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

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1. Introduction

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

These spatial and temporal changes in seasonal ice cover act as the major organizing feature and driver of the eastern Bering Sea ecosystem. We know that the timing and extent of the seasonal ice play essential roles in the productivity and community structure of this ecosystem, that sea-ice dynamics have been changing over recent decades (e.g. Stabeno et al., 2012), and that major changes in ice cover are predicted in the near future (e.g. Wang et al., 2012). Past and present changes in Bering Sea ice have attracted the curiosity of scientists, but it is the potential for future change and its consequences that are an increasing

44   cause of concern for scientists, resource managers, and a broad array of Native, local, and

45   regional stakeholders.

46

47   In response, the National Science Foundation (NSF) and the North Pacific Research Board

48   (NPRB) created a novel partnership in 2007 to support an ecosystem-scale study to examine

49   how a changing climate and changing sea-ice conditions affect the EBS ecosystem, from

50   physics and chemistry to lower trophic level organisms (e.g. plankton) to humans. The

51   "Bering Sea Project" (Fig. 1) integrated two major research programs, the NSF-funded Bering

52   Ecosystem Study (BEST) and the NPRB-funded Bering Sea Integrated Ecosystem Research

53   Program (BSIERP), and was underpinned by substantial in-kind contributions from National

54   Oceanic and Atmospheric Administration (NOAA) and additional contributions from other

55   agencies, universities, and institutions. The Bering Sea Project brought together nearly 100

56   principal investigators, leading a sprawling team of several hundred postdocs, graduate

57   students, technicians, ship officers and crew, and many others. Over its seven-year course

58   of activity (2007-2014, with primary fieldwork taking place during 2008-2010), the Bering Sea

59   Project has provided new insights into the functioning of the EBS ecosystem, particularly in

60   the north-central region (~59° – ~62°N) where data sets and temporal coverage previously

61   had been sparse.

62

63   Since the final full-project meeting in early 2014, Bering Sea Project participants have

64   focused on discussion, collaboration, data analysis, and publications, culminating in nearly

65   200 peer-reviewed Bering Sea Project papers to date published across a broad spectrum of

66 journals. This growing publication library includes 76 papers in the previous three Bering Sea

67 Project special issues in Deep-Sea Research II— volumes 65-70 published in 2012, volume

68 94 published in 2013, and volume 109 published in 2014. These special issues provide a

69 home for sharing peer-reviewed results across a broad audience, and facilitate project

70 integration and synthesis. On behalf of all Bering Sea Project participants and supporters,

71 we are pleased to share this collection of papers in the fourth and final Bering Sea Project

72 special issue.

73

74 The first two special issues presented papers that described new information about the EBS

75 ecosystem, focusing on how change will affect individual species and trophic levels (Wiese et

76 al., 2012, Harvey and Sigler, 2013). Papers in those issues placed new data in historical

77 context and assessed implications for the future of the Bering Sea ecosystem. They

78 addressed one or more of the core program hypotheses that guided the entire field program

79 and provide a framework for ongoing synthesis activities: 1) physical forcing, including

80 climate, affects food availability; 2) ocean conditions structure trophic relationships through

81 bottom-up processes; 3) ecosystem controls are dynamic; 4) location matters; and 5)

82 commercial and subsistence fisheries reflect climate.

83

84 The third special issue (Lomas and Stabeno, 2014) continued to address the core

85 hypotheses and had an increased focus on mid-level synthetic activities, striving to advance

86 our understanding of the ecosystem as an integrated whole, and how it might respond to

87 changes in climate. The third issue also featured a suite of papers focused on marine

88   ecosystem connections to regional human communities and other stakeholders, within the

89   scope of the Bering Sea Project's explicit consideration of humans as part of the EBS

90   ecosystem

91

92   This fourth and final special issue continues that evolution, with further focus on synthesis of

93   information across broader ranges of disciplines and inclusion of new collaborative author

94   teams. This issue also presents information on some of the extensive model-based research

95   directions within the project. In the following paragraphs, we provide some context and brief

96   summaries of each of the papers appearing in this fourth and final Bering Sea Project special

97   issue, grouped by broad topic or trophic level.

98

99   **2. Current and future Bering Sea physical conditions**

100   Stabeno and coauthors assembled a suite of physical measures to better understand the

101   complex pattern of current transport across the EBS shelf (**Stabeno et al.**, this issue).

102   Extensive data sets were required to capture the multiplicity of sources impacting the

103   northward flow of waters to the Bering Strait. Their analyses relied on data collected over two

104   decades originating from physical moorings, satellite-tracked drifters, and shipboard

105   hydrographic transects to develop integrated maps of flow patterns on the eastern shelf.

106   These estimates were then combined with data sets of sea ice and wind fields to calculate

107   annual estimates of flow paths and velocity for the region. Results showed that large

108   horizontal spatial scales and low bathymetric relief contribute to the relatively weak (< 0.1

109   Sv), but organized, transport. Winds were an important influence on surface flow fields, but

were variable and complicated by seasonal shifts in direction, ice, and varied bottom

topography. Other dynamics influenced the bottom flow on the southern middle shelf and on

the northern shelf near the M8 mooring. Stabeno and colleagues determined the waters that

transit the more shallow areas (especially along the 50-m and 100-m isobaths) are important

contributors to transport through Bering Strait, including the waters from the Gulf of Alaska

that flow through Unimak Pass. The relatively long (8-14 months) residence times estimated

for waters flowing north also implies that most of the heat entering into the Chukchi Sea

through Bering Strait originates from air-sea interactions in the Bering Sea, rather than from

the Gulf of Alaska. The impact of sea ice remained difficult to quantify, but important

differences were seen in currents in cold versus warm years.

Hermann et al. (this issue) used three global climate simulations to predict future trends in

temperature over the EBS shelf. Their research used the Intergovernmental Panel on

Climate Change Fourth Assessment (AR4) as physical forcing to drive a regional model that

included both physical and biological elements of the Bering Sea. They found considerable

variation among the three simulations, but each downscaled projection indicated a warming

of 1– 2 °C between 2010 and 2040 on the Bering Sea shelf. In a forecast to at least 2040,

Hermann et al. found that the magnitude of presently-observed interannual variability of

bottom temperatures and ice cover is expected to be maintained, but with a steadily

increasing probability of warm years with less ice on the southern shelf. Overall, their

modeling work indicates a trend toward warmer ocean temperatures, and reduced ice in the

southeastern Bering Sea, but continued ice cover in the northeastern Bering Sea. Hermann

et al. (this issue) also attempted to determine which factors were responsible for the modeled

133   increases in temperature. Sensitivity analyses suggest both increasing air temperature and

134   northward wind as primary drivers of future increases in water-column temperatures.

135

136   **Durski et al.** (this issue) used a high-resolution 2-km model to capture the regional

137   oceanographic processes and flow patterns. In general, their model simulations compared

138   well to observations, particularly in the passes in the Aleutian arc, where flow has been

139   difficult to model because of the narrowness of most of the passes compared to the spatial

140   resolution of the models. The model simulations replicated both temporal variability, including

141   the fortnightly signal, and the magnitude of flow. The Aleutian passes play an important role

142   in mixing nutrients into the surface waters via tidal mixing, and as a pathway for oceanic

143   zooplankton. These nutrients support local production, and are also advected eastward in

144   the Bering Slope Current and onto the shelf. In addition, the Durski et al. model provided

145   insight into the decay of the cold pool during the summer, which occurs on multiple time

146   scales. This model's very high resolution (2 km x 2 km) allowed the examination of processes

147   at spatial and temporal scales not previously possible.

148

149   The reliability and utility of temperature and salinity data collected by instrumenting research

150   fishing trawls on the annual NOAA Fisheries bottom trawl surveys in the EBS was explored in

151   **Cokelet** (this issue). Equipping each trawl made on the regular grid of the annual groundfish

152   survey with conductivity-temperature-depth (CTD) instruments permits an evaluation of

153   frontal structure, stratification and temporal variability, using gridded observations from

154 roughly 1000 CTD casts over three summers on the EBS shelf. These gridded data provide

155 information on both along- and across-shelf spatial patterns in temperature and salinity.

156

157 **3. Phytoplankton abundance and productivity**

158 The Marginal Ice Zone (MIZ), where ice breakup and melt occurs, has long been known to be

159 an important Bering Sea physiographic feature for enhanced primary production. This is due

160 to stabilization of the water column by ice melt and seeding of the water column with ice

161 algae melting out of the ice. **Sambrotto et al.** (this issue) show that while the contribution of

162 ice algal seed populations and the shallowing of the mixed layer depth were contributory

163 factors to the establishment of MIZ blooms, those factors were by themselves not sufficient to

164 explain the spatial variations in bloom intensity. Rather, in situ observations suggest that ice

165 melt was releasing additional growth factors (e.g. particulate and dissolved iron and dissolved

166 organics) into the salinity stratified water column that were leading to enhanced primary

167 production and phytoplankton growth. On the western regions of the shelf and near the St.

168 Lawrence Island polynya, advection of MIZ water under the ice, coupled with light

169 transmission through the ice, allowed for continued primary production that was not readily

170 observed in ocean color data by satellites. This 'hidden' production may account for nearly

171 one third of the annual production in the non-shelf break regions of the EBS.

172

173 Physical and chemical control of phytoplankton production and abundance occur year round,

174 and the Bering Sea Project aimed to encompass studies that examine control mechanisms

175 across all seasons. **Eisner et al.** (this issue) analyzed a 10-year record (2003-2012) of late

176 summer/early fall phytoplankton abundance (estimated by chlorophyll-*a*) on the EBS, and

177   observed that warm years in the early part of the record (2003-2005) were characterized by

178   higher chlorophyll-*a* concentrations on the southern outer and middle shelf domains than

179   those same regions in cold years (2007-2012). These elevated chlorophyll-*a* conditions in

180   warm years were also associated with a higher prevalence of larger phytoplankton cells.

181   Eisner et al. observed that the frequency of wind-mixing and sea surface temperature were

182   positively correlated with both total chlorophyll-*a* and the large size fraction of phytoplankton

183   chlorophyll-*a*, suggesting that a combination of repetitive nutrient injection and temperature-

184   enhanced growth supported this accumulation of phytoplankton biomass on the southern

185   shelf. In a companion study, **Gann et al.** (this issue) examined processes during a single,

186   cold year (2007) when there was a particularly obvious absence of wind mixing and thus

187   nutrient entrainment. During that summer of 2007, they observed some of the lowest

188   measured rates of primary production on the southern shelf. While the differences in

189   chlorophyll-*a* between warm and cold temperature stanzas were obvious over the

190   southeastern Bering Sea shelf, they were not observed on the northern shelf— consistent

191   with prior Bering Sea Project studies that showed a decoupling of change between the

192   northern and southern shelf (e.g. Stabeno et al., 2012). These patterns in phytoplankton

193   abundance and productivity in the late summer are curiously out of phase with patterns in

194   large crustacean zooplankton abundance and biomass, which are highest during cold

195   stanzas, suggesting a trophic connection complicated not only by physics, but by biology as

196   well.

197

198   Previous field observations indicate that spring and fall phytoplankton blooms on the EBS

199   continental shelf co-vary, so that a year with a strong spring bloom also tends to have a

200   strong fall bloom (Sigler et al., 2014). Similar co-variability of primary production is also seen

201 in the multi-year (1987–2007) integration of a coupled physical–biological model described in

202 earlier Bering Sea Project publications (e.g. Gibson and Spitz, 2011; Gibson et al., 2013;

203 Hermann et al., 2013). **Cheng et al.** (this issue) used a coupled, physical–biological model

204 simulation to examine the relative contributions to this co-variability of wind mixing, local

205 nutrient recycling/regeneration, horizontal nutrient advection, and water-column stability.

206 They found no significant correlation between the spring and fall surface wind mixing, and

207 concluded that although wind mixing is an important mechanism for bringing nutrients in the

208 lower water column to the surface layers in the EBS, it is not the mechanism tying the two

209 seasons' productivity together. They highlight the importance of local recycling and

210 regeneration of nutrients assimilated during spring phytoplankton bloom in linking together

211 the spring and fall primary productions on EBS shelf region.

212

213 The work by **Liu et al.** (this issue) examined phytoplankton carbon cycling using an analytical

214 model to estimate daily, mixed-layer gross primary production (GPP) together with 8-day,

215 chlorophyll-*a* composite satellite images of phytoplankton biomass fields to describe the total

216 phytoplankton loss from the mixed layer. The model was applied to five regions of the EBS

217 shelf over the major domains to quantify GPP and total phytoplankton losses, and to compare

218 differences between warm and cold stanzas of years. Additional information including

219 calculated SST and mixed layer depth were obtained from database and field archives. The

220 annual shelf-wide mean modeled Chl-*a* concentration was slightly higher in warm years than

221 in cold years, but the difference was not significant. This is consistent with findings for

222 August-September by Eisner et al. (this issue), who saw higher Chl-*a* during warm years, but

223 results were not significant over the majority of the shelf. Although the dynamic nature of

224 phytoplankton blooms over the water column and their spatial extent complicate the

10

225 observations, maximum GPP values were seen during the spring bloom and minimum values

226 in the summer. Warm years were slightly higher than cold years for annual GPP and carbon

227 loss terms, but differences between climate regimes were not significant in most instances.

228 Modeled estimates of losses from microzooplankton grazers were consistent with published

229 field observations that microzooplankton grazing loss is a relatively small fraction of

230 phytoplankton standing biomass (<10%), but can be a significant impact on daily primary

231 production, with the percent grazed higher in summer than spring. Overall, respiration

232 dominated total loss, following by the losses due to zooplankton grazing and sinking. The

233 authors noted that the summation of all loss processes did not account for phytoplankton total

234 loss, suggesting that additional processes or more detailed information are needed to fully

235 calibrate chlorophyll estimates determined by satellite.

236

237 **4. Zooplankton**

238 Euphausiids and large copepods are important parts of the EBS marine food web and are

239 essential components of fish, seabird, and marine mammal diets in the region. In particular,

240 for walleye pollock (*Gadus chalcogrammus*— a commercially and ecologically important

241 species and a focal fish species in the Bering Sea Project—hereafter referred to as 'pollock'),

242 large copepod and euphausiid populations have been shown to be an important predictor of

243 recruitment (Heintz et al., 2013, Siddon et al., 2013). Several manuscripts in this special

244 issue address the ecology of these important zooplankton taxa and their role in the

245 ecosystem. **Campbell et al.** (this issue) documented spring grazing rates and diet of major

246 crustacean zooplankton taxa during three sequential cold years for the middle and outer EBS

247 shelf. The proportion of microzooplankton in crustacean zooplankton diets was higher than

248 that found in the prey field for six of the eight taxa examined, indicating selection for

249 microzooplankton. However, phytoplankton and ice algae were the most important

250 component of the diet because they accounted for a much greater fraction of the prey

251 biomass. The grazing impact of zooplankton as a whole (comprising both micro- and

252 mesozooplankton) was a small fraction of the total standing stock of chlorophyll, and was

253 generally 50% or less of primary production during spring phytoplankton blooms. This leaves

254 a large fraction of primary production available for direct transport to the benthos to support

255 high biomasses of infauna and epifauna, including many flatfishes.

256

257 **Bailey et al.** (this issue) applied molecular bar coding techniques to understand the

258 distribution and abundance of *Pseudocalanus* adult females during a single year. From

259 specimens collected over the outer and middle shelf regions, they found four species— two

260 temperate (*P. mimus*, *P. newmani*) and two arctic (*P. acuspes*, *P. minutus*). Temperate

261 species were more abundant over the outer shelf, while the arctic species were more

262 abundant over the middle shelf. Low genetic diversity within each species suggests high

263 levels of connectivity across the shelf. *Pseudocalanus* nauplii and copepodites are an

264 important prey item for early feeding larval pollock, and the loss of the two Arctic

265 *Pseudocalanus* species during warm periods or due to climate-induced warming of the whole

266 ecosystem could impact the condition of larval pollock, because the arctic species typically

267 contain higher lipid levels than the temperate species.

268

269 A second study on *Pseudocalanus* examined feeding differences across species using a

270 different molecular technique (18S rDNA) to identify prey items in the water and guts of

271 *Pseudocalanus* (**Cleary et al.**, this issue). In this case, copepodites of various stages were

272   used from some of the same 2010 collections used in the Bailey et al. study. Their diets were

273   generally very broad (and included other metazoans), but there were dietary differences

274   discovered across species. *P. acuspes,* an arctic species, had a high proportion of

275   heterotrophic dinoflagellates in its diet, while *P. minutus*, another arctic species, had a high

276   proportion of material from gelatinous plankton, except when captured in waters with high

277   chlorophyll concentrations when they had a high proportion of diatoms in their diet. These

278   results describe both niche separation as well as an ability to use multiple prey types— an

279   ability that may be useful if the structure and function of the southeastern Bering Sea

280   changes due to climate induced warming.

281

282   **Pleuthner et al.** (this issue) examined the feeding and lipid storage of euphausiids, during

283   both late spring and early summer through a series of feeding and starvation experiments,

284   and analysis of the lipid composition of the euphausiids and of their prey. They found

285   seasonal differences in the extent to which euphausiids lost lipid under starvation, with the

286   early summer euphausiids losing less lipid than the late spring euphausiids. They also found

287   that although the individual lipid biomarkers in the euphausiids in spring versus summer

288   reflected the longer-term seasonal switch from ice algal diatom to heterotrophic prey (e.g.

289   microzooplankton), shorter-term changes in euphausiid diet were not consistently reflected in

290   lipid composition.

291

292   In a review of the available information on euphausiids, **Hunt et al.** (this issue) use a

293   synthesis approach to summarize the state of knowledge of bottom-up and top-down controls

294   of euphausiids. This was attempted to understand the implications for higher trophic level

295   species such as pollock and the marine mammals that rely upon them for food. Based upon

296 modeled rates of euphausiid production, the authors found sufficient primary production to

297 support euphausiid production. Pollock were estimated to consume only 20-35% of that

298 euphausiid production in spring and summer. These observations complicate the explanation

299 of a strong, negative correlation between pollock biomass and euphausiid biomass, and the

300 simultaneous negative correlation between euphausiid biomass and water temperature. In

301 fact it is likely that neither top-down control by pollock, nor bottom-up control by the

302 availability of food is the sole determinant of euphausiid biomass; rather, controls on

303 euphausiid biomass, and thus its central role in the EBS ecosystem, vary as a function of the

304 mean temperature state of the system.

305

306 The **Sigler et al.** (this issue) team brought insights from previous papers together with some

307 new results in a synthesis that explored: 1) linkages between primary and secondary

308 production, particularly in cold versus warm years; 2) bioenergetics and seasonality of

309 copepods, euphausiids, and pollock; 3) the importance of location and the different conditions

310 of sea ice and the timing of production for the success of larval pollock and their crustacean

311 prey; and 4) annual to multi-year shifts (associated with large-scale atmospheric drivers) in

312 the intensity of top-down control of crustacean zooplankton by pollock. They found that

313 production is closely linked to sea-ice conditions and seasonal timing. Favorable locations

314 for crustacean zooplankton, and thus for pollock, are defined not only by water temperature

315 and depth, but also by the extent and timing of sea ice in the spring. Predation pressure and

316 top-down control is greater during cold periods when pollock are successful because of

317 enhanced availability of their crustacean prey; warm years lead to less intense predation

318 pressure because reduced prey availability limits pollock success. During switches from

319 warm to cold periods, the faster-responding planktonic system rebounds first and enjoys a

320   brief period (1-2 years) of reduced predation pressure before the pollock in turn respond to

321   the favorable feeding conditions. In cold years, crustacean zooplankton exploit high primary

322   production and in turn sustain vigorous pollock populations, while in warm years the life

323   cycles of the crustacean zooplankton are not well matched to the timing of primary production

324   so zooplankton abundance, and availability as prey to pollock, remains low. The Sigler et al.

325   synthesis highlighted key influences on patterns of primary and secondary production— and

326   ultimately on the success of pollock populations— including the importance of the extent and

327   timing of sea ice, the alternation of periods of warm and cold years shaped by these changes

328   in sea ice, location-specific sea-ice characteristics, and the overlying atmospheric drivers on

329   the Bering Sea ecosystem.

330

331   **5. Fish ecology**

332   Our understanding of the life history and ecology of important fish species reached a new

333   level over the course of the Bering Sea Project. For example, **Andrews et al.** (this issue)

334   examined the effects of warm and cold periods on two forage fish species, capelin (*Mallotus*

335   *villosus*) and Pacific herring (*Clupea pallasii*). Time series that were begun before the

336   coordinated effort of the Bering Sea Project were essential to documenting patterns in

337   distribution and abundance. Andrews and colleagues found that the catch per unit effort

338   (CPUE) of both species was higher in the northeastern than the southeastern Bering Sea,

339   and was higher during cold conditions than during warm conditions. Fish length was not

340   significantly different between warm and cold periods, but herring length did show differences

341   among geographic regions, with increasing size toward the shelf break, most likely due to

342   migratory behavior. Diet also differed between warm and cold conditions, with warm year

15

343   forage fish diets in the southeastern Bering Sea exhibiting the same lack of large, lipid-rich

344   crustacean zooplankton as seen for other fish species. One interesting result was the high

345   proportion of age-0 pollock in the diet of herring in warm years. Herring had not previously

346   been identified as a major predator of young pollock.

347

348   An analogous approach was taken with the ecology of Pacific cod (*Gadus macrocephalus*)

349   age-0 diet, using collections from surface trawls to examine size, diet, and condition of age-0

350   Pacific cod during warm, average, and cold periods (**Farley et al.**, this issue). Similar to

351   capelin and herring, young cod were found to have a high proportion of age-0 pollock in their

352   diets in warm years, and high proportions of large crustacean zooplankton in their stomachs

353   in cold years. Similar to age-0 pollock, energetic status (body condition) of age-0 Pacific cod

354   was highest in the cold years when their diet focused on large crustacean zooplankton.

355   Therefore, although there are distinct life history differences between these two gadid

356   species, there are also strong similarities in how their early pelagic stages respond to

357   alternating periods of warm and cold conditions. This suggests that gadid recruitment in this

358   region is being controlled by direct and indirect effects on prey quality and quantity, and by

359   their condition or caloric density prior to the first winter.

360

361   **Parker-Stetter et al.** (this issue) examined the environmental factors affecting spatial

362   distributions of forage fish species. They examined the distributions of capelin, age-0 pollock,

363   and age-0 Pacific cod, and evaluated the influence of both local and annual environmental

364   indices, with the latter accounting for the possibility that overall distributions changed with

16

365 annual conditions. They found that local, but not annual, environmental indices were most

366 important for capelin (e.g., local temperature), whereas both local and annual indices were

367 important for age-0 pollock and age-0 cod (e.g., local temperature and annual sea-ice

368 anomaly). Only two indices (local temperature and depth) influenced all three species,

369 emphasizing the importance of these two indices, but also demonstrating that the prediction

370 of distributions is complex. The results of Parker-Stetter et al. are applicable to our

371 understanding of climate effects on spatial distributions, and also to future distribution and

372 recruitment modeling efforts that build on the five model-based papers described in this

373 issue.

374

375 **Miller et al.** (this issue) conducted an investigation—not formally part of the Bering Sea

376 Project, but closely related to it—that attempted to connect juvenile (age-0) Pacific cod and

377 their collection locations to known natal areas, using the isotopic signatures contained in

378 otoliths. Although it was not possible to make the connection, they did identify chemically

379 distinct larval source signatures with mixing patterns that appeared to vary between the two

380 years (2006 and 2008) for which they had samples. The varying mixing patterns between the

381 two years may have been attributed to differential spawning locations and shelf circulation

382 between the average and cold years (e.g. Petrik et al., 2015). Identification of unique

383 chemical signatures on the open shelf provides support for the further application of this

384 technique to understand the relative contributions of different natal areas to eventual

385 recruitment, and the demonstrated ability of the technique to identify collection site based on

386 otolith edge chemistry suggests an ability to discern the relative productivity of multiple

387 juvenile nursery areas.

388

Duffy-Anderson et al. (this issue) used the many Bering Sea Project discipline-specific and

component studies, plus the historical literature, to synthesize the present state of knowledge

for the first year of life for a focal fish species, pollock. The eastern Bering Sea is at the

northern end of the current range of pollock, so environmental variability is expected to have

a significant influence on recruitment. The first year of life, and in particular the nutritional

status leading up to the first winter, has been identified as the recruitment bottleneck. The

Duffy-Anderson et al. synthesis resulted in an evaluation of the strengths and weaknesses of

our current paradigms to explain pollock recruitment variability in mechanistic terms. The

review covers a critical discussion of knowledge regarding the distribution, feeding ecology,

growth, and predation for each early life history stage (spawning, egg, larvae, and juvenile)

and different approaches to modeling of the first year of life. In addition, they critically

evaluate current recruitment control paradigms: Differential transport; nutrition and condition;

and predation. Duffy-Anderson et al. conclude with a discussion of current knowledge gaps,

and recommend nine research areas that, if successfully developed, would enable us to

reach a higher level in understanding pollock recruitment variability. In brief, these research

areas and data gaps are: Full seasonal sampling, particularly through the first winter;

predation dynamics and trophic consequences of predation, particularly those factors which

affect young pollock vulnerability to predation; a more complete understanding of the

relationship between diet and condition, and physiological and behavioral responses to prey

shift; laboratory-based studies of physiology and growth to produce data necessary to

parameterize models; development of coupled, spatially-explicit models of the first year of

life; stage-specific predictive models to test and quantify the impact of variable mortality on

411 recruitment; identification of critical production areas for each early life history stage;

412 assessment of the potential impacts of competition with other planktivorous fishes and

413 invertebrates; and development of approaches that can successfully resolve the daily ages of

414 larval and juvenile pollock in the cold eastern Bering Sea.

415 In a related paper, **Buckley et al.** (this issue) used Bering Sea Project results in combination

416 with several additional long time series (1987-2011) to examine interannual, regional, and

417 size-dependent differences in summer feeding by pollock. Copepods were a small fraction of

418 the diet in the inner shelf, where mysiids and euphausiids tended to dominate the diet. In the

419 northern-most regions sampled, amphipods and other fishes had increasing importance in

420 diets as the size of the predator increased. Summer feeding success (indexed by stomach

421 fullness) for intermediate-sized pollock was related to copepod consumption, while that for

422 slightly larger pollock was related to prey that were not euphausiids. Interannual patterns in

423 copepod prey availability appeared to be important in the diet of younger pollock, while

424 patterns in the availability of euphausiids were observed in the diets of older, larger pollock (≥

425 60 cm fork length). Thus the impacts of climate change on pollock may differ with the age of

426 the fish, depending on what part of the zooplankton community is most affected, and the

427 region where young pollock spend their summer.

428

429 **6. Marine Mammals**

430 The EBS has historically been important habitat for a wide range of marine mammal species,

431 including baleen whales such as fin whales (*Balaenoptera physalus*), humpback whales

432 (*Megaptera novaeangliae*), minke whales (*B. acutorostrata*), and North Pacific right whales

433   (*Eubalaena japonica*). Intensive commercial harvest of baleen whales in the 1900s resulted

434   in depletion of most baleen whale populations in the EBS; since the cessation of commercial

435   whaling in the mid-20th century, some populations are recovering (fin and humpback whales),

436   while North Pacific right whales are not recovering. Currently, baleen whale populations are

437   seasonal in their use of the EBS region, with maximum numbers during their spring and

438   summer feeding periods. In a study that combines extensive at-sea observational data and

439   environmental and prey data together with a detailed statistical model, **Zerbini et al.** (this

440   issue) provide a novel habitat baseline for baleen whales in the EBS, based on a quantitative

441   assessment of the relationship between whale abundance, environmental variables such as

442   sea surface temperature and chlorophyll concentration, and the density of key prey species:

443   euphausiids and age-1 pollock. This work demonstrates the added value provided by

444   working within the broadly integrated Bering Sea Project, although Zerbini and colleagues

445   note that the robustness of the relationships—and their applicability to forecasting—still

446   needs fuller validation with additional years of survey data.

447

448   **7. Fisheries management**

449   Application of project results to the top trophic level— humans— has been a consistent and

450   important goal of the Bering Sea Project. For example, in the third special issue, project

451   participants reported on how ecological information emerging from the Bering Sea Project

452   connected to subsistence harvests of local communities (e.g. Renner and Huntington, 2014).

453   In this issue we publish a set of six related articles by a group of authors on resource

454   assessment and modeling, incorporating focus on an ecosystem-based approach to fisheries

455   management (EBFM). Increasing awareness of the interconnections among species and

456   ecosystem conditions, together with concern over long-term cumulative impacts of

457   commercial fishing on marine ecosystems, have led to calls for a move towards EBFM, either

458   in addition to, or as replacement for, traditional single-species management. This topic fits

459   squarely within the core aims of the Bering Sea Project, which included providing information

460   relevant to the commercial fishing industry and of direct or indirect use to fishery managers.

461   However, moves toward multispecies and ecosystem-based management are complex and

462   have proven challenging to bring to implementation. In an innovative modeling study,

463   **Uchiyama et al.** (this issue) used biomass estimates and predation data derived from annual

464   groundfish surveys in the Bering Sea, and then developed two forms of age-aggregated

465   biomass models—a multispecies biomass dynamics (MBD) model, and a multispecies delay

466   difference (MDD) model —to study the biomass dynamics of the four major groundfish

467   species or species groups in the eastern Bering Sea. Despite a need for model

468   improvements and additional model evaluations, Uchiyama et al. provide a useful step

469   forward in multi-species management approach, and their work can be used as a tool to

470   improve single-species stock assessments currently used, and enable further exploration of

471   the performance of harvest control rules aiming to maintain healthy populations of the Bering

472   Sea groundfish complex as a whole.

473

474   In the EBS there are strong trophic connections between pollock, arrowtooth flounder

475   (*Atheresthes stomias*), and Pacific cod due to interspecific predation of juveniles (Aydin and

476   Mueter, 2007). **Moffit et al.** (this issue) explore how to develop and test multi-species

477   biological reference points (MBRP) for use in setting harvest control rules of commercially-

478   exploited species. Their work explored a range of approaches, from use of a relatively

479   simple, two-species model (pollock and cod) to using system wide, multi-species maximum

480   sustainable yield models (MMSY). In the simplest case, they calculated the fishing mortality

481   for each species' $F_{x\%}$ (the fishing mortality which reduces the spawning biomass per recruit of

482   that species to x% of unfished biomass (B_0)) while assuming the average fishing mortality

483   applied to all other species. In this method the natural and fishing mortality for each species

484   is calculated from the multi-species model. The pollock-cod model predicted that pollock

485   recruitment increased with increasing fishing mortality of cod (due to predation), while cod

486   recruitment suffered as pollock fishing mortality increased (lower food availability for cod).

487   Plots of the modeled fishing rate of pollock ($F_{40\%}$) as a function of the fishing rate of cod

488   enabled them to identify combinations of fishing rates on the two species that exceeded the

489   overfishing limit. This simplest case is the one closest to how reference points are computed

490   with the current single-species management in Alaska. When comparing the relatively simple

491   method of obtaining MBRP with the more complicated MMSY models, it appeared that in

492   some cases the more complicated models yielded catch rates that were as high or higher

493   than the rates calculated from the simpler models.

494

495   **Holsman et al.** (this issue) expanded upon the work of Moffit et al. and asked if multi-species

496   assessment models could be used to quantify the direct and indirect effects of climate and

497   fisheries harvest on fish populations. The question was addressed using single species and

498   multi-species, statistical catch-at-age (MSCAA) models. This particular model (Climate-

499   Enhanced, Age-based model with Temperature-specific Trophic Linkages and Energetics, or

500   'CEATTLE') included three interacting species from the EBS— pollock, Pacific cod, and

501   arrowtooth flounder— and incorporated temperature-specific growth and predation rates.

502   The strength of temperature effects depended upon species and model type. Biological

503   reference points for arrowtooth flounder were the most sensitive to changes in temperature,

504   while temperature effects on the MBRP for pollock and cod were difficult to discern due to

505   resulting high variability caused by different harvest scenarios and predation rates in the

506   absence of temperature change. The model demonstrated the large impact of annual

507   predation on juvenile pollock; this predation (primarily cannibalism) represented an important

508   control on population dynamics. Interactions between climate (temperature) and trophic

509   drivers did influence the MBRPs, but trophic and management-driven changes (i.e. fishing

510   rates on the predators) can exceed or at least make it difficult to detect the direct effects of

511   temperature on growth and predation. Results from this study provide a good example of the

512   complexity of fisheries management under changing climate conditions, and how MSCAA

513   models could be implemented for the annual setting of fishery quotas in the EBS.

514   Once multiple models (e.g., single species, multi-species, etc.) are developed for a

515   geographic region or large marine ecosystem, the question "which model is right?" arises. In

516   other words, which model provides harvest recommendations and biological reference points

517   that ensure the sustainability of the target populations? Each model will have its own

518   strengths and weaknesses based on the underlying construction, and the variation in

519   agreement among models, even among similar models, can be large. **Ianelli et al.** (this

520   issue) advocate for combining results from "competing" stock assessment model using a

521   method called ensemble forecasting, commonly used in climate forecasting. They review

522   alternative ways to implement model averaging for EBFM, and then apply averaging to three

523   types of stock assessment models (single-species, single species with temperature-specific

524   weight at age, and temperature-specific multispecies) to examine how fishing in the EBS

under four different temperature scenarios may impact the spawning stock biomass of

pollock, Pacific cod, and arrowtooth flounder in the future (present to 2039). The authors

advocate the use of multiple models and model averaging to provide new and improved

insight into uncertainty in our stock assessments. This improved understanding of

uncertainty may then help managers set harvest control rules that improve our ability to meet

management goals such as avoiding overfishing.

Ortiz et al. (this issue) explored ecological processes with a novel integrated "end-to-end"

ecosystem model that brought a physical oceanographic model (ROMS- Bering10K) together

with a lower trophic nutrient-phytoplankton-zooplankton model (BESTNPZ) and an upper

trophic fish model ("Forage and Euphausiid Abundance in Space and Time", or FEAST). By

combining field data and end-to-end model output, Ortiz et al calculated weekly climatologies

and times series of physical and biological drivers from 1971-2009 for multiple distinct

regions of the EBS shelf and slope, and evaluated the reliability of such a complex

ecosystem model through comparison with observations. The model illustrated two large-

scale gradients that characterize overall EBS dynamics and also revealed specific ecosystem

processes, including how the seasonal warming of air temperature and the spring-summer

expansion of the warm pelagic and bottom habitats influence the seasonal sea-ice retreat

and the associated ice edge and open-water spring phytoplankton blooms, as well as the

subsequent production of copepods and euphausiids. The Ortiz et al. hindcast exhibited skill

in reproducing seasonal and temporal patterns in hydrography and biology, provides a year-

round framework for local or seasonal observations, and has helped identify gaps and guide

research, both in the design of new surveys and the targeted temporal focus of surveys.

548

Finally, the **Punt et al.** (this issue) essay describes how a "Field-integrated End-to-End"

modeling approach that includes management strategy evaluation can be developed to

implement an EBFM approach in the EBS. The approach advocates future creation of

harvest control rules that incorporate ecosystem information, rather than the present system

that relies solely on estimates of stock biomass relative to reference biomass levels. In

addition, an important part of this essay is the presentation of guidelines and principles for the

development of ecosystem models and recommendations for best practices based on the

Bering Sea Project experience. In retrospect, principal investigators working on model-based

components found the breadth and depth of Bering Sea Project models challenging to

implement. In this essay, Punt et al. provide perspectives that may help in the design of

future ecological modeling work, based on their hard-earned Bering Sea Project experience.

These include: logistical support of large-scale software development should be on par with

fieldwork support; ensure clear separation of scientific versus logistics oversight; promote

open and frequent communication with field biologists; ensure the adequacy and availability

of field data for model validation and testing; recognize that most modeling work is sequential

and iterative as opposed to simultaneous and independent; and recognize there is a

mismatch of required performance levels and performance measures between single

discipline approaches and multi-disciplinary approaches.

567

8. Syntheses and Conclusions

569

570   The Bering Sea Project's internal steering committee (the "Science Advisory Board" or SAB)

571   initially envisioned that the series of four special issues in Deep-Sea Research Part II would

572   show a progression from relatively directed and focused reports, to broader syntheses. In

573   practice, elements of both types of study appear in this final special issue. Some of this can

574   be attributed to special studies added to the project well after its inception (e.g. Bailey et al.,

575   this issue, Cleary et al., this issue), but other directed investigations are just now emerging

576   (e.g. Cokelet, this issue). After this massive effort involving nearly 100 principal investigators

577   and some 25,000 person-field days, results will continue to find their way into the literature for

578   years to come. At this point we know that several intermediary syntheses have been

579   completed and others are well underway, and we look forward to the emergence of future

580   work.

581

582   *8.1 Synthesis examples*

583   To date, there are many examples of synthesis-focused advancements in our understanding

584   of the Bering Sea ecosystem stemming from the Bering Sea Project. To supplement

585   individual paper descriptions, here we highlight three selected examples that span multiple

586   papers across the whole program (including some within this special issue series and some

587   published elsewhere), are indicative of the success of the project as a whole, and represent

588   some of the project breadth. First is an important and complex story emerging from a group

589   of the lower-trophic level studies. Investigators were able to describe how bottom-up

590   processes in a marginal ice zone influence both lower and upper trophic levels. In the

591   eastern Bering Sea ice, ice algae and cold winters help to promote the establishment of

592   strong year-classes of large crustacean zooplankton (copepods and euphausiids). This

593 combination of conditions promotes lipid storage in those taxa, which in turn provides a

594 critical energy source for juvenile fish, such as pollock. Although the number of early juvenile

595 pollock in warm years is often higher than that in cold years, winter survival of juveniles

596 produced during a warm year is low. It is the late summer ingestion of abundant, lipid-rich,

597 crustacean zooplankton during cold years that enable juvenile pollock to store enough energy

598 reserves of their own to survive the first winter.

599

600 Warming of the ocean, and loss of sea ice at high latitudes in particular, are cause for

601 concern. One question on the minds of those that harvest resources from the Bering Sea is

602 how will warming impact the distribution and availability of those resources. In a second

603 example of broad, synthesis advancement in understanding, Bering Sea Project studies

604 concluded that many subarctic demersal and semi-demersal fishes will not be able to

605 penetrate very far into the high arctic, even after the southeastern Bering Sea loses its

606 winter/spring sea ice. This is because at high latitudes (> ca. 62° N) physical conditions

607 combine to result in the region remaining dark and frigid in the winter, with continued

608 advection and formation of sea ice. Thus in the near future the shelf in this northern region is

609 likely to continue to be covered by cold (< 2° C) bottom water during the summer, and this

610 landscape-scale feature will continue to be a barrier to demersal and semi-demersal

611 subarctic fishes. The situation for pelagic fishes, such as Pacific salmon, while less certain,

612 appears different, and an increase in salmon species in the northern Bering Sea and Chukchi

613 Sea has already been observed (Eisner et al. 2013).

614

615   Teams of researchers within the Bering Sea Project also investigated bottom-up processes

616   affecting higher trophic levels. In a third example of a broad, multi-investigator advance,

617   comparison was made of food availability between two colonies of Northern fur seals

618   (*Callorhinus ursinus*), one situated on the shelf (Pribilof Islands) and the other on a tiny island

619   in the oceanic basin (Bogoslof Island). It was known that the Pribilof population on the shelf

620   has seen pup production decline by some 80% since the 1950s, and the population of adults

621   has been declining at an annual rate of ~5% since 1998, while in recent decades the

622   population from the Bogoslof oceanic site was increasing (Battaile et al. 2015). What hasn't

623   been understood is the cause of the Pribilof decline, particularly because scientists often view

624   the shelf as a more productive region than the oceanic basin. Previous tagging studies ruled

625   out immigration or emigration. Using a combination of sophisticated logging instrumentation

626   and at-sea oceanographic and bioacoustic work, Bering Sea Project scientists discovered

627   that prey availability and foraging efficiency for fur seals was higher at the oceanic rookery

628   than at the shelf site. Prey available to fur seals at the oceanic rookery were both closer

629   (requiring shorter trips for lactating females), and more energy-rich than the prey available to

630   fur seals traveling from the shelf Pribilof rookery.

631

632   *8.2 Reflection and conclusion*

633   Large, interdisciplinary programs come with large risks, but also with potentially large

634   rewards. At every level, success depends on the talent, ingenuity, and the altruism of

635   participating scientists. Luck, timing, and serendipity also play roles in the success of large

636   research programs. Have methods and technology used in the independent fields of study

637   progressed far enough for the next big advancement? Are the project hypotheses cleverly

638 constructed to enable meaningful conclusions? Will the conditions under which the field

639 years are conducted allow the scientists to actually test the hypotheses? Will scientists work

640 well in teams that go beyond their immediate projects? Will scientists allow themselves and

641 the program to be guided by a team of peers? If the Bering Sea Project is seen as fully

642 successful, it is only because the participants succeeded in meeting many of these

643 challenges.

644

645 As described in this special issue's opening "Appreciation", many key individuals working in a

646 variety of programs helped to set the stage and collect datasets that were later used in this

647 project. Building from earlier work, teams of scientists crafted framework hypotheses and

648 questions after much discussion and multiple workshops. Then, as the project was launched,

649 nature had a surprise in store and provided a challenge— following a series of warming years

650 prior to project inception, Bering Sea Project participants were faced with three "cold"

651 fieldwork years during which atmospheric conditions resulted in extensive sea-ice coverage

652 and colder-than-average ocean temperatures. The next "warm" year wouldn't occur until four

653 years after field research was concluded.

654

655 Fortunately, thanks to the efforts of many scientists working in the region prior to the Bering

656 Sea Project, data from previous programs conducted during warm climate regimes were

657 available for reference, and were successfully used by scientists in their analyses and

658 syntheses. Project scientists willingly extended themselves to work in groups that went well

659 beyond their own components. Common interests and curiosity helped to form powerful and

660   productive partnerships. And participating scientists were responsive to suggestions and

661   challenges from both those who prepared and launched the Bering Sea Project on this

662   journey (see Appreciation) and the members of the SAB and program managers who guided

663   the project to this concluding issue.

664

665   Investment in an integrated ecosystem research approach to the EBS ecosystem paid many

666   dividends. First and foremost, the results achieved by the project researchers would likely

667   not have been accomplished by a series of individual projects spaced over a longer time

668   period. The breadth of the team of investigators resulted in a deep and broad publication

669   record, and empowered the ability to answer questions about the conservation and

670   management of living marine resources. Finally, the success of individual projects helped to

671   establish new collaborative relationships among scientists that will last into the future for

672   additional studies in this and other ecosystems.

673

674   This large expansion of information suggests that there has been a worthy payoff of the risks

675   taken by NSF and NPRB to partner with each other and with NOAA and other organizations

676   in a broad, complex, integrated ecosystem research program. The Bering Sea Project has

677   resulted in a large increase of knowledge in an important ecosystem; it was able to address

678   many of the program hypotheses, it increased our knowledge of how warming and loss of sea

679   may impact the ecosystem in the future, and it was able to address some of the questions

680   posed by those that use and manage resources from the region. We look forward to

681   continued advancement of understanding in the ecology of this rich and vital region. And we

682 expect that future scientists will re-examine what we learned, refute parts of it, and build upon

683 other parts to provide a more mechanistic, predictive, and holistic understanding of the Bering

684 Sea ecosystem, just as we built upon results and insights from earlier researchers.

685

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704

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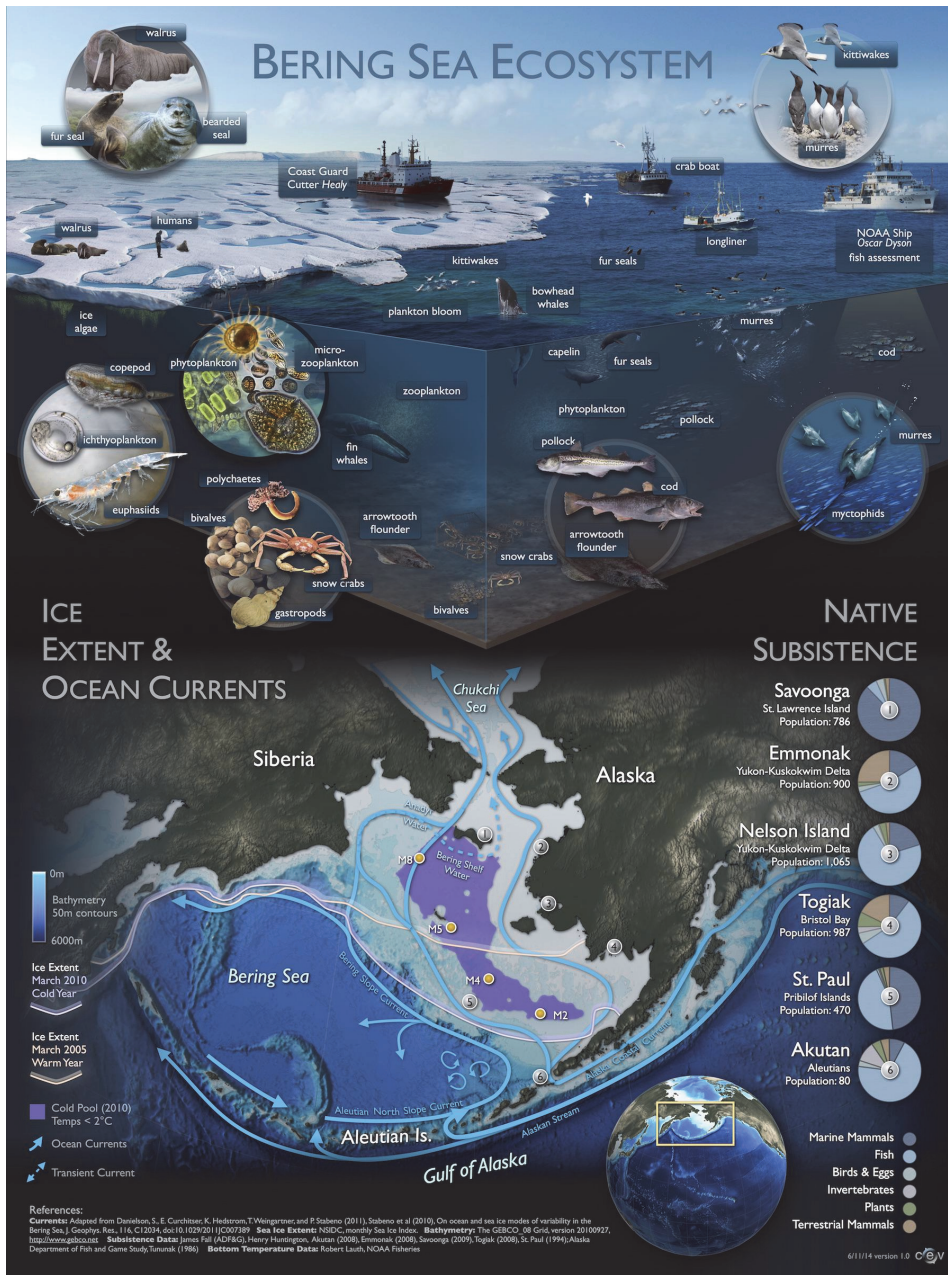
Figure 1. An illustration of the eastern Bering Sea shelf ecosystem and the framework of the
Bering Sea Project, showing the predominant currents and species, research platforms, ice
extent, location of the 'cold pool', and also depicting the focal coastal communities and their
primary subsistence harvest.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

869   and basin, extending south from the Bering Strait and north from the Alaska Peninsula and
870   eastern Aleutian Islands.