and  
241 abundance of *Pseudocalanus* adult females during a single year. From specimens collected over the  
242 outer and middle shelf regions, they found four species— two temperate (*P. mimus*, *P. newmani*) and  
243 two arctic (*P. acuspes*, *P. minutus*). Temperate species were more abundant over the outer shelf,  
244 while the arctic species were more abundant over the middle shelf. Low genetic diversity within each  
245 species suggests high levels of connectivity across the shelf. *Pseudocalanus* nauplii and copepodites  
246 are an important prey item for early feeding larval pollock, and the loss of the two Arctic  
247 *Pseudocalanus* species during warm periods or due to climate-induced warming of the whole  
248 ecosystem could impact the condition of larval pollock, because the arctic species typically contain  
249 higher lipid levels than the temperate species.

250

251 A second study on *Pseudocalanus* examined feeding differences across species using a different  
252 molecular technique (18S rDNA) to identify prey items in the water and guts of *Pseudocalanus* (**Cleary**  
253 **et al.**, this issue). In this case, copepodites of various stages were used from some of the same 2010  
254 collections used in the Bailey et al. study. Their diets were generally very broad (and included other  
255 metazoans), but there were dietary differences discovered across species. *P. acuspes*, an arctic  
256 species, had a high proportion of heterotrophic dinoflagellates in its diet, while *P. minutus*, another

257 arctic species, had a high proportion of material from gelatinous plankton, except when captured in  
258 waters with high chlorophyll concentrations when they had a high proportion of diatoms in their diet.  
259 These results describe both niche separation as well as an ability to use multiple prey types— an  
260 ability that may be useful if the structure and function of the southeastern Bering Sea changes due to  
261 climate induced warming.

262

263 **Pleuthner et al.** (this issue) examined the feeding and lipid storage of euphausiids, during both late  
264 spring and early summer through a series of feeding and starvation experiments, and analysis of the  
265 lipid composition of the euphausiids and of their prey. They found seasonal differences in the extent  
266 to which euphausiids lost lipid under starvation, with the early summer euphausiids losing less lipid  
267 than the late spring euphausiids. They also found that although the individual lipid biomarkers in the  
268 euphausiids in spring versus summer reflected the longer-term seasonal switch from ice algal diatom  
269 to heterotrophic prey (e.g. microzooplankton), shorter-term changes in euphausiid diet were not  
270 consistently reflected in lipid composition.

271

272 In a review of the available information on euphausiids, **Hunt et al.** (this issue) use a synthesis  
273 approach to summarize the state of knowledge of bottom-up and top-down controls of euphausiids.  
274 This was attempted to understand the implications for higher trophic level species such as pollock  
275 and the marine mammals that rely upon them for food. Based upon modeled rates of euphausiid  
276 production, the authors found sufficient primary production to support euphausiid production.  
277 Pollock were estimated to consume only 20-35% of that euphausiid production in spring and summer.  
278 These observations complicate the explanation of a strong, negative correlation between pollock

279 biomass and euphausiid biomass, and the simultaneous negative correlation between euphausiid  
280 biomass and water temperature. In fact it is likely that neither top-down control by pollock, nor  
281 bottom-up control by the availability of food is the sole determinant of euphausiid biomass; rather,  
282 controls on euphausiid biomass, and thus its central role in the EBS ecosystem, vary as a function of  
283 the mean temperature state of the system.

284

285 The **Sigler et al.** (this issue) team brought insights from previous papers together with some new  
286 results in a synthesis that explored: 1) linkages between primary and secondary production,  
287 particularly in cold versus warm years; 2) bioenergetics and seasonality of copepods, euphausiids,  
288 and pollock; 3) the importance of location and the different conditions of sea ice and the timing of  
289 production for the success of larval pollock and their crustacean prey; and 4) annual to multi-year  
290 shifts (associated with large-scale atmospheric drivers) in the intensity of top-down control of  
291 crustacean zooplankton by pollock. They found that production is closely linked to sea-ice conditions  
292 and seasonal timing. Favorable locations for crustacean zooplankton, and thus for pollock, are  
293 defined not only by water temperature and depth, but also by the extent and timing of sea ice in the  
294 spring. Predation pressure and top-down control is greater during cold periods when pollock are  
295 successful because of enhanced availability of their crustacean prey; warm years lead to less intense  
296 predation pressure because reduced prey availability limits pollock success. During switches from  
297 warm to cold periods, the faster-responding planktonic system rebounds first and enjoys a brief  
298 period (1-2 years) of reduced predation pressure before the pollock in turn respond to the favorable  
299 feeding conditions. In cold years, crustacean zooplankton exploit high primary production and in turn  
300 sustain vigorous pollock populations, while in warm years the life cycles of the crustacean

301 zooplankton are not well matched to the timing of primary production so zooplankton abundance,  
302 and availability as prey to pollock, remains low. The Sigler et al. synthesis highlighted key influences  
303 on patterns of primary and secondary production— and ultimately on the success of pollock  
304 populations— including the importance of the extent and timing of sea ice, the alternation of periods  
305 of warm and cold years shaped by these changes in sea ice, location-specific sea-ice characteristics,  
306 and the overlying atmospheric drivers on the Bering Sea ecosystem.

307

## 308 **5. Fish ecology**

309 Our understanding of the life history and ecology of important fish species reached a new level over  
310 the course of the Bering Sea Project. For example, **Andrews et al.** (this issue) examined the effects of  
311 warm and cold periods on two forage fish species, capelin (*Mallotus villosus*) and Pacific herring  
312 (*Clupea pallasii*). Time series that were begun before the coordinated effort of the Bering Sea Project  
313 were essential to documenting patterns in distribution and abundance. Andrews and colleagues  
314 found that the catch per unit effort (CPUE) of both species was higher in the northeastern than the  
315 southeastern Bering Sea, and was higher during cold conditions than during warm conditions. Fish  
316 length was not significantly different between warm and cold periods, but herring length did show  
317 differences among geographic regions, with increasing size toward the shelf break, most likely due to  
318 migratory behavior. Diet also differed between warm and cold conditions, with warm year forage  
319 fish diets in the southeastern Bering Sea exhibiting the same lack of large, lipid-rich crustacean  
320 zooplankton as seen for other fish species. One interesting result was the high proportion of age-0  
321 pollock in the diet of herring in warm years. Herring had not previously been identified as a major  
322 predator of young pollock.

323

324 An analogous approach was taken with the ecology of Pacific cod (*Gadus macrocephalus*) age-0 diet,  
325 using collections from surface trawls to examine size, diet, and condition of age-0 Pacific cod during  
326 warm, average, and cold periods (**Farley et al.**, this issue). Similar to capelin and herring, young cod  
327 were found to have a high proportion of age-0 pollock in their diets in warm years, and high  
328 proportions of large crustacean zooplankton in their stomachs in cold years. Similar to age-0 pollock,  
329 energetic status (body condition) of age-0 Pacific cod was highest in the cold years when their diet  
330 focused on large crustacean zooplankton. Therefore, although there are distinct life history  
331 differences between these two gadid species, there are also strong similarities in how their early  
332 pelagic stages respond to alternating periods of warm and cold conditions. This suggests that gadid  
333 recruitment in this region is being controlled by direct and indirect effects on prey quality and  
334 quantity, and by their condition or caloric density prior to the first winter.

335

336 **Parker-Stetter et al.** (this issue) examined the environmental factors affecting spatial distributions of  
337 forage fish species. They examined the distributions of capelin, age-0 pollock, and age-0 Pacific cod,  
338 and evaluated the influence of both local and annual environmental indices, with the latter  
339 accounting for the possibility that overall distributions changed with annual conditions. They found  
340 that local, but not annual, environmental indices were most important for capelin (e.g., local  
341 temperature), whereas both local and annual indices were important for age-0 pollock and age-0 cod  
342 (e.g., local temperature and annual sea-ice anomaly). Only two indices (local temperature and depth)  
343 influenced all three species, emphasizing the importance of these two indices, but also



344 demonstrating that the prediction of distributions is complex. The results of Parker-Stetter et al. are  
345 applicable to our understanding of climate effects on spatial distributions, and also to future  
346 distribution and recruitment modeling efforts that build on the five model-based papers described in  
347 this issue.

348

349 **Miller et al.** (this issue) conducted an investigation—not formally part of the Bering Sea Project, but  
350 closely related to it—that attempted to connect juvenile (age-0) Pacific cod and their collection  
351 locations to known natal areas, using the isotopic signatures contained in otoliths. Although it was  
352 not possible to make the connection, they did identify chemically distinct larval source signatures  
353 with mixing patterns that appeared to vary between the two years (2006 and 2008) for which they  
354 had samples. The varying mixing patterns between the two years may have been attributed to  
355 differential spawning locations and shelf circulation between the average and cold years (e.g. Petrik  
356 et al., 2015). Identification of unique chemical signatures on the open shelf provides support for the  
357 further application of this technique to understand the relative contributions of different natal areas  
358 to eventual recruitment, and the demonstrated ability of the technique to identify collection site  
359 based on otolith edge chemistry suggests an ability to discern the relative productivity of multiple  
360 juvenile nursery areas.

361

362 **Duffy-Anderson et al.** (this issue) used the many Bering Sea Project discipline-specific and component  
363 studies, plus the historical literature, to synthesize the present state of knowledge for the first year of  
364 life for a focal fish species, pollock. The eastern Bering Sea is at the northern end of the current range

365 of pollock, so environmental variability is expected to have a significant influence on recruitment.  
366 The first year of life, and in particular the nutritional status leading up to the first winter, has been  
367 identified as the recruitment bottleneck. The Duffy-Anderson et al. synthesis resulted in an  
368 evaluation of the strengths and weaknesses of our current paradigms to explain pollock recruitment  
369 variability in mechanistic terms. The review covers a critical discussion of knowledge regarding the  
370 distribution, feeding ecology, growth, and predation for each early life history stage (spawning, egg,  
371 larvae, and juvenile) and different approaches to modeling of the first year of life. In addition, they  
372 critically evaluate current recruitment control paradigms: Differential transport; nutrition and  
373 condition; and predation. Duffy-Anderson et al. conclude with a discussion of current knowledge  
374 gaps, and recommend nine research areas that, if successfully developed, would enable us to reach a  
375 higher level in understanding pollock recruitment variability. In brief, these research areas and data  
376 gaps are: Full seasonal sampling, particularly through the first winter; predation dynamics and  
377 trophic consequences of predation, particularly those factors which affect young pollock vulnerability  
378 to predation; a more complete understanding of the relationship between diet and condition, and  
379 physiological and behavioral responses to prey shift; laboratory-based studies of physiology and  
380 growth to produce data necessary to parameterize models; development of coupled, spatially-explicit  
381 models of the first year of life; stage-specific predictive models to test and quantify the impact of  
382 variable mortality on recruitment; identification of critical production areas for each early life history  
383 stage; assessment of the potential impacts of competition with other planktivorous fishes and  
384 invertebrates; and development of approaches that can successfully resolve the daily ages of larval  
385 and juvenile pollock in the cold eastern Bering Sea.

386 In a related paper, **Buckley et al.** (this issue) used Bering Sea Project results in combination with  
387 several additional long time series (1987-2011) to examine interannual, regional, and size-dependent  
388 differences in summer feeding by pollock. Copepods were a small fraction of the diet in the inner  
389 shelf, where mysids and euphausiids tended to dominate the diet. In the northern-most regions  
390 sampled, amphipods and other fishes had increasing importance in diets as the size of the predator  
391 increased. Summer feeding success (indexed by stomach fullness) for intermediate-sized pollock was  
392 related to copepod consumption, while that for slightly larger pollock was related to prey that were  
393 not euphausiids. Interannual patterns in copepod prey availability appeared to be important in the  
394 diet of younger pollock, while patterns in the availability of euphausiids were observed in the diets of  
395 older, larger pollock ( $\geq 60$  cm fork length). Thus the impacts of climate change on pollock may differ  
396 with the age of the fish, depending on what part of the zooplankton community is most affected, and  
397 the region where young pollock spend their summer.

398

## 399 **6. Marine Mammals**

400 The EBS has historically been important habitat for a wide range of marine mammal species, including  
401 baleen whales such as fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera*  
402 *novaeangliae*), minke whales (*B. acutorostrata*), and North Pacific right whales (*Eubalaena japonica*).  
403 Intensive commercial harvest of baleen whales in the 1900s resulted in depletion of most baleen  
404 whale populations in the EBS; since the cessation of commercial whaling in the mid-20<sup>th</sup> century,  
405 some populations are recovering (fin and humpback whales), while North Pacific right whales are not  
406 recovering. Currently, baleen whale populations are seasonal in their use of the EBS region, with

407 maximum numbers during their spring and summer feeding periods. In a study that combines  
408 extensive at-sea observational data and environmental and prey data together with a detailed  
409 statistical model, **Zerbini et al.** (this issue) provide a novel habitat baseline for baleen whales in the  
410 EBS, based on a quantitative assessment of the relationship between whale abundance,  
411 environmental variables such as sea surface temperature and chlorophyll concentration, and the  
412 density of key prey species: euphausiids and age-1 pollock. This work demonstrates the added value  
413 provided by working within the broadly integrated Bering Sea Project, although Zerbini and  
414 colleagues note that the robustness of the relationships—and their applicability to forecasting—still  
415 needs fuller validation with additional years of survey data.

416

## 417 **7. Fisheries management**

418 Application of project results to the top trophic level— humans— has been a consistent and  
419 important goal of the Bering Sea Project. For example, in the third special issue, project participants  
420 reported on how ecological information emerging from the Bering Sea Project connected to  
421 subsistence harvests of local communities (e.g. Renner and Huntington, 2014). In this issue we  
422 publish a set of six related articles by a group of authors on resource assessment and modeling,  
423 incorporating focus on an ecosystem-based approach to fisheries management (EBFM). Increasing  
424 awareness of the interconnections among species and ecosystem conditions, together with concern  
425 over long-term cumulative impacts of commercial fishing on marine ecosystems, have led to calls for  
426 a move towards EBFM, either in addition to, or as replacement for, traditional single-species  
427 management. This topic fits squarely within the core aims of the Bering Sea Project, which included

428 providing information relevant to the commercial fishing industry and of direct or indirect use to  
429 fishery managers.

430 However, moves toward multispecies and ecosystem-based management are complex and have  
431 proven challenging to bring to implementation. In an innovative modeling study, **Uchiyama et al.**  
432 (this issue) used biomass estimates and predation data derived from annual groundfish surveys in the  
433 Bering Sea, and then developed two forms of age-aggregated biomass models—a multispecies  
434 biomass dynamics (MBD) model, and a multispecies delay difference (MDD) model—to study the  
435 biomass dynamics of the four major groundfish species or species groups in the eastern Bering Sea.  
436 Despite a need for model improvements and additional model evaluations, Uchiyama et al. provide a  
437 useful step forward in multi-species management approach, and their work can be used as a tool to  
438 improve single-species stock assessments currently used, and enable further exploration of the  
439 performance of harvest control rules aiming to maintain healthy populations of the Bering Sea  
440 groundfish complex as a whole.

441

442 In the EBS there are strong trophic connections between pollock, arrowtooth flounder (*Atheresthes*  
443 *stomias*), and Pacific cod due to interspecific predation of juveniles (Aydin and Mueter, 2007). **Moffit**  
444 **et al.** (this issue) explore how to develop and test multi-species biological reference points (MBRP) for  
445 use in setting harvest control rules of commercially-exploited species. Their work explored a range of  
446 approaches, from use of a relatively simple, two-species model (pollock and cod) to using system  
447 wide, multi-species maximum sustainable yield models (MMSY). In the simplest case, they calculated  
448 the fishing mortality for each species'  $F_{x\%}$  (the fishing mortality which reduces the spawning biomass

449 per recruit of that species to  $x\%$  of unfished biomass ( $B_0$ ) while assuming the average fishing  
450 mortality applied to all other species. In this method the natural and fishing mortality for each  
451 species is calculated from the multi-species model. The pollock-cod model predicted that pollock  
452 recruitment increased with increasing fishing mortality of cod (due to predation), while cod  
453 recruitment suffered as pollock fishing mortality increased (lower food availability for cod). Plots of  
454 the modeled fishing rate of pollock ( $F_{40\%}$ ) as a function of the fishing rate of cod enabled them to  
455 identify combinations of fishing rates on the two species that exceeded the overfishing limit. This  
456 simplest case is the one closest to how reference points are computed with the current single-species  
457 management in Alaska. When comparing the relatively simple method of obtaining MBRP with the  
458 more complicated MMSY models, it appeared that in some cases the more complicated models  
459 yielded catch rates that were as high or higher than the rates calculated from the simpler models.

460

461 **Holsman et al.** (this issue) expanded upon the work of Moffit et al. and asked if multi-species  
462 assessment models could be used to quantify the direct and indirect effects of climate and fisheries  
463 harvest on fish populations. The question was addressed using single species and multi-species,  
464 statistical catch-at-age (MSCAA) models. This particular model (Climate-Enhanced, Age-based model  
465 with Temperature-specific Trophic Linkages and Energetics, or 'CEATTLE') included three interacting  
466 species from the EBS— pollock, Pacific cod, and arrowtooth flounder— and incorporated  
467 temperature-specific growth and predation rates. The strength of temperature effects depended  
468 upon species and model type. Biological reference points for arrowtooth flounder were the most  
469 sensitive to changes in temperature, while temperature effects on the MBRP for pollock and cod  
470 were difficult to discern due to resulting high variability caused by different harvest scenarios and

471 predation rates in the absence of temperature change. The model demonstrated the large impact of  
472 annual predation on juvenile pollock; this predation (primarily cannibalism) represented an important  
473 control on population dynamics. Interactions between climate (temperature) and trophic drivers did  
474 influence the MBRPs, but trophic and management-driven changes (i.e. fishing rates on the  
475 predators) can exceed or at least make it difficult to detect the direct effects of temperature on  
476 growth and predation. Results from this study provide a good example of the complexity of fisheries  
477 management under changing climate conditions, and how MSCAA models could be implemented for  
478 the annual setting of fishery quotas in the EBS.

479 Once multiple models (e.g., single species, multi-species, etc.) are developed for a geographic region  
480 or large marine ecosystem, the question "which model is right?" arises. In other words, which model  
481 provides harvest recommendations and biological reference points that ensure the sustainability of  
482 the target populations? Each model will have its own strengths and weaknesses based on the  
483 underlying construction, and the variation in agreement among models, even among similar models,  
484 can be large. **Ianelli et al.** (this issue) advocate for combining results from "competing" stock  
485 assessment model using a method called ensemble forecasting, commonly used in climate  
486 forecasting. They review alternative ways to implement model averaging for EBFM, and then apply  
487 averaging to three types of stock assessment models (single-species, single species with temperature-  
488 specific weight at age, and temperature-specific multispecies) to examine how fishing in the EBS  
489 under four different temperature scenarios may impact the spawning stock biomass of pollock,  
490 Pacific cod, and arrowtooth flounder in the future (present to 2039). The authors advocate the use of  
491 multiple models and model averaging to provide new and improved insight into uncertainty in our

492 stock assessments. This improved understanding of uncertainty may then help managers set harvest  
493 control rules that improve our ability to meet management goals such as avoiding overfishing.

494

495 **Ortiz et al.** (this issue) explored ecological processes with a novel integrated “end-to-end” ecosystem  
496 model that brought a physical oceanographic model (ROMS- Bering10K) together with a lower trophic  
497 nutrient-phytoplankton-zooplankton model (BESTNPZ) and an upper trophic fish model (“Forage and  
498 Euphausiid Abundance in Space and Time”, or FEAST). By combining field data and end-to-end model  
499 output, Ortiz et al calculated weekly climatologies and times series of physical and biological drivers  
500 from 1971-2009 for multiple distinct regions of the EBS shelf and slope, and evaluated the reliability  
501 of such a complex ecosystem model through comparison with observations. The model illustrated  
502 two large-scale gradients that characterize overall EBS dynamics and also revealed specific ecosystem  
503 processes, including how the seasonal warming of air temperature and the spring-summer expansion  
504 of the warm pelagic and bottom habitats influence the seasonal sea-ice retreat and the associated ice  
505 edge and open-water spring phytoplankton blooms, as well as the subsequent production of  
506 copepods and euphausiids. The Ortiz et al. hindcast exhibited skill in reproducing seasonal and  
507 temporal patterns in hydrography and biology, provides a year-round framework for local or seasonal  
508 observations, and has helped identify gaps and guide research, both in the design of new surveys and  
509 the targeted temporal focus of surveys.

510

511 Finally, the **Punt et al.** (this issue) essay describes how a “Field-integrated End-to-End” modeling  
512 approach that includes management strategy evaluation can be developed to implement an EBFM



513 approach in the EBS. The approach advocates future creation of harvest control rules that  
514 incorporate ecosystem information, rather than the present system that relies solely on estimates of  
515 stock biomass relative to reference biomass levels. In addition, an important part of this essay is the  
516 presentation of guidelines and principles for the development of ecosystem models and  
517 recommendations for best practices based on the Bering Sea Project experience. In retrospect,  
518 principal investigators working on model-based components found the breadth and depth of Bering  
519 Sea Project models challenging to implement. In this essay, Punt et al. provide perspectives that may  
520 help in the design of future ecological modeling work, based on their hard-earned Bering Sea Project  
521 experience. These include: logistical support of large-scale software development should be on par  
522 with fieldwork support; ensure clear separation of scientific versus logistics oversight; promote open  
523 and frequent communication with field biologists; ensure the adequacy and availability of field data  
524 for model validation and testing; recognize that most modeling work is sequential and iterative as  
525 opposed to simultaneous and independent; and recognize there is a mismatch of required  
526 performance levels and performance measures between single discipline approaches and multi-  
527 disciplinary approaches.

528

## 529 **8. Syntheses and Conclusions**

530

531 The Bering Sea Project's internal steering committee (the "Science Advisory Board" or SAB) initially  
532 envisioned that the series of four special issues in Deep-Sea Research Part II would show a  
533 progression from relatively directed and focused reports, to broader syntheses. In practice, elements  
534 of both types of study appear in this final special issue. Some of this can be attributed to special

535 studies added to the project well after its inception (e.g. Bailey et al., this issue, Cleary et al., this  
536 issue), but other directed investigations are just now emerging (e.g. Cokelet, this issue). After this  
537 massive effort involving nearly 100 principal investigators and some 25,000 person-field days, results  
538 will continue to find their way into the literature for years to come. At this point we know that  
539 several intermediary syntheses have been completed and others are well underway, and we look  
540 forward to the emergence of future work.

541

#### 542 *8.1 Synthesis examples*

543 To date, there are many examples of synthesis-focused advancements in our understanding of the  
544 Bering Sea ecosystem stemming from the Bering Sea Project. To supplement individual paper  
545 descriptions, here we highlight three selected examples that span multiple papers across the whole  
546 program (including some within this special issue series and some published elsewhere), are  
547 indicative of the success of the project as a whole, and represent some of the project breadth. First is  
548 an important and complex story emerging from a group of the lower-trophic level studies.  
549 Investigators were able to describe how bottom-up processes in a marginal ice zone influence both  
550 lower and upper trophic levels. In the eastern Bering Sea ice, ice algae and cold winters help to  
551 promote the establishment of strong year-classes of large crustacean zooplankton (copepods and  
552 euphausiids). This combination of conditions promotes lipid storage in those taxa, which in turn  
553 provides a critical energy source for juvenile fish, such as pollock. Although the number of early  
554 juvenile pollock in warm years is often higher than that in cold years, winter survival of juveniles  
555 produced during a warm year is low. It is the late summer ingestion of abundant, lipid-rich,

556 crustacean zooplankton during cold years that enable juvenile pollock to store enough energy  
557 reserves of their own to survive the first winter.

558

559 Warming of the ocean, and loss of sea ice at high latitudes in particular, are cause for concern. One  
560 question on the minds of those that harvest resources from the Bering Sea is how will warming  
561 impact the distribution and availability of those resources. In a second example of broad, synthesis  
562 advancement in understanding, Bering Sea Project studies concluded that many subarctic demersal  
563 and semi-demersal fishes will not be able to penetrate very far into the high arctic, even after the  
564 southeastern Bering Sea loses its winter/spring sea ice. This is because at high latitudes (> ca. 62° N)  
565 physical conditions combine to result in the region remaining dark and frigid in the winter, with  
566 continued advection and formation of sea ice. Thus in the near future the shelf in this northern  
567 region is likely to continue to be covered by cold (< 2° C) bottom water during the summer, and this  
568 landscape-scale feature will continue to be a barrier to demersal and semi-demersal subarctic fishes.  
569 The situation for pelagic fishes, such as Pacific salmon, while less certain, appears different, and an  
570 increase in salmon species in the northern Bering Sea and Chukchi Sea has already been observed  
571 (Eisner et al. 2013).

572

573 Teams of researchers within the Bering Sea Project also investigated bottom-up processes affecting  
574 higher trophic levels. In a third example of a broad, multi-investigator advance, comparison was  
575 made of food availability between two colonies of Northern fur seals (*Callorhinus ursinus*), one  
576 situated on the shelf (Pribilof Islands) and the other on a tiny island in the oceanic basin (Bogoslof

577 Island). It was known that the Pribilof population on the shelf has seen pup production decline by  
578 some 80% since the 1950s, and the population of adults has been declining at an annual rate of ~5%  
579 since 1998, while in recent decades the population from the Bogoslof oceanic site was increasing  
580 (Battaile et al. 2015). What hasn't been understood is the cause of the Pribilof decline, particularly  
581 because scientists often view the shelf as a more productive region than the oceanic basin. Previous  
582 tagging studies ruled out immigration or emigration. Using a combination of sophisticated logging  
583 instrumentation and at-sea oceanographic and bioacoustic work, Bering Sea Project scientists  
584 discovered that prey availability and foraging efficiency for fur seals was higher at the oceanic rookery  
585 than at the shelf site. Prey available to fur seals at the oceanic rookery were both closer (requiring  
586 shorter trips for lactating females), and more energy-rich than the prey available to fur seals traveling  
587 from the shelf Pribilof rookery.

588

## 589 *8.2 Reflection and conclusion*

590 Large, interdisciplinary programs come with large risks, but also with potentially large rewards. At  
591 every level, success depends on the talent, ingenuity, and the altruism of participating scientists.  
592 Luck, timing, and serendipity also play roles in the success of large research programs. Have methods  
593 and technology used in the independent fields of study progressed far enough for the next big  
594 advancement? Are the project hypotheses cleverly constructed to enable meaningful conclusions?  
595 Will the conditions under which the field years are conducted allow the scientists to actually test the  
596 hypotheses? Will scientists work well in teams that go beyond their immediate projects? Will  
597 scientists allow themselves and the program to be guided by a team of peers? If the Bering Sea

598 Project is seen as fully successful, it is only because the participants succeeded in meeting many of  
599 these challenges.

600

601 As described in this special issue's opening "Appreciation", many key individuals working in a variety  
602 of programs helped to set the stage and collect datasets that were later used in this project. Building  
603 from earlier work, teams of scientists crafted framework hypotheses and questions after much  
604 discussion and multiple workshops. Then, as the project was launched, nature had a surprise in store  
605 and provided a challenge— following a series of warming years prior to project inception, Bering Sea  
606 Project participants were faced with three "cold" fieldwork years during which atmospheric  
607 conditions resulted in extensive sea-ice coverage and colder-than-average ocean temperatures. The  
608 next "warm" year wouldn't occur until four years after field research was concluded.

609

610 Fortunately, thanks to the efforts of many scientists working in the region prior to the Bering Sea  
611 Project, data from previous programs conducted during warm climate regimes were available for  
612 reference, and were successfully used by scientists in their analyses and syntheses. Project scientists  
613 willingly extended themselves to work in groups that went well beyond their own components.  
614 Common interests and curiosity helped to form powerful and productive partnerships. And  
615 participating scientists were responsive to suggestions and challenges from both those who prepared  
616 and launched the Bering Sea Project on this journey (see Appreciation) and the members of the SAB  
617 and program managers who guided the project to this concluding issue.

618

619 Investment in an integrated ecosystem research approach to the EBS ecosystem paid many  
620 dividends. First and foremost, the results achieved by the project researchers would likely not have  
621 been accomplished by a series of individual projects spaced over a longer time period. The breadth  
622 of the team of investigators resulted in a deep and broad publication record, and empowered the  
623 ability to answer questions about the conservation and management of living marine resources.  
624 Finally, the success of individual projects helped to establish new collaborative relationships among  
625 scientists that will last into the future for additional studies in this and other ecosystems.

626

627 This large expansion of information suggests that there has been a worthy payoff of the risks taken by  
628 NSF and NPRB to partner with each other and with NOAA and other organizations in a broad,  
629 complex, integrated ecosystem research program. The Bering Sea Project has resulted in a large  
630 increase of knowledge in an important ecosystem; it was able to address many of the program  
631 hypotheses, it increased our knowledge of how warming and loss of sea may impact the ecosystem in  
632 the future, and it was able to address some of the questions posed by those that use and manage  
633 resources from the region. We look forward to continued advancement of understanding in the  
634 ecology of this rich and vital region. And we expect that future scientists will re-examine what we  
635 learned, refute parts of it, and build upon other parts to provide a more mechanistic, predictive, and  
636 holistic understanding of the Bering Sea ecosystem, just as we built upon results and insights from  
637 earlier researchers.

638

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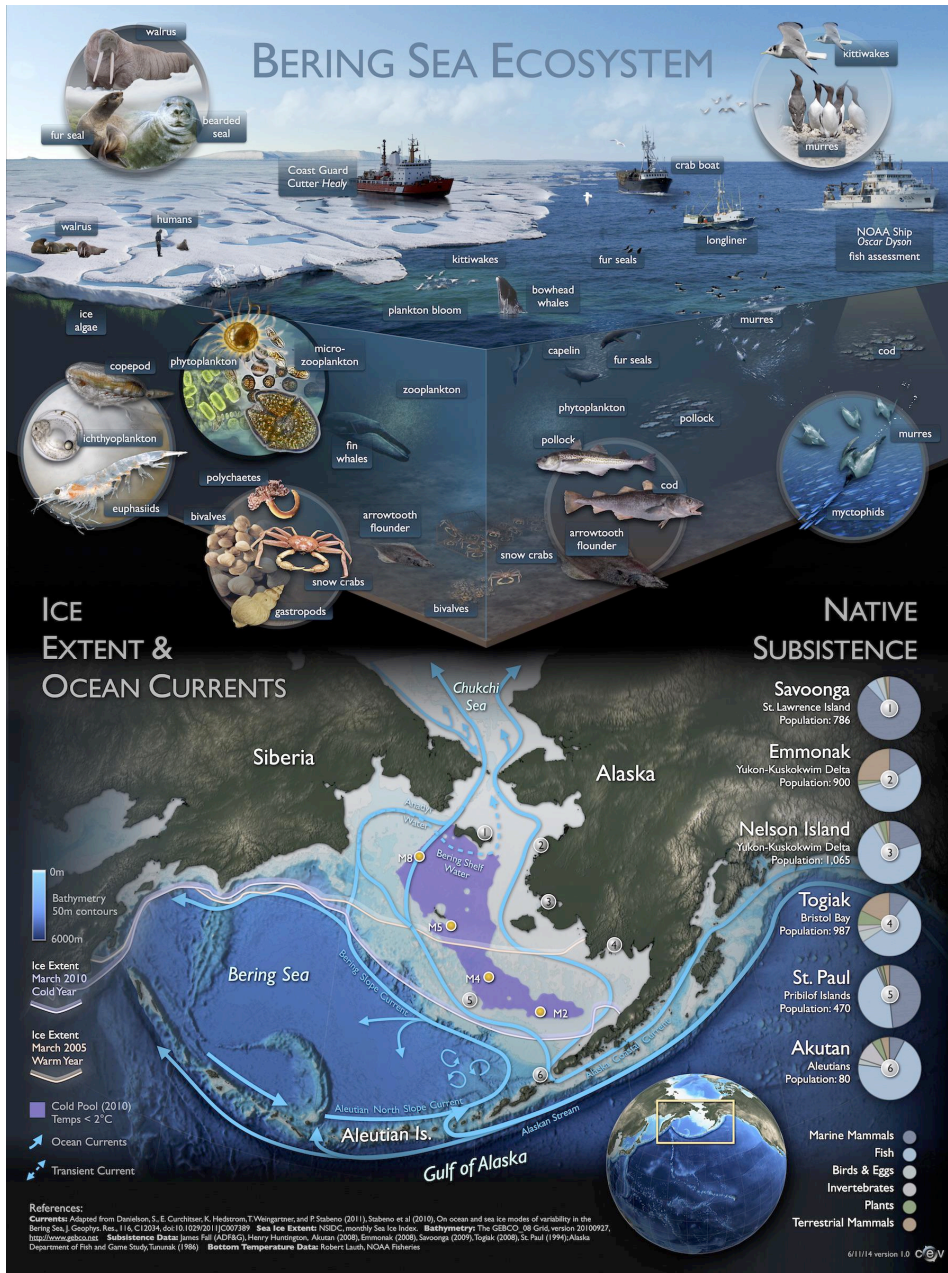
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806 Figure 1. An illustration of the eastern Bering Sea shelf ecosystem and the framework of the Bering  
 807 Sea Project, showing the predominant currents and species, research platforms, ice extent, location  
 808 of the 'cold pool', and also depicting the focal coastal communities and their primary subsistence  
 809 harvest. Biophysical moorings are noted as M2-M8. The seven-year Bering Sea Project focused on US

810 waters across the entire eastern Bering Sea shelf, slope, and basin, extending south from the Bering  
811 Strait and north from the Alaska Peninsula and eastern Aleutian Islands.