

1 **NORTH PACIFIC RESEARCH BOARD PROJECT FINAL REPORT**

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8 **Correlative Biomass Dynamics Model**

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14 NPRB Project B75 Final Report

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35 **Abstract**

36 Our first goal was to develop an age-aggregated multispecies model describing biomass dynamics of
37 some commercially and ecologically important groundfish species in the eastern Bering Sea. We
38 constructed multispecies models including walleye pollock, Pacific cod, arrowtooth flounder, and three
39 other flatfish species, including their trophic interactions. Two alternative model formulations were
40 developed: a multispecies biomass dynamics (MBD) model and a multispecies delay difference (MDD)
41 model. Both models were able to capture observed trends in survey biomass data over 1982-2009 and
42 both predicted the multi-species B_0 , MSY , and F_{MSY} to be lower than the sum of the estimates from single-
43 species assessment models. Although the MDD model fit survey biomass estimates better than the MBD
44 model, the MDD model and its maximum likelihood parameters produced biologically unrealistic
45 biomass projections at $F > 0.14$. Using the MBD model, our second goal was to test a hypothesis that
46 reduction in the extent of the cold pool intensifies predation on juvenile pollock. We found that warmer
47 temperatures increase cannibalism and predation on age-1 pollock by adult pollock (age 3+) and
48 arrowtooth flounder, respectively, and decreases cannibalism on age-0 pollock by adult pollock. The
49 opposite effect of water temperature on age-0 and age-1 pollock likely reflects different distributions of
50 these pollock age classes in relation to the cold pool. Our multispecies models provide useful tools for
51 management strategy evaluations and they can be used to examine the effects of future climate change on
52 the groundfish community on the eastern Bering Sea continental shelf.

53 **Key words:**

54 Multispecies model, eastern Bering Sea, biomass dynamics model, delay-difference model, predator-prey
55 interaction, cold pool

56 **Citation**

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78 **Study Chronology**

79 By design, this Bering Sea Integrated Ecosystem Research Program (BSIERP) project began in
80 September 2009 – one year after the start of other BSIERP projects. The delayed start was necessary to
81 allow the modeling effort to be informed by preliminary results from project B68 *Trophic Interactions -*
82 *Retrospective Analysis*. In addition, delays were encountered while conducting this research owing the
83 following issues: (1) a short course on model development using AD model builder (ADMB) was not
84 available until April 2010, (2) parameter estimation was more difficult than anticipated owing to strong
85 correlations among number of parameters in the preliminary models, large uncertainty with parameter
86 estimates, and apparent overparameterization, (3) two alternative model forms (multispecies biomass
87 dynamics models and multispecies delay difference models) were developed, which took longer to
88 develop and test, (4) receipt of groundfish diet data from NMFS, used for parameter estimation, was
89 delayed, (5) models were modified to include more age classes (age 0, 1, 2) in juvenile pollock than
90 originally planned based on results of AFSC fish diet study, and (6) an additional hypothesis regarding a
91 climate effect on inter-specific interactions was addressed. Owing to these delays, we requested and
92 received a no-cost extension for this project September 30, 2012 to September 30, 2013.

93 **Introduction**

94 Fisheries harvests off Alaska accounted for 56% of the total U.S. commercial fishery harvest and 36% of
95 the U.S. exvessel value in 2011 (McDowell Group 2013). The Bering Sea and Aleutian Islands region
96 alone produced seafood valued at \$2.4 billion; fisheries for groundfish in this region accounted for 40%
97 of the entire U.S. commercial fishery harvest. Walleye pollock (*Gadus chalcogrammus*) is the most
98 abundant and commercially important groundfish species in the Bering Sea. Pollock represent 56% of
99 exploitable groundfish biomass in the Bering Sea and Aleutian Islands management area (NPFMC 2010),
100 and pollock catches averaged 76% of the total groundfish catch by weight from 1990 to 2009 (NPFMC
101 2009).

102 These valuable fisheries are managed under a federal Fishery Management Plan under the auspices of the
103 North Pacific Fishery Management Council. The Council’s policy for groundfish fisheries includes the
104 adoption of ecosystem-based fishery management principles, including the incorporation of ecosystem
105 considerations into its management decisions (NPFMC 2010). In so doing, the Council recognizes that
106 “potential changes in productivity may be caused by fluctuations in natural oceanographic conditions,
107 fisheries, and other, non-fishing activities” and intends to “protect managed species from overfishing, and
108 where appropriate and practicable, increase habitat protection and bycatch constraints.”

109 Central to ecosystem-based fishery management is the need to account for ecological interactions among
110 species. To understand variability of multiple species in the ocean, scientists often develop whole
111 ecosystem models that attempt to explain the flow of energy from phytoplankton throughout the marine
112 ecosystem. Such ecosystem models tend to be very complicated and require large quantities of data, many
113 assumptions, and large teams of modelers and other researchers. Instead, multispecies models, informed
114 by routinely collected assessment and ecological data, may provide a more practical tool to better
115 understand trends of the most commercially important fish species, based on their trophic interactions and
116 environmental relationships.

117 We explored two hypotheses:

118 H_{01} : Multispecies models, which incorporate species interactions, can provide good fits to historical
119 biomass estimates for key groundfish species on the eastern Bering Sea shelf.

120 H_{02} : The extent of the cold pool is related to the predation rate on juvenile pollock by their major
121 predators, including adult pollock.

122 In essence, the first hypothesis represented development of quantitative tools to evaluate the second
123 hypothesis about effects of temperature on groundfish predation rates.

124 Although multispecies models, such as ours, are unlikely to replace single-species models for annual
125 stock assessment and management over the near term, they can lead to improvements in single-species
126 models. For example, multispecies models typically demonstrate that the lack of separate accounting of
127 predation mortality in single-species models often results in natural mortality estimates that are biased
128 low. Such errors can lead to misspecification of harvest control rules used to manage the fishery. In
129 addition, multispecies models can be used to provide strategic management advice. For instance,
130 multispecies models can be used to evaluate the implications of single-species harvest strategies on
131 expected biomass of their predators and prey. Moreover, because they incorporate these trophic
132 interactions, multispecies models can be used to estimate the effects of environmental conditions (e.g.,
133 temperature) on predation rate, thus providing a tool to forecast responses of the groundfish community to
134 future climate changes.

135 **Overall Objectives**

136 The three objectives of our research were:

137 Objective 1: Develop multispecies biomass dynamics models [and multispecies delay difference
138 models] for commercially or ecologically important groundfish in the eastern Bering Sea.

139 Objective 2: Examine inter-specific (predator-prey and competitive) interactions among a group of
140 species that show clear evidence of covariation in productivity.

141 Objective 3: Examine shared climate effects on productivity and on the strength and magnitude of the
142 inter-specific interactions among species or species groups.

143 For objective 1, we developed two alternative multispecies models. The first is based on the multispecies
144 biomass dynamics model of Collie & DeLong (1999) for the groundfish community on Georges Bank in
145 the northwest Atlantic Ocean. Biomass dynamics models aggregate the effects of recruitment, growth,
146 and mortality into a single production function (Haddon, 2000). As an alternative, we also modified
147 Deriso's (1980) single-species delay difference model and reformulated it for multiple species. Unlike the
148 biomass dynamics model, the delay difference model separates the effects of growth, mortality, and
149 recruitment. It describes biomass dynamics of an age-structured population by assuming a von
150 Bertalanffy growth function. In these regards, it is more realistic than the biomass dynamics model, yet
151 still requires the same undifferentiated biomass data as does the biomass dynamics model. Details are
152 provided in the Methods section of Chapter 1.

153 For objective 2 concerning interspecific interactions, we found that high F s on all species depleted the
154 biomass of predators, which in turn reduced predation on juvenile pollock by Pacific cod and arrowtooth
155 flounder, resulted in a rapid increase in pollock biomass. However, strong positive correlations among
156 many of the predation parameters resulted in extremely large relative errors. This suggests that the diet
157 data do not contain enough information to reliably estimate these parameters and that the model is
158 overparameterized. Interspecific interactions are described in equations 5-7 and 9-27 in the Methods
159 section of Chapter 1. Predation parameters are defined in Table 1 of Chapter 1, and parameter estimates
160 (and relative errors) are shown in Figure 5 and 8 of Chapter 1. Correlations among selected interaction
161 (predation) parameters are shown in Figures 6 and 7 of Chapter 1. Parameter estimates and correlations
162 are explained in the Result and discussed in the Discussion of Chapter 1.

163 Objective 3 is the topic of Chapter 2. Our results suggest that variability in the extent of the cold pool on
164 the EBS shelf affects important predator-prey interactions. Our results imply that increasing abundances
165 of arrowtooth flounder (and to a lesser extent, adult pollock), in combination with anticipated decreases in
166 ice extent and duration, may increase predation on age-1 pollock. These results are consistent with the
167 hypothesis that an extensive cold pool provides a refuge for age-1 pollock from these predators (see
168 Figure 1b of Chapter 2). Decreases in ice extent and enhanced summer temperatures have previously been
169 shown to reduce the overwinter survival and subsequent recruitment of young-of-year pollock due to
170 reduced prey availability (Hunt et al. 2011, Heintz et al. 2013). Our study suggests that recruitment may
171 be further reduced in warm years because of increased predation mortality on age-1 pollock. Therefore,
172 anticipated declines in the future recruitment and abundance of walleye pollock in a warming climate may
173 be even more pronounced than predicted by Mueter et al. (2011). Our main findings on the effects of
174 temperature on predation appear in the Results, shown graphically in Figures 4 and 5, and are discussed in
175 the Discussion of Chapter 2.

176

177 **Chapter 1: A Multi-species Biomass Dynamics Model for Investigating Predator-prey Interactions**
178 **in the Bering Sea Groundfish Community**

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183 **Abstract**

184 Concerns over long-term cumulative impacts of fishing on marine ecosystems and the status of many
185 marine species have led to calls for ecosystem-based approaches to fishery management. Single species
186 population dynamics models traditionally used in fisheries stock assessment lack separate accounting of
187 predation mortality and often underestimate natural mortality. Age-structured models used for stock
188 assessment in the Alaska region are biologically realistic, but their applicability is limited to a relatively
189 small number of commercially exploited species because they require accurate survey and fishery age
190 composition data. The objective of this study was to develop a relatively simple age-aggregated
191 multispecies model that describes biomass dynamics of some commercially and ecologically important
192 groundfish species in the eastern Bering Sea by accounting for their trophic interactions. We developed
193 and contrasted two alternative model formulations: a multispecies biomass dynamics (MBD) model and a
194 multispecies delay difference (MDD) model. Both MBD and MDD models were able to capture observed
195 trends in survey biomass data over 1982-2009. Although the MDD model fit the survey biomass
196 estimates better than the MBD model, the MDD model and its maximum likelihood parameters produced
197 biologically unrealistic biomass projections at $F > 0.14$. Strong positive correlations among many of the
198 predation parameters resulted in highly uncertain parameter estimates. Consistent with previous studies,
199 both multispecies models predicted the multi-species B_0 , MSY , and F_{MSY} to be lower than the sum of the
200 estimates from single-species assessment models. Although the results of the current study should be
201 taken with caution because of high estimation uncertainty, our multispecies models provide useful tools
202 for exploring long-term effects of choosing a particular harvest strategy for one species on the stock
203 dynamics of other members of the groundfish community.

204 **Keywords:**

205 Multispecies model, Bering Sea, biomass dynamics model, delay-difference model, predator-prey
206 interaction

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208 Deep-Sea Research Part II: Topical Studies in Oceanography

209 **Introduction**

210 Increasing awareness of long-term cumulative impacts of fishing on marine ecosystems, including
211 overfishing, have prompted serious concerns over the status of many marine species (Myers and Worm,
212 2003; Pauly et al., 2002; Pikitch et al., 2004). Recognition of these broader impacts has led to calls for
213 more holistic approaches to fishery management, specifically ecosystem-based approaches. Central to
214 ecosystem-based fishery management is the need to account for ecological interactions among species.
215 Such interactions can be incorporated into fishery management using multispecies stock assessment
216 models. Traditionally, fisheries stock assessment has relied on single species population dynamics models
217 that treat natural mortality as time-invariant. This assumption, coupled to a lack of separate accounting of
218 predation mortality, very often results in underestimation of natural mortality (Tyrrell et al., 2011).

219 Fisheries harvests off Alaska accounted for 56% of the total U.S. commercial fishery harvest and 36% of
220 the U.S. exvessel value in 2011 (McDowell Group 2013). The Bering Sea and Aleutian Islands region
221 alone produced seafood valued at \$2.4 billion; fisheries for groundfish in this region accounted for 40%
222 of the entire U.S. commercial fishery harvest. These valuable fisheries are managed under a federal
223 Fishery Management Plan under the auspices of the North Pacific Fishery Management Council. The
224 Council's policy for groundfish fisheries includes the adoption of ecosystem-based fishery management
225 principles, including the incorporation of ecosystem considerations into its management decisions
226 (NPFMC 2010). In so doing, the Council recognizes that "potential changes in productivity may be
227 caused by fluctuations in natural oceanographic conditions, fisheries, and other, non-fishing activities"
228 and intends to "protect managed species from overfishing, and where appropriate and practicable,
229 increase habitat protection and bycatch constraints."

230 Although all stock assessment models in use for the Alaska region are single-species population models,
231 multispecies models are also used indirectly to incorporate trophic ecology into management decisions.
232 For instance, linked predator-prey population models have been used to identify temporal changes in

233 natural mortality and stock productivity (Hollowed et al., 2011). Models used for these types of analysis
234 include multispecies virtual population analysis (MSVPA; Livingston & Jurado-Molina 2000, Jurado-
235 Molina & Livingston 2002), multispecies statistical catch-at-age models (MSM; Jurado-Molina et al.
236 2005), and multispecies age-structured models (MSASA; Van Kirk et al., 2010). These are age-structured
237 population dynamics models similar to the single species models used for stock assessment, but they
238 include predator-prey linkages among two to five strongly interacting species.

239 Age-structured assessments subdivide the stock into age classes (cohorts) and model the dynamics of each
240 cohort separately, requiring accurate survey and fishery age composition data. A simpler alternative to an
241 age-structured model is the biomass dynamics model (also called surplus production model), which
242 describes the dynamics of a stock using total biomass without regard to age, thus not requiring age
243 composition data. Although the age-structured model is biologically more realistic, its applicability is
244 limited to a relatively small number of commercially exploited species because of demanding data
245 requirements. Also, simpler models can produce more precise biomass estimates than more realistic
246 models, if available data do not provide sufficient contrast in historical information about stock status
247 (Ludwig and Walters, 1985).

248 The goal of our study is to develop a relatively simple age-aggregated model that describes biomass
249 dynamics of some commercially and ecologically important groundfish species in the eastern Bering Sea
250 by accounting for their trophic interactions. We developed and contrasted two alternative model
251 formulations. The first is based on the multispecies biomass dynamics model developed by Collie &
252 DeLong (1999) for the groundfish community on Georges Bank in the northwest Atlantic Ocean.
253 Biomass dynamics models aggregate the effects of recruitment, growth, and mortality into a single
254 production function (Haddon, 2000). As an alternative, we also modified Deriso's (1980) single-species
255 delay difference model and reformulated it for multiple species. Unlike the biomass dynamics model, the
256 delay difference model separates the effects of growth, mortality, and recruitment. It describes biomass
257 dynamics of an age-structured population by assuming a von Bertalanffy growth function. In these
258 regards, it is more realistic than the biomass dynamics model, yet still requires the same undifferentiated
259 biomass data as does the biomass dynamics model.

260 Both multispecies models were developed for seven groundfish species in the eastern Bering Sea: walleye
261 pollock (*Gadus chalcogrammus*) – a species that supports the largest commercial fishery in the U.S.,
262 arrowtooth flounder (*Atheresthes stomias*) – a very abundant predatory flatfish species of low economic
263 value but high ecologically importance, Pacific cod (*Gadus macrocephalus*) – a predatory fish that
264 supports valuable fisheries, and four commercially important flatfish species – yellowfin sole (*Limanda*

265 *aspera*), northern rock sole (*Lepidopsetta polyxystra*), flathead sole (*Hippoglossoides elassodon*), and
266 Alaska plaice (*Pleuronectes quadrituberculatus*). Yellowfin sole alone supports the largest flatfish fishery
267 in the U.S. For modeling purposes, we aggregated these last four flatfish species into a ‘small-mouth
268 flatfish’ group, owing to their similar decadal trends in stock biomass and the similarity of their
269 ecological relationships. Walleye pollock was divided into two age groups, juveniles (ages 0, 1, and 2)
270 and adults (age 3+), because juvenile pollock serve as important forage for many other predators in the
271 Bering Sea ecosystem. This separation also allowed us to explicitly model predation on juveniles, as well
272 as cannibalism of juveniles by adult pollock, which is important component of their population dynamics
273 (Wespestad et al., 2000). These seven species display tight trophic coupling owing to predator-prey
274 relationships inferred from stomach content analyses (Figure 1), which forms the basis for our
275 multispecies models.

276 **Methods**

277 Data

278 Biomass estimates from the summer bottom trawl survey (all species), echo-integrated trawl survey
279 (walleye pollock only), and annual commercial catch data for all species were obtained from the Stock
280 Assessment and Fishery Evaluation (SAFE) report for 2009 (NPFMC, 2009). The trawl survey estimates
281 and catch data were available from 1982 to 2009, while EIT survey estimates for walleye pollock were
282 only available in 1982, 1985, 1988, 1991, 1994, 1996, 1997, 1999, 2000, 2002, 2004, and 2006 – 2009.

283 Mean body weight for age-0 pollock was taken from Kooka (2012), and mean body weights for age-1, -2,
284 -3, and -3+ pollock were taken from Ianelli et al (2009). Estimates of biomass lost to predation for each
285 species for each predator were compiled from Alaska Fisheries Science Center’s groundfish food habits
286 reports for 1984 – 2001 (Lang et al., 2005, 2003, 1991; Livingston and DeReynier, 1996; Livingston et
287 al., 1993). The biomass of a particular prey species lost to predation was estimated by multiplying
288 together the daily ration of the predator by the biomass estimate of the predator, proportion of the prey
289 species by weight in the predator’s stomach, and the estimated number of feeding days by the predator.
290 Methodological details are provided in Lang et al. (1991).

291 **Correction for age-specific survey selectivity**

292 To obtain an estimate of total biomass, survey biomass estimates were corrected for age-specific
293 selectivity and model-estimated age compositions reported in NPFMC (2009). Assuming that observed
294 biomass in year y (B_y^{obs}) is composed of age classes $a = \{1, 2, 3, \dots, A\}$ and that each age class has a

295 different degree of vulnerability to the survey gear (i.e., age-specific selectivity, S_a), then B_y^{obs} can be
 296 estimated as:

$$297 \quad B_y^{obs} = \sum_{a=1}^A B_{a,y}^{obs} = \sum_{a=1}^A B_{a,y} S_a = \sum_{a=1}^A N_{a,y} \bar{w}_a S_a = \sum_{a=1}^A N_y P_{a,y} \bar{w}_a S_a = N_y \sum_{a=1}^A P_{a,y} \bar{w}_a S_a, \quad [1]$$

298 where:

$B_{a,y}^{obs}$ = observed biomass of age class a in year y

S_a = selectivity of age class a

299 $N_{a,y}$ = number of individuals in age class a in year y

\bar{w}_a = average weight of an individual of age class a

$P_{a,y}$ = proportion of population in age class a in year y

N_y = total abundance in year y

300 From this,

$$301 \quad N_y = B_y^{obs} / \sum_{a=1}^A P_{a,y} \bar{w}_a S_a. \quad [2]$$

302 A selectivity-corrected biomass estimate, \tilde{B}_y^{obs} , is then obtained by setting all selectivities S_a in equation

303 [1] equal to 1:

$$304 \quad \tilde{B}_y^{obs} = N_y \sum_{a=1}^A P_{a,y} \bar{w}_a = \frac{B_y^{obs}}{\sum_{a=1}^A P_{a,y} \bar{w}_a S_a} \sum_{a=1}^A P_{a,y} \bar{w}_a. \quad [3]$$

305 If selectivity, age proportions, and/or average weight-at-age differ between sexes, then selectivity-

306 corrected estimates can be generalized to:

$$307 \quad \tilde{B}_y^{obs} = N_y \sum_{s=1}^2 \sum_{a=1}^A P_{s,a,y} \bar{w}_{s,a} = \frac{B_y^{obs}}{\sum_{s=1}^2 \sum_{a=1}^A P_{s,a,y} \bar{w}_{s,a} S_{s,a}} \sum_{s=1}^2 \sum_{a=1}^A P_{s,a,y} \bar{w}_{s,a}, \quad [4]$$

308 where subscript s denotes sex.

309 Models

310 Two forms of age-aggregated biomass models were used to model biomass dynamics of four major
311 groundfish species/species groups in the eastern Bering Sea. The biomass dynamics equations of these
312 species groups are connected to each other through predation terms.

313 Multispecies Biomass Dynamics (MBD) model

314 Biomass dynamics equations for all species or species group have a common basic form as follows for
315 species x :

316
$$\hat{B}_{x,y+1} = \hat{B}_{x,y} + r_x \hat{B}_{x,y} \left(1 - \frac{\hat{B}_{x,y}}{k_x} \right) - C_{x,y} - \hat{B}_{pred,x,y}, \quad [5]$$

317 where $\hat{B}_{x,y}$ = biomass estimate of species x in year y

318 $C_{x,y}$ = commercial catch in year y

319 $\hat{B}_{pred,x,y}$ = estimated predation on species x in year y , and

320 r_x, k_x = population growth and carrying capacity parameters, respectively, for species x .

321 In addition to the basic form above, the biomass dynamics equation for walleye pollock (subscript p) also
322 includes a recruitment term $R_{p,y+1}$ that captures the part of the juvenile pollock biomass that recruits into
323 adult biomass in year $y+1$:

324
$$\hat{B}_{p,y+1} = \hat{B}_{p,y} + r_p \hat{B}_{p,y} \left(1 - \frac{\hat{B}_{p,y}}{k_p} \right) - C_{p,y} - \hat{B}_{pred,p,y} + \hat{R}_{p,y+1}, \quad [6]$$

325 where $\hat{R}_{p,y+1}$ = predicted recruitment.

326 Multispecies Delay Difference (MDD) model

327 Biomasses of adult walleye pollock (age 3+), arrowtooth flounder (age 1+), Pacific cod (age 1+), and the
328 small-mouth flatfish group (age 1+) were modeled based on Deriso's delay difference model (Quinn &
329 Deriso 1999). In the models, the biomass of these species (or species group) were connected to each other
330 by predation terms. The form of the biomass equation common to these species and species group was
331 calculated following Quinn and Deriso (1999). For a given species x , predicted biomass in year $y + 1$ was
332 calculated as:

333
$$\hat{B}_{x,y+1} = (1 + \rho_x) s_{x,y} \hat{B}_{x,y} - \rho_x s_{x,y} s_{x,y-1} \hat{B}_{x,y-1} + \hat{R}_{x,y+1}, \quad [7]$$

334 where:

335 ρ_x = Ford growth parameter for species x

336 $s_{x,y}$ = surviving fraction of $\hat{B}_{x,y}$ in the previous year y

337
$$= \frac{(\hat{B}_{x,y} - \hat{B}_{pred,x,y} - C_{x,y}) e^{-m_{0,x}}}{\hat{B}_{x,y}}$$

338 $m_{0,x}$ = residual mortality rate of species x in year y , and

339 $\hat{R}_{x,y+1}$ = predicted recruitment of species x in year $y+1$.

340 Recruitment for all species except pollock was modeled using a Ricker stock-recruit relationship.

341 Spawning biomass was defined as the fraction of the biomass that survived all predation and fishing:

342
$$\hat{R}_{x,y+1} = \alpha_x s_{x,y} \hat{B}_{x,y} \exp(-\beta_x s_{x,y} \hat{B}_{x,y}). \quad [8]$$

343 Modeling of juvenile pollock biomass for both MBD and MDD models

344 Biomass of juvenile pollock (ages 0, 1, 2) was modeled with age structure to account for the effect of
345 predation on recruitment through multiple juvenile age classes, which have very different spatial
346 distributions. Juvenile pollock biomass was modeled identically for both the MBD and the MDD models.

347 Age-0 pollock biomass was modeled to be proportional to adult (age-3+) pollock biomass:

$$348 \quad \hat{B}_{P0,y} = f\hat{B}_{P3+,y}, \quad [9]$$

349 where f is a parameter combining fecundity, growth, and larval mortality.

350 In the subsequent two years, the surviving portion of juvenile biomass was multiplied by $\frac{W_{a+1}}{W_a}$, the ratio

351 of the mean age- $a+1$ pollock body weight to the mean age- a pollock body weight to account for
352 individual growth:

$$353 \quad \hat{B}_{P1,y+1} = \left(\hat{B}_{P0,y} - \hat{B}_{pred,P0,y} \right) \frac{W_{P1,y+1}}{W_{P0,y}}, \text{ and} \quad [10]$$

$$354 \quad \hat{B}_{P2,y+1} = \left(\hat{B}_{P1,y} - \hat{B}_{pred,P1,y} - C_{P1,y} \right) \exp(m_{0,P1}) \frac{W_{P2,y+1}}{W_{P1,y}}. \quad [11]$$

355 Finally, the surviving portion of age-2 pollock biomass that recruits into the adult pollock biomass the
356 next year is given by:

$$357 \quad \hat{R}_{P,y+1} = \left(\hat{B}_{P2,y} - \hat{B}_{pred,P2,y} - C_{P2,y} \right) \exp(m_{0,P2}) \frac{W_{P3,y+1}}{W_{P2,y}}. \quad [12]$$

358 In equations [9 – 12],

$$359 \quad \hat{B}_{P0,y}, \hat{B}_{P1,y}, \hat{B}_{P2,y}, \hat{B}_{P3+,y}$$

360 = predicted biomass of pollock at age 0, 1, 2, and 3+ in year y , respectively.

361 $w_{P0,y}, w_{P1,y}, w_{P2,y}, w_{P3,y}$ = mean body weight at age 0, 1, 2, and 3 in year y , respectively

362 $\hat{B}_{pred,P0,y}, \hat{B}_{pred,P1,y}, \hat{B}_{pred,P2,y}$ = predicted biomass of pollock age 0, 1, 2 lost to predation in year y

363 $C_{P1,y}, C_{P2,y}$ = observed catch of pollock at age 1, and 2 in year y , and

364 $m_{0,P1}, m_{0,P2}$ = residual mortality parameter for pollock age1, and 2, respectively.

365 Predation terms

366 Predator-prey relationships among study species were modeled based on known trophic interactions from
 367 stomach analyses. The predation term for each prey species consisted of estimated biomass consumed by
 368 each of its predators. A Holling Type III predator functional response was used to model predator-prey
 369 relationships. In equations shown below, d_{xz} is a predation parameter for prey x and predator z , and a_{zx} is a
 370 search-and-handling parameter for predator z feeding on prey x . Species notations are; $P0$ = age-0
 371 pollock, $P1$ = age-1 pollock, $P2$ = age-2 pollock, $P3+$ = adult pollock, A = arrowtooth flounder, C =
 372 Pacific cod, and F = small-mouth flatfish.

373 Predation by adult pollock on juvenile (ages 0-2) walleye pollock is estimated as:

374
$$\hat{B}_{dPP,y} = \frac{d_{PP} \hat{B}_{P3+,y} \hat{B}_{J,y}^2}{1 + a_{PP} \hat{B}_{J,y}^2 + a_{PA} \hat{B}_{A,y}^2 + a_{PC} \hat{B}_{C,y}^2 + a_{PF} \hat{B}_{F,y}^2} . \quad [13]$$

375 Predation by arrowtooth flounder on juvenile and adult walleye pollock is estimated as:

376
$$\hat{B}_{dPA,y} = \frac{d_{PA} \hat{B}_{A,y} \hat{B}_{P,y}^2}{1 + a_{AP} \hat{B}_{P,y}^2 + a_{AF} \hat{B}_{F,y}^2} . \quad [14]$$

377 Predation by Pacific cod on juvenile and adult walleye pollock is estimated as:

378
$$\hat{B}_{dPC,y} = \frac{d_{PC} \hat{B}_{C,y} \hat{B}_{P,y}^2}{1 + a_{CP} \hat{B}_{P,y}^2 + a_{CA} \hat{B}_{A,y}^2 + a_{CF} \hat{B}_{F,y}^2} \quad [15]$$

379 and predation by small-mouth flatfish on juvenile walleye pollock is estimated as:

380
$$\hat{B}_{dPF,y} = \frac{d_{PF} \hat{B}_{F,y} \hat{B}_{J,y}^2}{1 + a_{FJ} \hat{B}_{J,y}^2} . \quad [16]$$

381 In equation [13 – 15] $\hat{B}_{J,y} = \hat{B}_{P0,y} + \hat{B}_{P1,y} + \hat{B}_{P2,y}$ and

382
$$\hat{B}_{P,y} = \hat{B}_{P0,y} + \hat{B}_{P1,y} + \hat{B}_{P2,y} + \hat{B}_{P3+,y} .$$

383 Pollock biomass lost to predation was then apportioned to each age class by multiplying it by the ratio of
 384 biomass in each age class to either the sum of juvenile pollock biomasses ($\hat{B}_{J,y}$) or the sum of the
 385 biomasses of all pollock age classes ($\hat{B}_{P,y}$). Pollock predation by adult pollock and by small-mouth
 386 flatfish were apportioned to juvenile pollock age classes only, while predation by arrowtooth flounder and
 387 by Pacific cod were apportioned to all age classes including adults (age 3+). Estimates of biomass lost to
 388 predation for juvenile and adult age classes were calculated as follows.

389 For juvenile age classes, $a = \{0, 1, 2\}$:

390
$$\hat{B}_{pred,Pa,y} = \frac{\hat{B}_{dPP,y} \hat{B}_{Pa,y}}{\hat{B}_{J,y}} + \frac{\hat{B}_{dPA,y} \hat{B}_{Pa,y}}{\hat{B}_{P,y}} + \frac{\hat{B}_{dPC,y} \hat{B}_{Pa,y}}{\hat{B}_{P,y}} + \frac{\hat{B}_{dPF,y} \hat{B}_{Pa,y}}{\hat{B}_{J,y}} . \quad [17]$$

391 For adult pollock (age 3+):

392
$$\hat{B}_{pred,P3+,y} = \frac{\hat{B}_{dPA,y} \hat{B}_{P3+,y}}{\hat{B}_{P,y}} + \frac{\hat{B}_{dPC,y} \hat{B}_{P3+,y}}{\hat{B}_{P,y}} . \quad [18]$$

393 An assumption implicit in equations [17 – 18] is that the rate of predation mortality caused by a particular
 394 predator was constant across all age classes of walleye pollock in a given year. This assumption is clearly
 395 not true, but was necessary to fit the models to age-aggregated estimates of biomass lost to predation.
 396 Despite constant predation mortality rates across all age classes, each cohort experiences different
 397 predation mortality through their juvenile life stage as predation mortality rates are time-variant.
 398 Therefore, pollock age classes 0-2 were modeled separately to reflect different predation mortality among
 399 cohorts from spawning to recruitment at age 3.

400 Predation on arrowtooth flounder by adult pollock and by Pacific cod, respectively, is modeled as
 401 follows:

402
$$\hat{B}_{dAP,y} = \frac{d_{AP} \hat{B}_{P3+,y} \hat{B}_{A,y}^2}{1 + a_{PP} \hat{B}_{J,y}^2 + a_{PA} \hat{B}_{A,y}^2 + a_{PC} \hat{B}_{C,y}^2 + a_{PF} \hat{B}_{F,y}^2} \quad \text{and [19]}$$

403
$$\hat{B}_{dAC,y} = \frac{d_{AC} \hat{B}_{C,y} \hat{B}_{A,y}^2}{1 + a_{CP} \hat{B}_{P,y}^2 + a_{CA} \hat{B}_{A,y}^2 + a_{CF} \hat{B}_{F,y}^2} \cdot \quad [20]$$

404 Therefore, total predation on arrowtooth flounder is:

405
$$\hat{B}_{pred,A,y} = \hat{B}_{dAP,y} + \hat{B}_{dAC,y} \cdot \quad [21]$$

406 Predation on Pacific cod by adult pollock is:
$$\hat{B}_{dCP,y} = \frac{d_{CP} \hat{B}_{P3+,y} \hat{B}_{C,y}^2}{1 + a_{PP} \hat{B}_{J,y}^2 + a_{PA} \hat{B}_{A,y}^2 + a_{PC} \hat{B}_{C,y}^2 + a_{PF} \hat{B}_{F,y}^2}$$

407 [22]

408 where $\hat{B}_{pred,C,y} = \hat{B}_{dCP,y} \cdot \quad [23]$

409 Predation on flatfish by adult pollock, by arrowtooth flounder, and by Pacific cod is estimated as:

410
$$\hat{B}_{dFP,y} = \frac{d_{FP} \hat{B}_{P3+,y} \hat{B}_{F,y}^2}{1 + a_{PP} \hat{B}_{J,y}^2 + a_{PA} \hat{B}_{A,y}^2 + a_{PC} \hat{B}_{C,y}^2 + a_{PF} \hat{B}_{F,y}^2} \cdot \quad [24]$$

411
$$\hat{B}_{dFA,y} = \frac{d_{FA} \hat{B}_{A,y} \hat{B}_{F,y}^2}{1 + a_{AP} \hat{B}_{P,y}^2 + a_{AF} \hat{B}_{F,y}^2} \cdot \text{ and } \quad [25]$$

412
$$\hat{B}_{dFC,y} = \frac{d_{FC} \hat{B}_{C,y} \hat{B}_{F,y}^2}{1 + a_{CP} \hat{B}_{P,y}^2 + a_{CA} \hat{B}_{A,y}^2 + a_{CF} \hat{B}_{F,y}^2} \cdot \quad [26]$$

413 Total predation on flatfish is therefore given by:

414
$$\hat{B}_{pred,F,y} = \hat{B}_{dFP,y} + \hat{B}_{dFA,y} + \hat{B}_{dFC,y} \cdot \quad [27]$$

415

416 Likelihood function

417 For pollock of all age classes, total survey catchability was assumed to equal 1, which was divided
 418 between two surveys, a bottom-trawl survey (BT) and an echo-integration trawl survey (EIT). Each
 419 survey is assumed to sample a distinct portion of the stock with no overlap in catch (Ianelli et al., 2009).
 420 Therefore, predicted biomass was related to selectivity-corrected survey biomass assuming a lognormal
 421 error structure:

$$422 \quad \tilde{B}_{BT,p,y}^{obs} = q_{BT,p} \hat{B}_{p,y} e^{\varepsilon_{BT,p,y}}, \varepsilon_{BT,p,y} \sim N(0, \sigma_{BT,p}^2) \text{ and} \quad [28]$$

$$423 \quad \tilde{B}_{EIT,p,y}^{obs} = q_{EIT,p} \hat{B}_{p,y} e^{\varepsilon_{EIT,p,y}}, \varepsilon_{EIT,p,y} \sim N(0, \sigma_{EIT,p}^2), \quad [29]$$

424 where $q_{BT,p} + q_{EIT,p} = 1$.

425 All other species (x) are surveyed with bottom trawl gear only and survey catchability was assumed to be
 426 1:

$$427 \quad \tilde{B}_{BT,x,y}^{obs} = q_{BT,x} \hat{B}_{x,y} e^{\varepsilon_{BT,x,y}}, \varepsilon_{BT,x,y} \sim N(0, \sigma_{BT,x}^2), \quad [30]$$

428 where $q_{BT,x} = 1$.

429 Lognormal errors were also assumed for the estimated biomass lost to predation:

$$430 \quad B_{dxz,y} = \hat{B}_{dxz,y} e^{\varepsilon_{dxz,y}}, \varepsilon_{dxz,y} \sim N(0, \sigma_{dxz}^2) \quad [32]$$

431 for prey species x and predator z .

432 First-year biomasses were estimated as free parameters. Based on the lognormal observation errors above,
 433 parameters were estimated by minimizing the following negative log likelihood function:

$$434 \quad -\ln L = \sum_{met} \sum_x \left\{ \sum_{y=1}^{n_{met,x}} \ln \tilde{B}_{met,x,y}^{obs} + \frac{n_{met,x}}{2} \left[\ln \left(\frac{2\pi \sum_{y=1}^{n_{met,x}} (\ln \tilde{B}_{met,x,y}^{obs} - \ln \hat{B}_{met,x,y})^2}{n_{met,x}} \right) + 1 \right] \right\}$$

$$435 \quad + \sum_x \sum_z \left\{ \sum_{y=1}^{n_{d,xz}} \ln B_{dxz,y} + \frac{n_{d,xz}}{2} \left[\ln \left(\frac{2\pi \sum_{y=1}^{n_{d,xz}} (\ln B_{dxz,y} - \ln \hat{B}_{dxz,y})^2}{n_{d,xz}} \right) + 1 \right] \right\} \quad [33]$$

436 where

met = survey method, {BT, EIT}

437 x = species

z = predator of species x

n = number of observations.

438 The list of estimated parameters is given in Table 1.

439 Biomass projection and calculation of biological reference points

440 Once parameters were estimated by fitting the models to data from 1982-2009, biomass of all species
 441 were projected forward using the estimated parameters for 100 years beginning with the predicted
 442 biomass for the last survey year (2009). Observed historical catches were subtracted from annual biomass
 443 estimates from 1982 to 2009. In forward projections, instantaneous fishing mortality rate (F) for each
 444 species was varied between 0 and 0.99 to find a combination of F s that produces the maximum
 445 sustainable yield (MSY) as the sum of the projected catches from all species at equilibrium. Catches were
 446 calculated as;

$$447 \quad C_{x,y} = (1 - \exp(-F_x)) \hat{B}_{x,y} \quad [34]$$

448 From biomass projections, five biological reference points (BRPs) of interest to fisheries management
 449 were calculated. Unfished equilibrium biomass, B_0 , was obtained as the biomass in the last year of a
 450 projection (equilibrium biomass) with no fishing ($F = 0$). Current depletion, B_{2009}/B_0 was predicted
 451 biomass in 2009 divided by B_0 . MSY was defined as the highest total yield in the last year of the
 452 projections (equilibrium yield) over all increments of F from 0 to 0.99 while maintaining biomasses of all
 453 species above 20% of their respective B_0 . F_{MSY} and B_{MSY} corresponded to the F and equilibrium biomass at
 454 which MSY was estimated to have occurred.

455

456 Monte Carlo simulations

457 Precision and bias in the estimates of the model parameters and the BRPs were evaluated for both types of
458 models using Monte Carlo (MC) simulations. The estimation models (MBD or MDD) and the maximum
459 likelihood parameters from the original model fits were used to simulate biomasses for all species for the
460 same number of years as in the original dataset (28 yr). From 1982 to 2009, annual catch rates in the
461 simulations were specified based on the observed catches and the biomass estimates from the original
462 model fit as $f_{x,y}^{MC} = C_{x,y} / \hat{B}_{x,y}$ for species x in year y . Simulated catches were then calculated as
463 $C_{x,y}^{MC} = f_{x,y}^{MC} B_{x,y}^{MC}$, in which $B_{x,y}^{MC}$ is the simulated biomass of species x in year y . In years after 2009 in
464 the simulations, one hundred projections were made by varying F from zero to 0.99 in increments of 0.01.
465 In each iterative MC simulation, the same F was applied to all species to limit the number of projections.
466 In each year, the simulated catch and biomass consumed by predators (calculated from the simulated
467 biomass using equations [13-27]) were subtracted from the simulated total biomass, and the remaining
468 biomass was multiplied by a lognormal process error with a standard deviation equal to 10% of the root-
469 mean-square error (RMSE) of the original model fit to the data. Process errors with a larger standard
470 deviation resulted in unstable biomass projections. The simulated "true" biomass was then projected
471 forward using either the MBD or the MDD models above and was multiplied by a lognormal observation
472 error with a standard deviation equal to 90% of RMSE of the original fit to produce a time series of
473 simulated "observations" $B_{x,y}^{MC,obs}$. Model parameters for both the MBD and MDD models, as well as the
474 five BRPs were estimated for each of 3000 simulated data sets following the procedure described above.
475 An additional set of 3000 simulated time series were generated using the MDD model as the operating
476 model and the MBD model as the assessment model to estimate the reference points. Estimation biases
477 were computed as the difference between the true parameters used to simulate biomass time series and the
478 median values of parameter estimates from the three thousand MC simulation runs. To summarize
479 variability in the parameter estimates we calculated the 2.5th and 97.5th percentiles of the estimates from
480 the MC simulations, respectively. These are referred to here as simulation intervals. Estimation biases are
481 reported as relative errors

482 $(= \frac{\text{Estimate} - \text{True parameter}}{\text{True parameter}} \times 100).$

483 **Results**

484 Both MBD and MDD models were able to capture the trends in the survey biomass data over 1982-2009
485 (Figure 2). Biomass estimates by the two types of models were almost identical for Pacific cod. For
486 small-mouth flatfish biomass, the MDD model seemed to be much more sensitive to fluctuations in
487 observed biomass compared to the MBD model. Overall, the MDD model fit the data only slightly better
488 than the MBD model based on the negative log likelihood (2445.11 and 2449.02 for the MDD and the
489 MBD models, respectively) at the expense of 11 additional parameters (42 and 53 parameters for the
490 MBD and the MDD models, respectively). Biomass projections by the MDD model exhibited limit cycles
491 in walleye pollock and small-mouth flatfish biomass trajectories at $F = 0$ (Figure 3). At higher F s ($F =$
492 0.34 is shown in Figure 3), pollock biomass projections by the MDD model increased exponentially over
493 time. To correct this biologically unrealistic behavior, it was necessary to adjust some parameters in the
494 MDD model (predation term for pollock and stock-recruit and growth parameters for the flatfish)
495 manually. The projections were allowed to stabilize (Figure 4); however, the resulting parameters were
496 not maximum likelihood parameters ($-\ln L = 2485.84$). Results presented below are based on models with
497 the adjusted parameter values.

498 Predicted biomass during 2010-2109 differed between the two models and depending upon F (Figure 4).
499 In the absence of fishing, the equilibrium biomass (B_0) predicted by both the MBD and the MDD models
500 were all smaller than the assessment estimates except for arrowtooth flounder (Table 2). The sum of B_0
501 estimates for all species from the assessment was about twice as large as those estimated by the MBD and
502 the MDD models. Current depletion (B_{2009}/B_0) estimated by the MBD and the MDD models were similar
503 to the one by the assessment model for Pacific cod, but much higher and close to 1 for walleye pollock
504 and flatfishes. The MDD model estimated B_0 for arrowtooth flounder to be about twice as large as
505 estimates from other models. When all seven species are combined, current depletion was estimated at
506 0.86 and 1.00 for the MBD and MDD models, respectively, compared to 0.40 for the 2009 stock
507 assessments. Estimates of MSY , F_{MSY} , and B_{MSY} for individual species varied considerably among models,
508 but all three models resulted in similar estimates of system-level B_{MSY} when summed across species (10 to
509 13 million metric tons). But, the both multispecies models predicted the eastern Bering Sea groundfish
510 stocks to be less productive than the assessment models, except for the flatfish group for which MSY was
511 estimated slightly higher by the MBD model (Table 2).

512 Model performance was assessed by examining relative errors in parameter estimates from the MC
513 simulations (Figures 5, 6, and 7). For the first year biomass estimates by species or group ($B_{P1,1982}$,
514 $B_{P2,1982}$, $B_{P3,1982}$, $B_{P,1982}$, $B_{A,1982}$, $B_{C,1982}$, $B_{F,1982}$; Table 1) the median parameter values from the simulations

515 are very close to the true parameters for both the MBD and the MDD model (Figure 5). Estimation biases
516 ranged from -21% ($B_{P3,1982}$) to 0.02% ($B_{F,1982}$), and were of similar magnitude in the two models.
517 However, the MDD model produced larger relative errors for all of these parameters except for $B_{P3,1982}$.

518 Bottom trawl catchability for the three juvenile and adult age classes of pollock ($q_{BT, P1}$, $q_{BT, P2}$, $q_{BT, P3}$, $q_{BT, P}$)
519 were also estimated accurately on average by both models, with median estimation biases ranging from
520 -0.9% to 3.2%. For these parameters, the MDD estimates were much more variable than the MBD
521 estimates (Figure 5). The median estimate of the fecundity parameter f was very close to the true
522 parameter for both the MBD and the MDD models, but relative error ranged from 1.5×10^{-3} (2.5th
523 percentile) to 6.5×10^{-2} (97.5th percentile) for the MDD model (Figure 5). In contrast, the MBD model
524 estimates had a much narrower distribution of f s.

525 The MBD model resulted in a much wider range of errors for many of the parameters related to predation
526 (d_{xz} , a_{zx}) and mortality ($m_{0,1}$, $m_{0,2}$) compared to the MDD model (Figure 5). While the MDD model
527 estimated $m_{0,1}$ and $m_{0,2}$ accurately, the estimates by the MBD model were strongly biased (3368% and
528 575% for $m_{0,1}$ and $m_{0,2}$, respectively). Error distributions were also wider for the MBD estimates for $m_{0,1}$
529 and $m_{0,2}$, whose 95% intervals both exceeded 100,000% of the true values, while the 95% interval of the
530 MDD estimates were about 200% of the true values for both.

531 Estimation biases for the 20 parameters in the predation equations of the MBD model were either small
532 (<10%; 2 parameters, d_{pf} and a_{pf}), moderate (>10%, <100%; 5 parameters, d_{ap} , d_{ac} , d_{fa} , d_{pa} , and a_{ap}), or
533 very large (>1000%; 13 parameters). Error distributions were narrow (2.5th and 97.5th percentiles were
534 within 100% of the true parameter values) for two parameters with large negative biases (d_{ap} and d_{ac} , due
535 to very small median estimates), but very large for the rest of the 20 parameters. Despite the wide 95%
536 intervals, the true parameter values were smaller than the 2.5th percentile for two parameters (d_{pp} , a_{pp}) and
537 larger than the 97.5th percentile for another two (d_{ap} , and d_{ac}). Five of the 13 parameters with extremely
538 large biases (d_{pp} , a_{pp} , d_{cp} , d_{fp} , a_{pf}) were strongly positively correlated with each other (Figure 6). Another
539 four (d_{pc} , a_{cp} , d_{ac} , d_{fc}) of the 13 parameters also showed strong positive correlations with each other. Three
540 of the five parameters with moderate biases (d_{pa} , a_{ap} , d_{fa}) were also highly positively correlated with each
541 other.

542 For the same 20 predation parameters, the MDD model estimated seven with small biases (<10%; d_{pa} , a_{ap} ,
543 a_{pa} , d_{cp} , a_{pc} , a_{af} , and a_{cf}), five with moderate biases (>10% and <100%; d_{pf} , a_{fp} , d_{ap} , d_{ac} , and d_{fa}), eight with
544 very large biases (>100%; d_{pp} , d_{pc} , a_{pp} , a_{cp} , a_{ca} , d_{fp} , d_{fc} and a_{pf}). Estimates were also highly variable for all
545 of the eight parameters with large estimation biases. For these eight parameters, and for four of the seven

546 parameters with small biases (a_{pa} , d_{cp} , a_{pc} , and a_{af}), the 97.5th percentile of relative errors were >1000% of
547 the true parameter value. Four of the eight parameters with large biases (d_{pp} , a_{pp} , d_{fp} , and a_{pf}) had strong
548 positive correlations with each other and with one parameter with a small estimation bias (d_{cp}). The other
549 three with large biases (d_{pc} , a_{cp} , and d_{fc}) also had strong positive correlation with each other (Figure 7).
550 Two pairs (d_{pf} and a_{fp} , d_{ap} and d_{ac}) of parameters out of the five with moderate biases were also positively
551 correlated with each other, while the last one of the five (d_{fa}) had strong positive correlation with two
552 parameters with small biases (d_{pa} and a_{ap}).

553 There are 8 and 19 other parameters unique to the MBD and MDD models, respectively. The MBD model
554 estimated these 8 parameters (r_p , k_p , r_a , k_a , r_c , k_c , r_f , k_f) fairly well (Figure 8). Estimated biases were all less
555 than 10%. The 95% intervals of relative errors for these parameters were fairly narrow except for the
556 carrying capacity parameter for small-mouth flatfish (k_f) Estimates of the 19 MDD parameters were less
557 accurate and precise (Figure 8). Out of the 19 parameters, six ($m_{0,p}$, $s_{p,1981}$, $B_{p,1981}$, ρ_C , α_C , $m_{0,F}$, and α_F) had
558 biases larger than 10%. For 12 of the 19 parameters, the range of the 95% intervals ranged from 108% to
559 556% of the true parameters. The other seven parameters exhibited the 95% intervals over 1000% of the
560 true parameter values. There was no apparent correlation between the magnitude of the estimation bias
561 and precision. Only three pairs of parameters (ρ_p and $m_{0,p}$, $m_{0,a}$ and α_a , $m_{0,c}$ and β_c) showed strong
562 correlation to each other.

563 The MDD model resulted in much larger biases in MSY and B_{MSY} (53% and 54%, respectively; Figure 9)
564 than the MBD model (3% and 2%, respectively). When the MBD model was used to estimate the
565 reference points from simulated biomasses generated by the MDD model, the biases were intermediate
566 and negative (-27% and -4% for MSY and B_{MSY} , respectively). Using MBD as both the operating model
567 and the assessment model produced the most precise estimates of MSY and B_{MSY} , while using the MDD
568 model to estimate these reference points from MDD simulated biomasses were least precise.

569 Estimation biases for B_0 were similarly small for all three simulation sets (4%, 2%, and 4% for the MBD,
570 the MDD, and the MDD/MBD, respectively). However, relative errors for the MDD estimates were much
571 larger compared to the other two (Figure 9). For B_{2009}/B_0 , estimation biases were similar among the three
572 simulation sets and were moderately large around -20%. The MBD estimates for B_{2009}/B_0 was much more
573 precise compared to the other two sets. Regardless of the model used to project biomass (whether the
574 MBD model or the MDD model), the estimates produced by the MBD model were more precise than the
575 estimates by the MDD model. The only exception was F_{MSY} , the MBD estimate of which was both less
576 accurate and precise.

577 Estimates of MSY , B_{MSY} , B_0 , and B_{2009}/B_0 by the MDD model were all strongly correlated (Figure 10).
578 These same estimates plus F_{MSY} from the MBD models also showed moderate correlations (Figure 11 &
579 12).

580 Discussion

581 Although the MDD model fit the survey biomass estimates of the eastern Bering Sea groundfish species
582 better than did the MBD model, the MDD model and its maximum likelihood parameters produced
583 biologically unrealistic biomass projections involving exponential increases of pollock biomass at $F >$
584 0.14 . High F s on all species depleted the biomass of predators, which in turn reduced predation on
585 juvenile pollock by Pacific cod and arrowtooth flounder, resulting in a rapid increase in pollock biomass.
586 Biomass projections for pollock were stabilized by manually adjusting the model parameters to increase
587 the amount of cannibalism, which introduced a tighter density-dependent control on pollock biomass.
588 However, after this ad-hoc correction the negative log likelihood of the MDD model, given the survey
589 biomass estimates, became greater than that of the MBD model in spite of the 11 additional parameters
590 used in the MDD model.

591 Similar to the results from the multispecies biomass dynamics model of Collie and DeLong (1999), our
592 parameter estimates were highly uncertain. Strong positive correlations among many of the predation
593 parameters resulted in extremely large relative errors. This suggests that the diet data do not contain
594 enough information to reliably estimate these parameters and that the model is overparameterized.
595 Although many of the predation parameters estimated by the MDD model had narrower error ranges than
596 the MBD model estimates, these MDD estimates were associated with large variation in the sum-of-
597 squared biomass residuals. This indicates that the smaller estimation error was achieved at the expense of
598 increased errors or bias in the survey biomass estimates. While neither model is clearly better in terms of
599 parameter estimation, unstable biomass projections is a major concern for the MDD model. Small
600 changes in parameter values quite often lead to unrealistic or chaotic behaviors of biomass trajectories for
601 the MDD model. Lack of self-regulation in the MDD-model biomass dynamics is particularly problematic
602 in estimating BRPs as this requires projected biomass to reach equilibrium.

603 The estimates of unfished biomass (B_0) from the multispecies models were lower than the estimates from
604 single-species assessment models because surplus production in the absence of fishing is consumed by
605 predators. This also means that, under various harvesting scenarios, the biomass of a given species can be
606 greater than its B_0 if predator biomass is reduced by fishing. For example, the equilibrium biomass of
607 walleye pollock was predicted to be above its B_0 when maximizing the total yield of the system (Table 2),

608 as a result of fishing down predators of walleye pollock to $B_{20\%}$, the lowest biomass level specified in the
609 chosen harvest strategy. In the MDD-model predictions, MSY for the system was obtained by harvesting
610 two predator species (Pacific cod and arrowtooth flounder) down to low biomass levels, thereby
611 increasing production of pollock and flatfish. In the MBD-model predictions, Pacific cod was similarly
612 depleted to a low biomass level to increase the production of pollock and flatfish, but arrowtooth flounder
613 were not harvested at all because reducing the availability of arrowtooth flounder as prey in the system
614 increases predation on juvenile pollock, especially by adult pollock (prey switching). In either case,
615 multispecies models predicted the system-wide MSY to be much lower than that estimated by the
616 assessment models. As a result, F_{MSY} for each species was also predicted to be lower than the estimates in
617 the stock assessments, except for some species in the flatfish group. These results are consistent with
618 other studies that have shown that multi-species or system level MSY is generally lower than the sum of
619 single-species MSY (Walters et al. 2005, Mueter and Megrey 2006, Tyrrell et al. 2011).

620 Multispecies models are currently not used as primary assessment tools or to determine reference points.
621 The results of the current study need to be considered carefully because of the high estimation
622 uncertainty. However, the multispecies models developed in this study provide useful tools for exploring
623 long-term effects of choosing a particular harvest strategy for one species on the stock dynamics of other
624 species. In the current study, we explored the consequences of one particular harvesting strategy, in which
625 the total sustainable yield of the multi-species system was maximized. Simulations of other harvesting
626 strategies with different management objectives, such as maximizing economic values of catches or
627 rebuilding a depleted stock, are also possible and worth exploring. Another fruitful area of research would
628 be to incorporate effects of climate change on trophic interactions and to study how it may affect
629 management decisions on these fishery resources.

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687 Wespestad, V.G., Fritz, L.W., Ingraham, W.J., Megrey, B.A., 2000. On relationships between
688 cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye
689 pollock (*Theragra chalcogramma*). ICES Journal of Marine Science 57, 272–278.

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691 Table 1. List of estimated parameters.
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Parameters common to both models

$B_{P1,1982}$	Biomass of age-1 pollock in 1982
$B_{P2,1982}$	Biomass of age-2 pollock in 1982
$B_{P3,1982}$	Biomass of age-3 pollock in 1982
$B_{P,1982}$	Biomass of age-3+ pollock in 1982
$B_{A,1982}$	Biomass of arrowtooth flounder in 1982
$B_{C,1982}$	Biomass of Pacific cod in 1982
$B_{F,1982}$	Biomass of small-mouth flatfish in 1982
$q_{BT, P1}$	Bottom trawl survey catchability for age-1 pollock
$q_{BT, P2}$	Bottom trawl survey catchability for age-2 pollock
$q_{BT, P3}$	Bottom trawl survey catchability for age-3 pollock
$q_{BT, P}$	Bottom trawl survey catchability for age-3+ pollock
f	Parameter combining fecundity, growth, and larval mortality of pollock
$m_{0,P1}$	Residual mortality of age-1 pollock
$m_{0,P2}$	Residual mortality of age-2 pollock

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Parameters in predation equations

d_{PP}	Predation rate parameter for pollock prey and pollock predator
d_{PA}	Predation rate parameter for pollock prey and arrowtooth predator
d_{PC}	Predation rate parameter for pollock prey and cod predator
d_{PF}	Predation rate parameter for pollock prey and flatfish predator
a_{PP}	Search-and-handling parameter for pollock prey and pollock predator
a_{AP}	Search-and-handling parameter for pollock prey and arrowtooth predator
a_{CP}	Search-and-handling parameter for pollock prey and cod predator
a_{FP}	Search-and-handling parameter for pollock prey and flatfish predator
d_{AP}	Predation rate parameter for arrowtooth prey and pollock predator
d_{AC}	Predation rate parameter for arrowtooth prey and cod predator
a_{PA}	Search-and-handling parameter for arrowtooth prey and pollock predator
a_{CA}	Search-and-handling parameter for arrowtooth prey and cod predator
d_{CP}	Predation rate parameter for cod prey and pollock predator
a_{PC}	Search-and-handling parameter for cod prey and pollock predator
d_{FP}	Predation rate parameter for flatfish prey and pollock predator
d_{FA}	Predation rate parameter for flatfish prey and arrowtooth predator
d_{FC}	Predation rate parameter for flatfish prey and cod predator
a_{PF}	Search-and-handling parameter for flatfish prey and pollock predator
a_{AF}	Search-and-handling parameter for flatfish prey and arrowtooth predator
a_{CF}	Search-and-handling parameter for flatfish prey and cod predator

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697 Table 1. Continued.
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Parameters unique to MBD model

r_P	Growth parameter for walleye pollock
k_P	Carrying capacity parameter for walleye pollock
r_A	Growth parameter for arrowtooth flounder
k_A	Carrying capacity parameter for arrowtooth flounder
r_C	Growth parameter for Pacific cod
k_C	Carrying capacity parameter for Pacific cod
r_F	Growth parameter for small-mouth flatfish
k_F	Carrying capacity parameter for small-mouth flatfish

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Parameters unique to MDD model

ρ_P	Ford growth parameter for walleye pollock
$m_{0,P}$	Residual mortality rate for walleye pollock
$s_{P2,1981}B_{P2,1981}$	Surviving portion of age-2 pollock biomass in 1981
$s_{P,1981}B_{P,1981}$	Surviving portion of age-3+ pollock biomass in 1981
ρ_A	Ford growth parameter for arrowtooth flounder
$m_{0,A}$	Residual mortality rate for arrowtooth flounder
α_A	Ricker stock-recruit parameter for arrowtooth flounder
β_A	Ricker stock-recruit parameter for arrowtooth flounder
$s_{A,1981}B_{A,1981}$	Surviving portion of arrowtooth biomass in 1981
ρ_C	Ford growth parameter for Pacific cod
$m_{0,C}$	Residual mortality rate for Pacific cod
α_C	Ricker stock-recruit parameter for Pacific cod
β_C	Ricker stock-recruit parameter for Pacific cod
$s_{C,1981}B_{C,1981}$	Surviving portion of cod biomass in 1981
ρ_F	Ford growth parameter for small-mouth flatfish
$m_{0,F}$	Residual mortality rate for small-mouth flatfish
α_F	Ricker stock-recruit parameter for small-mouth flatfish
β_F	Ricker stock-recruit parameter for small-mouth flatfish
$s_{F,1981}B_{F,1981}$	Surviving portion of small-mouth flatfish biomass in 1981

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713 Table 2. Estimates of biological reference points for the MBD, MDD, and assessment models.
 714 Assessment model estimates were taken from NPFMC (2009). The unit for MSY, B_{MSY} , and B_0 are in
 715 1,000 metric tons.

<u>Species</u>	<u>Model</u>	<u>F_{MSY}</u>	<u>MSY</u>	<u>B_{MSY}</u>	<u>B_0</u>	<u>B_{2009}/B_0</u>
Pollock	MBD	0.22	1,605	9,206	8,942	0.92
	MDD	0.17	946	7,085	5,213	1.34
	Assessment	0.47	3,022	8,102	21,457	0.29
Cod	MBD	0.24	90	417	2,086	0.31
	MDD	0.26	87	379	1,825	0.35
	Assessment	0.35	355	1,202	3,428	0.33
Arrowtooth	MBD	0.00	0	945	942	0.97
	MDD	0.24	64	296	1,357	0.72
	Assessment	0.30	94	368	1,051	1.08
Flatfish	MBD	0.45	904	2,473	5,857	0.95
	MDD	0.27	673	2,838	6,221	0.97
	Assessment	0.12 - 0.77	717	2,820	9,696	0.59
Total	MBD		2,599	13,041	17,826	0.86
	MDD		1,769	10,597	14,615	1.00
	Assessment		4,188	12,492	35,633	0.40

716 * F_{MSY} estimates varied among the four species of flatfishes.

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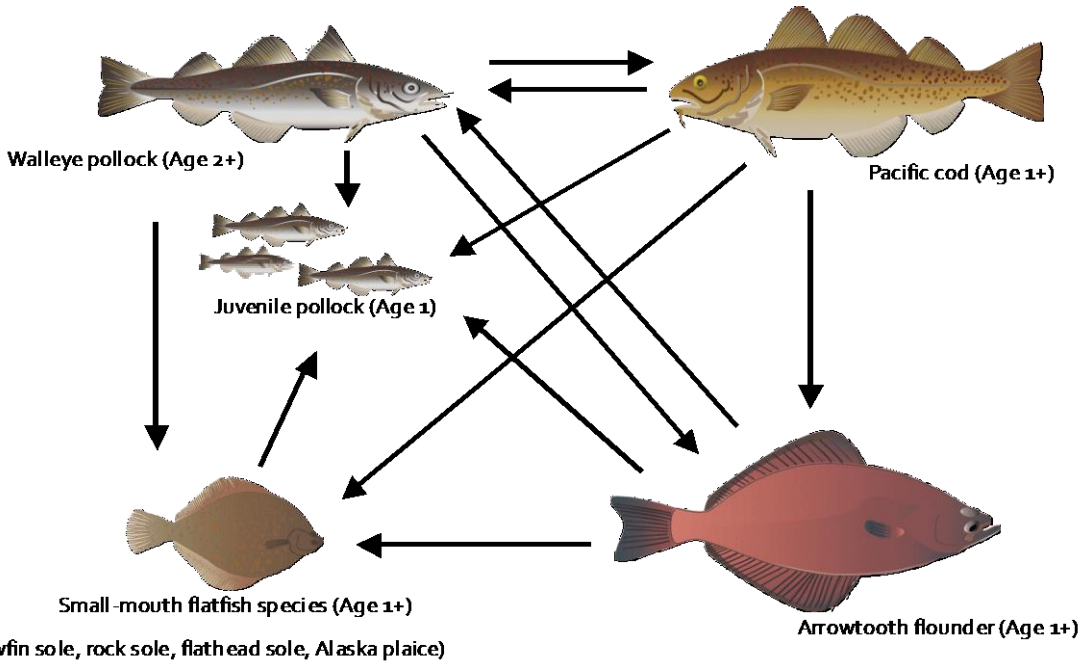


Figure 1. Predator-prey relationships among eastern Bering Sea fish species as modeled in this study.

Arrows represent directions of predator → prey.

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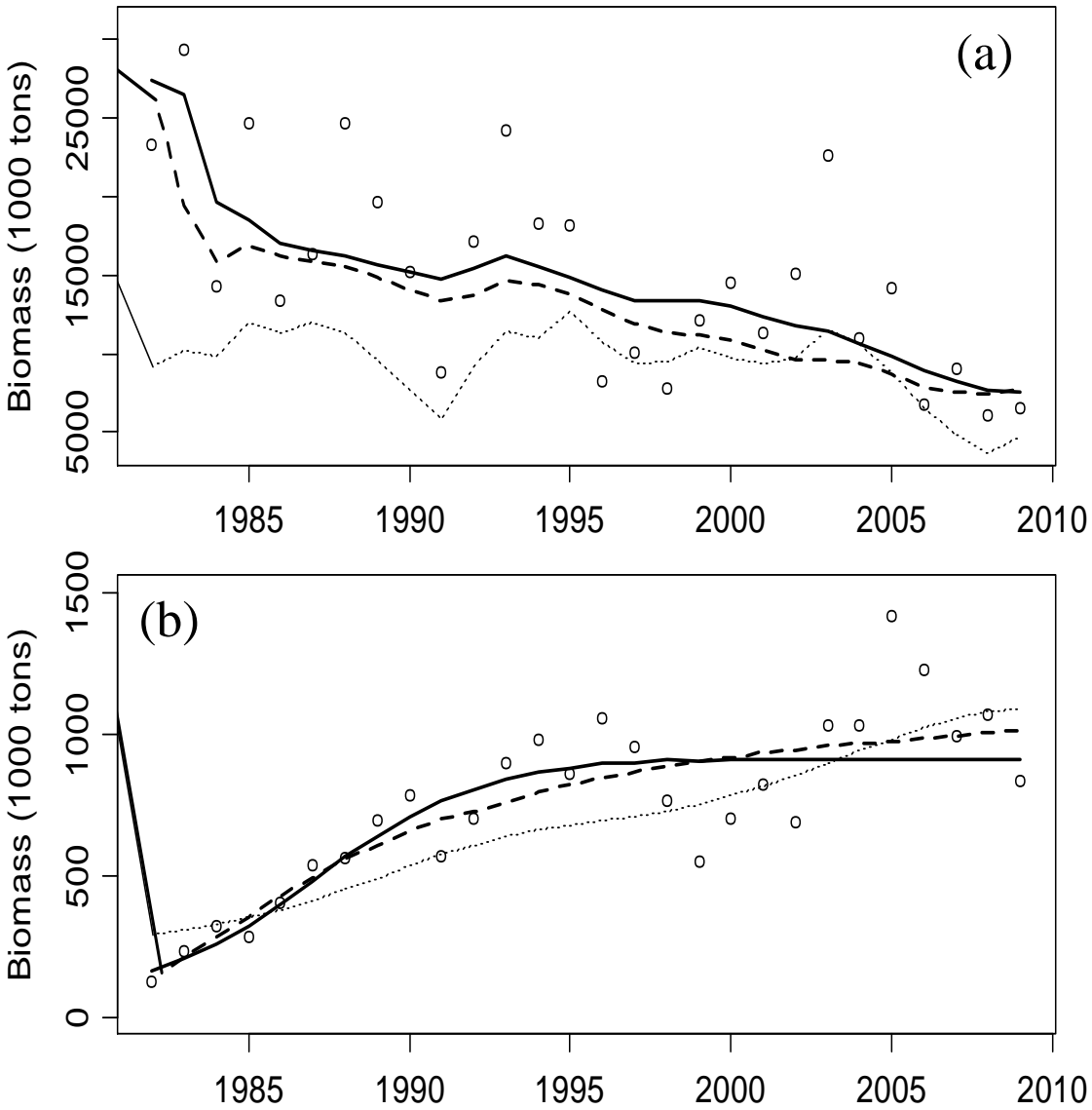


Figure 2. Estimated biomass for (a) walleye pollock, (b) arrowtooth flounder, (c) Pacific cod, and (d) small-mouth flatfish for 1982-2009. Biomass was predicted from the multispecies biomass dynamics (MBD, solid line) and the multispecies delay difference (MDD, dashed line) model. Open circles are biomass estimates from the summer bottom trawl survey based on area-swept methods, and the dashed lines are biomass estimates from the single-species stock assessment models (NPFMC, 2009).

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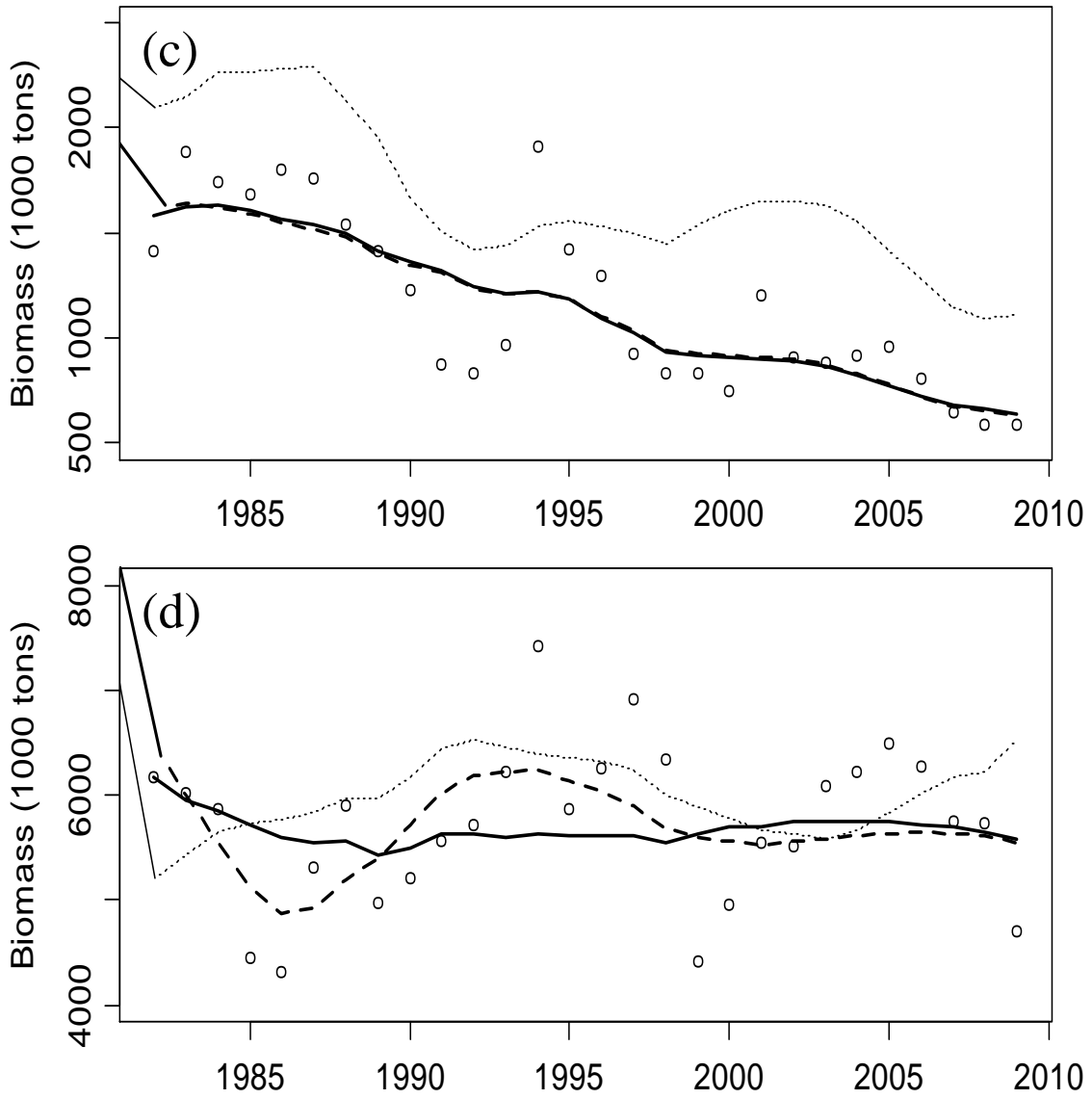


Figure 2. continued.

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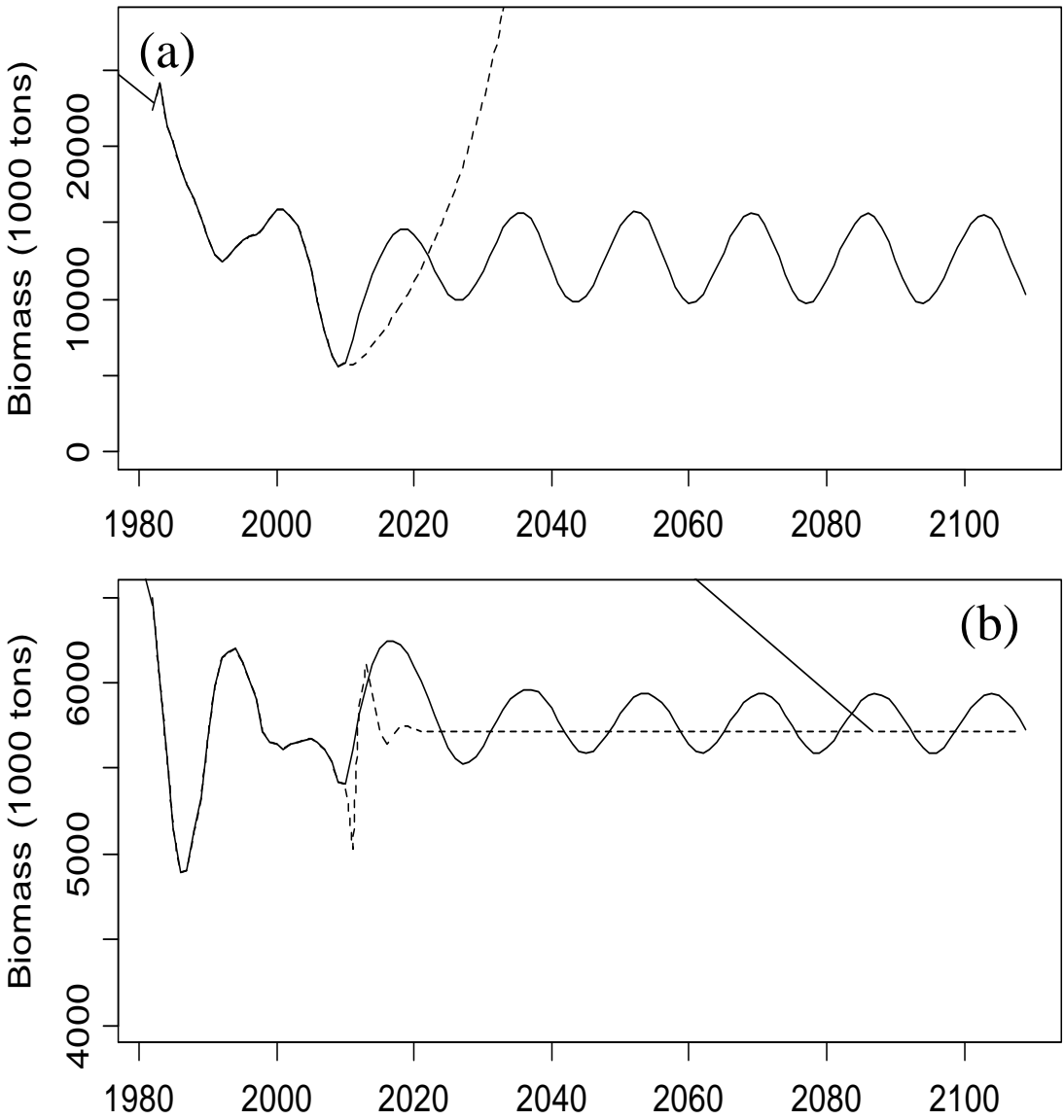


Figure 3. Fitted biomass over 1982-2009 and projected biomass through 2109 for (a) walleye pollock and (b) small-mouth flatfish produced by the MDD model with the maximum likelihood parameters. Historical observed catches were applied over 1982-2009, then constant F was applied over 2010-2109. Solid lines are projections with $F = 0$. Dashed lines show projections with $F = 0.34$.

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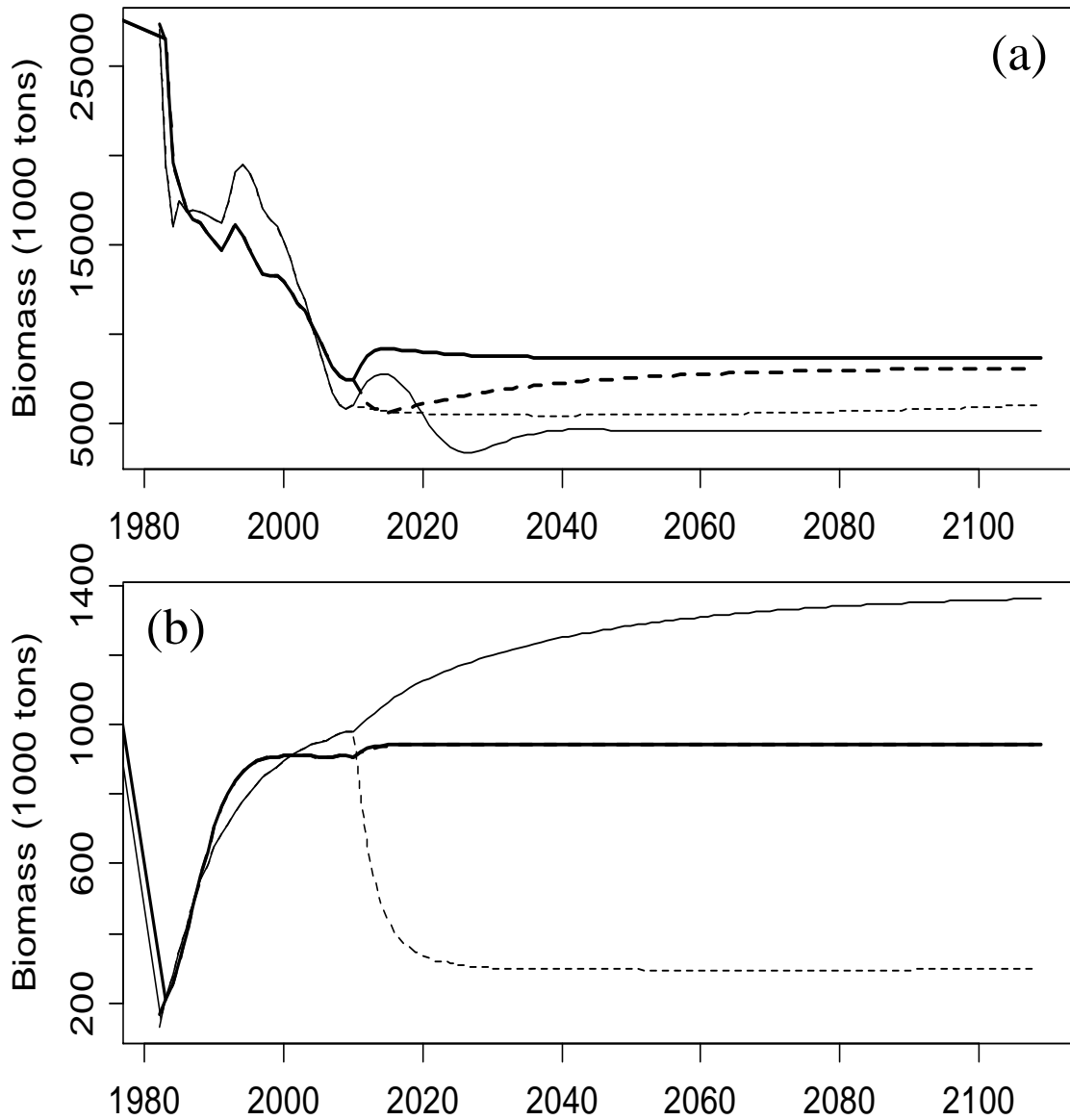


Figure 4. Biomass projections for (a) walleye pollock, (b) arrowtooth flounder, (c) Pacific cod, (d) small-mouth flatfish from the MBD (thick lines) and the MDD (thin lines) models from 1982 to 2109. Solid lines are projections with $F = 0$ after 2009, and dashed lines are projections with $F = F_{MSY}$. For the MBD models, $F_{MSY,pollock} = 0.22$, $F_{MSY,cod} = 0.24$, $F_{MSY,arrowtooth} = 0$, $F_{MSY,flatfish} = 0.45$. For the MDD models, $F_{MSY,pollock} = 0.17$, $F_{MSY,cod} = 0.26$, $F_{MSY,arrowtooth} = 0.24$, $F_{MSY,flatfish} = 0.27$.

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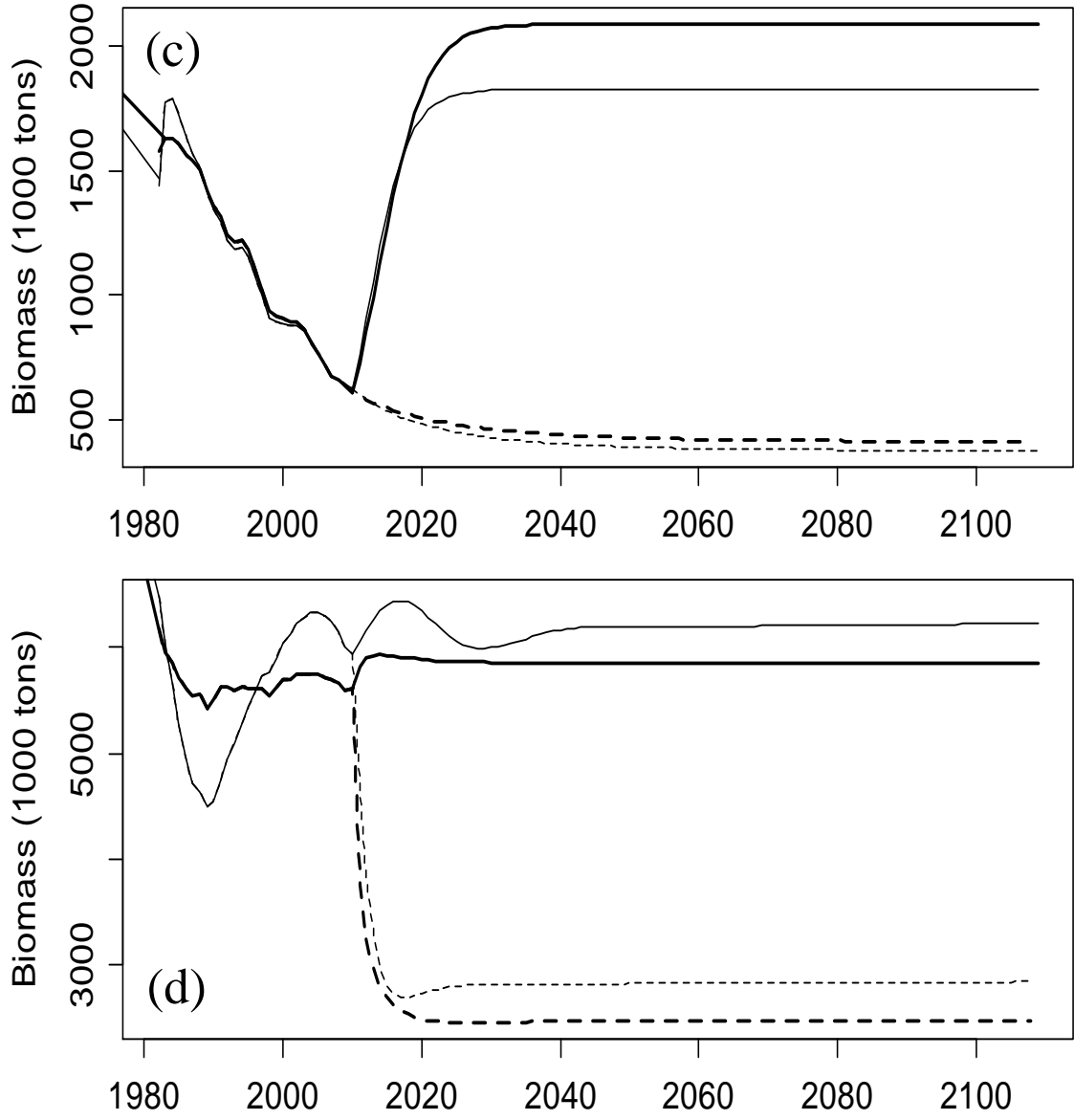
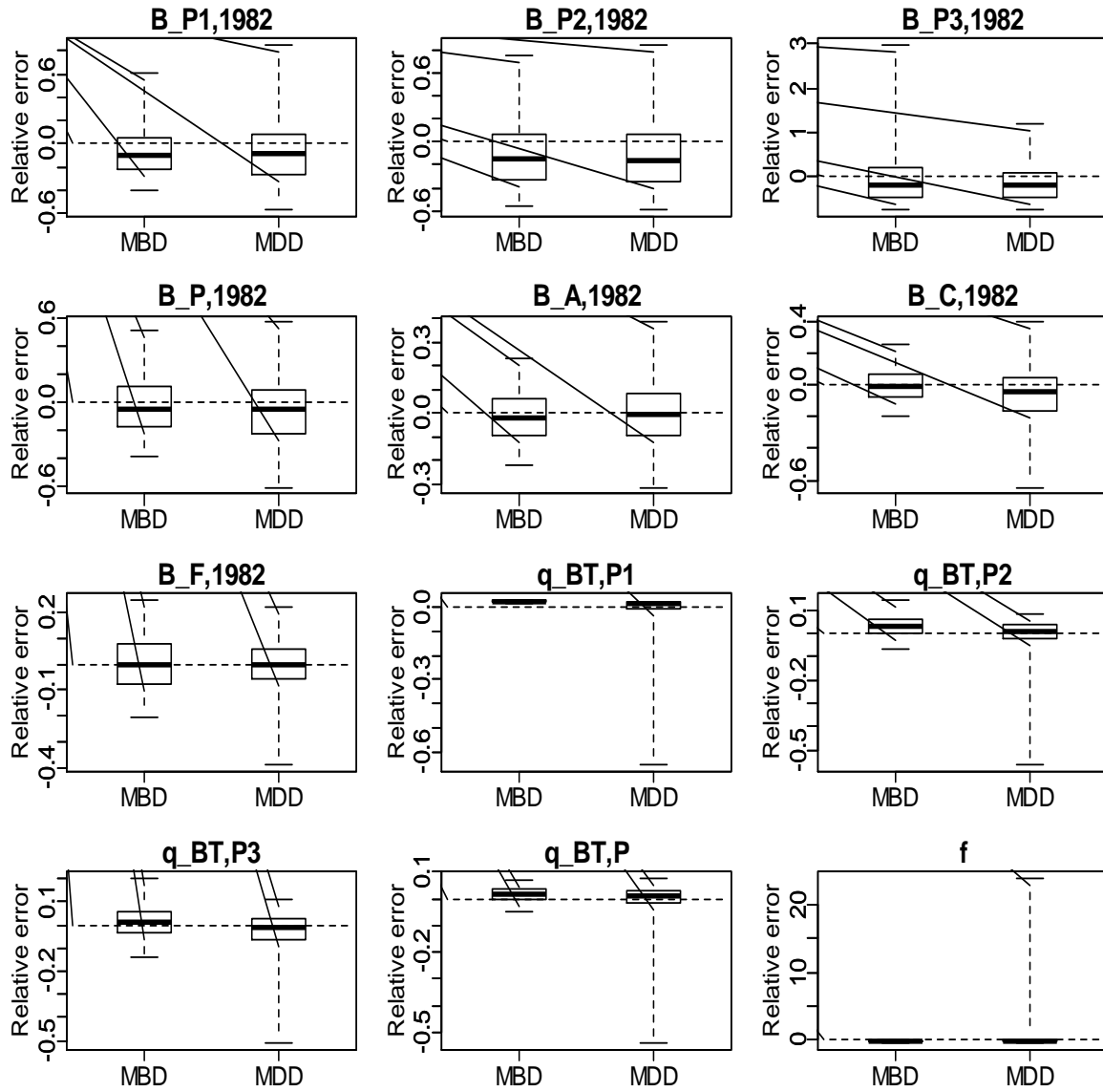
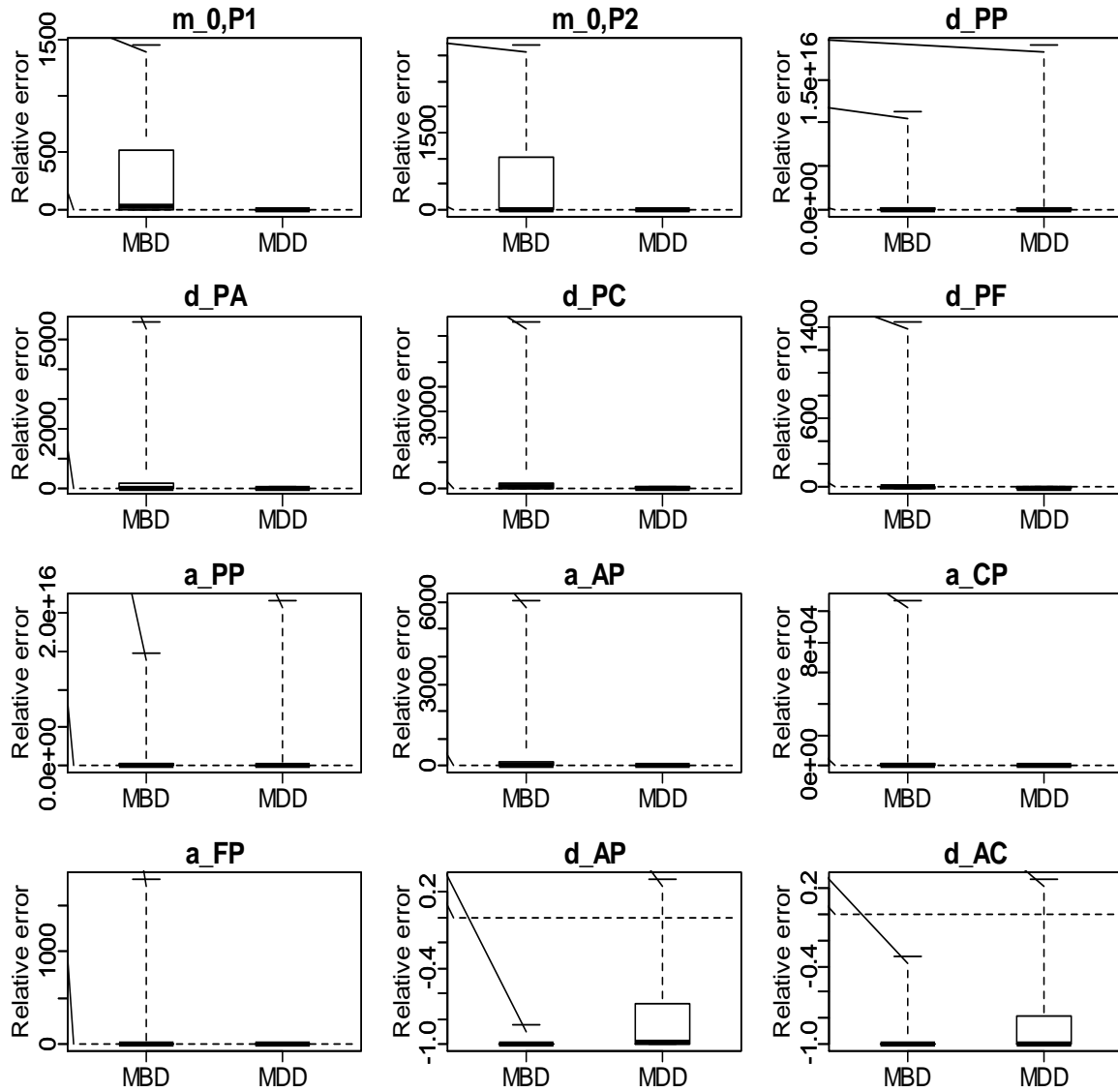


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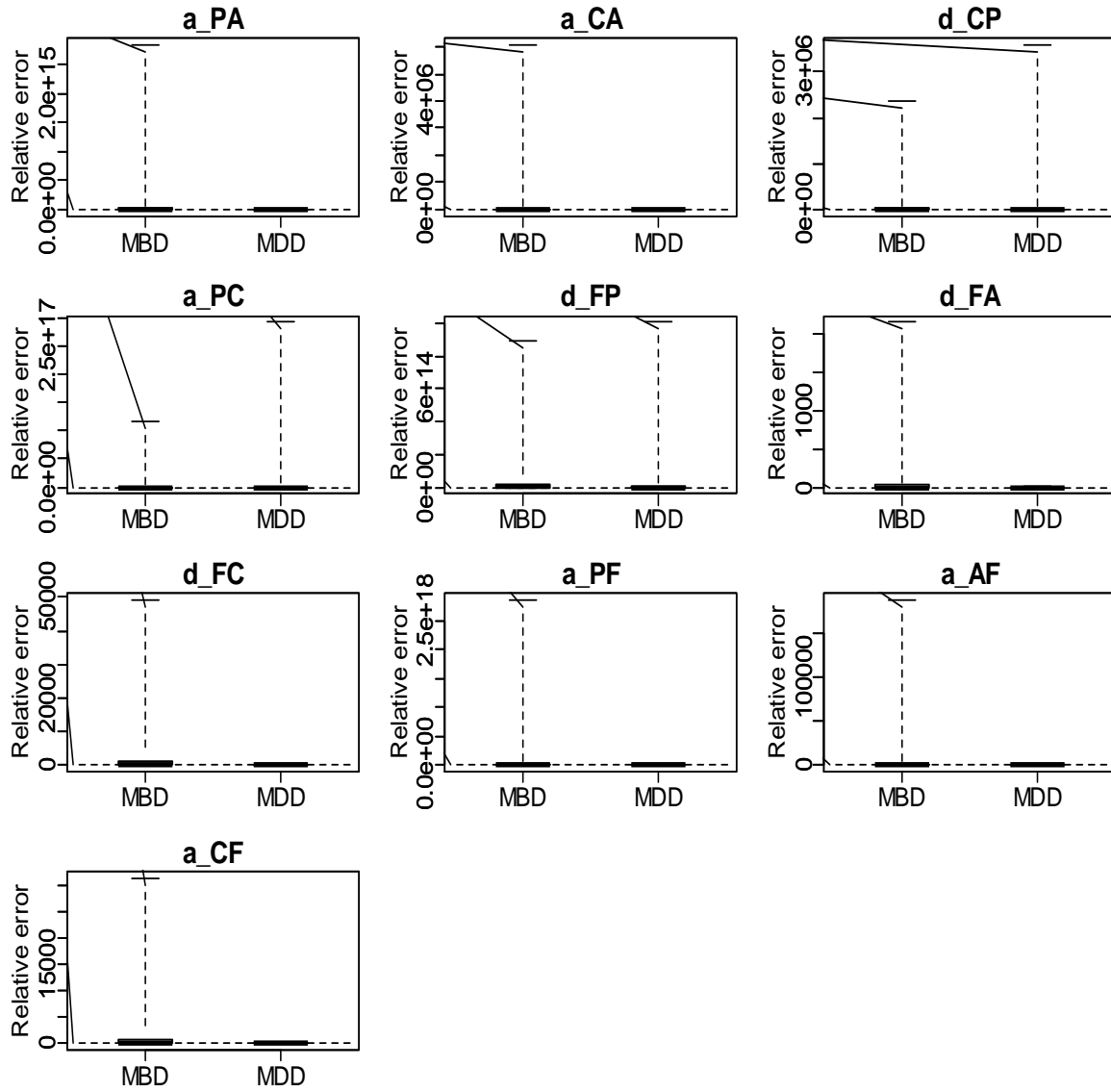
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Figure 5. Boxplots of parameter estimates from Monte Carlo simulations expressed as relative errors, i.e., true parameters are at 0 (dotted horizontal lines). For definitions of the parameters see Table 1. Lower and upper bounds of the boxes indicate 25th and 75th percentiles, respectively. Thick horizontal lines inside the boxes indicate median errors. Whiskers indicate 2.5th and 97.5th percentiles.



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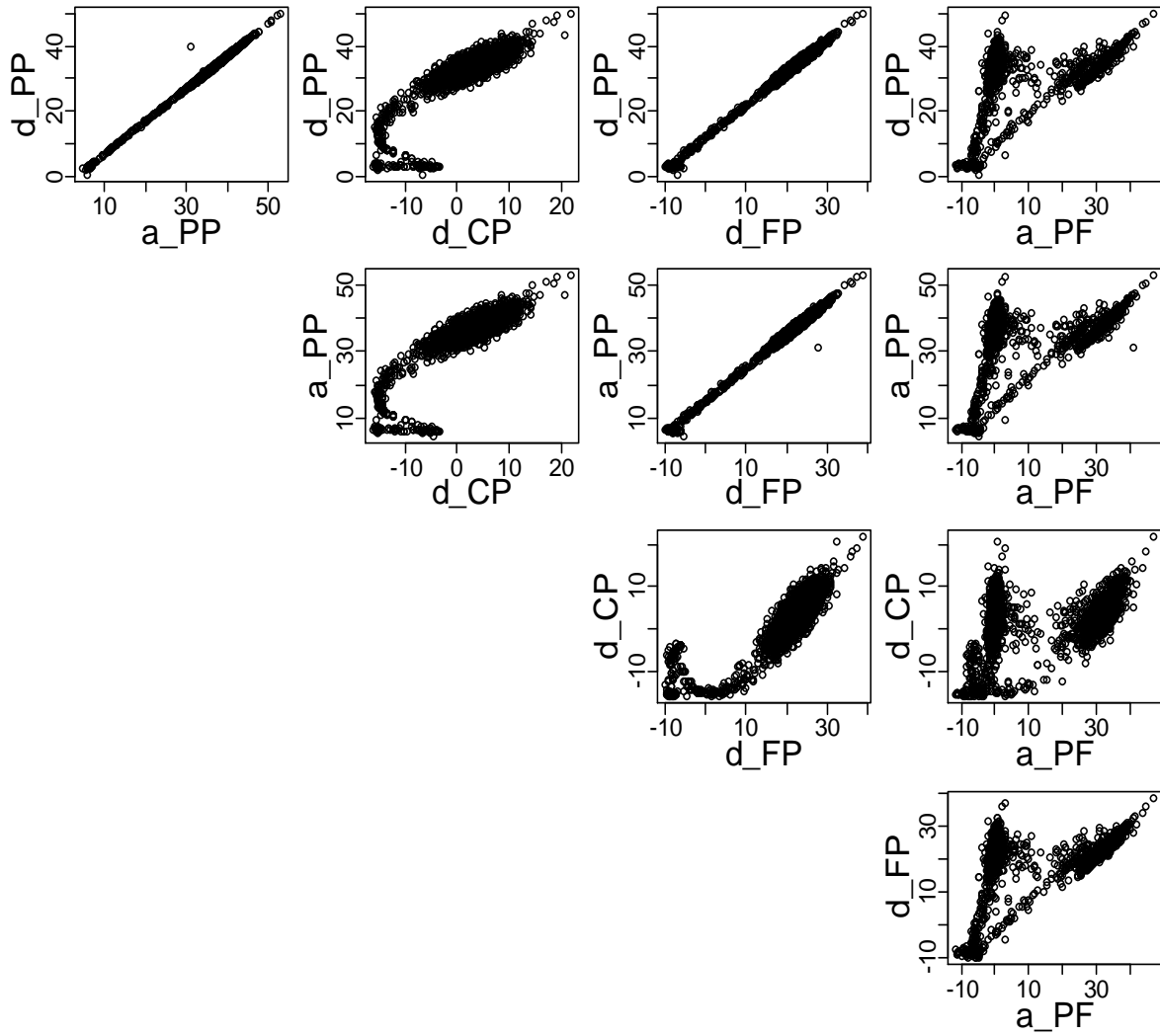
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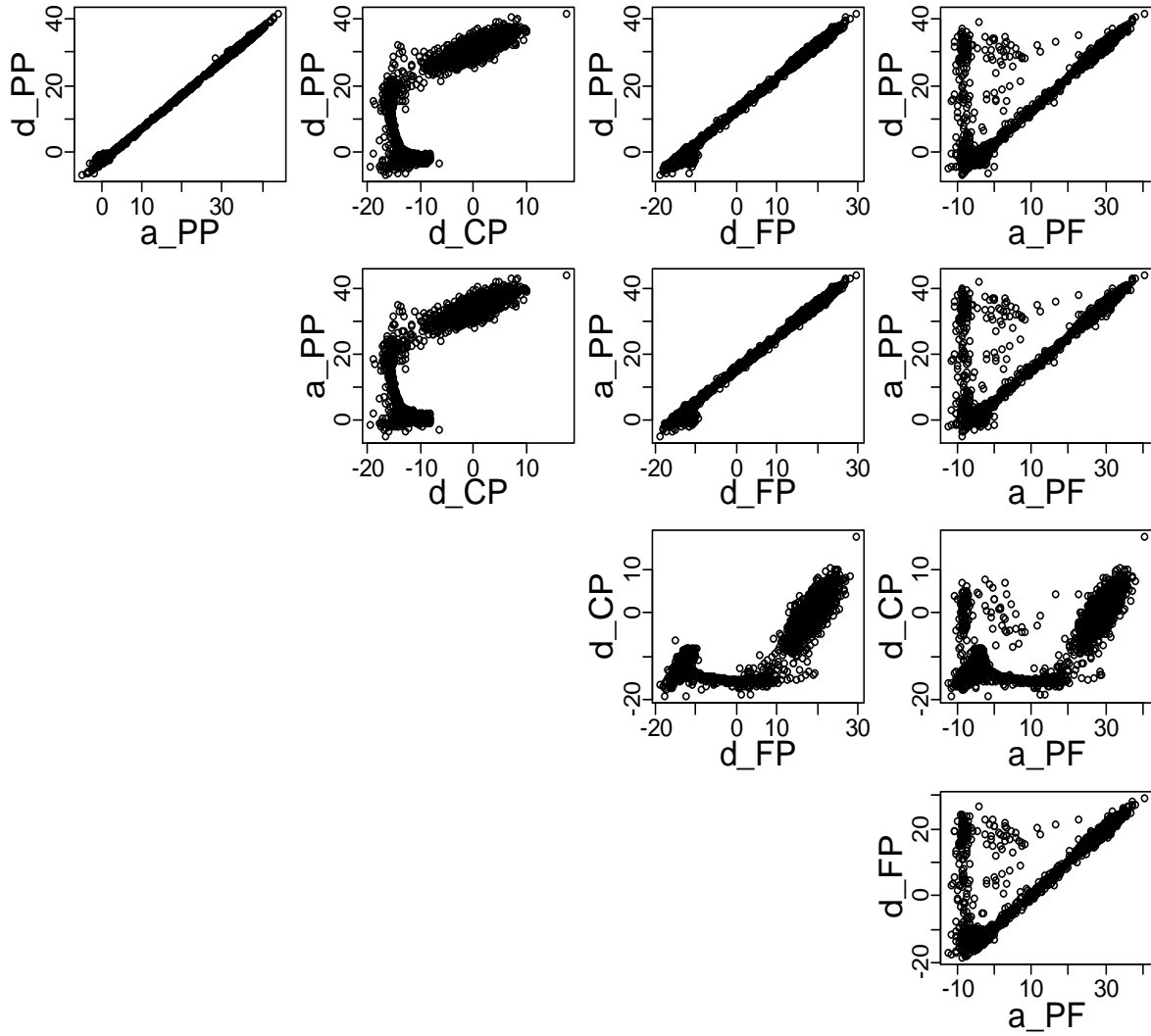
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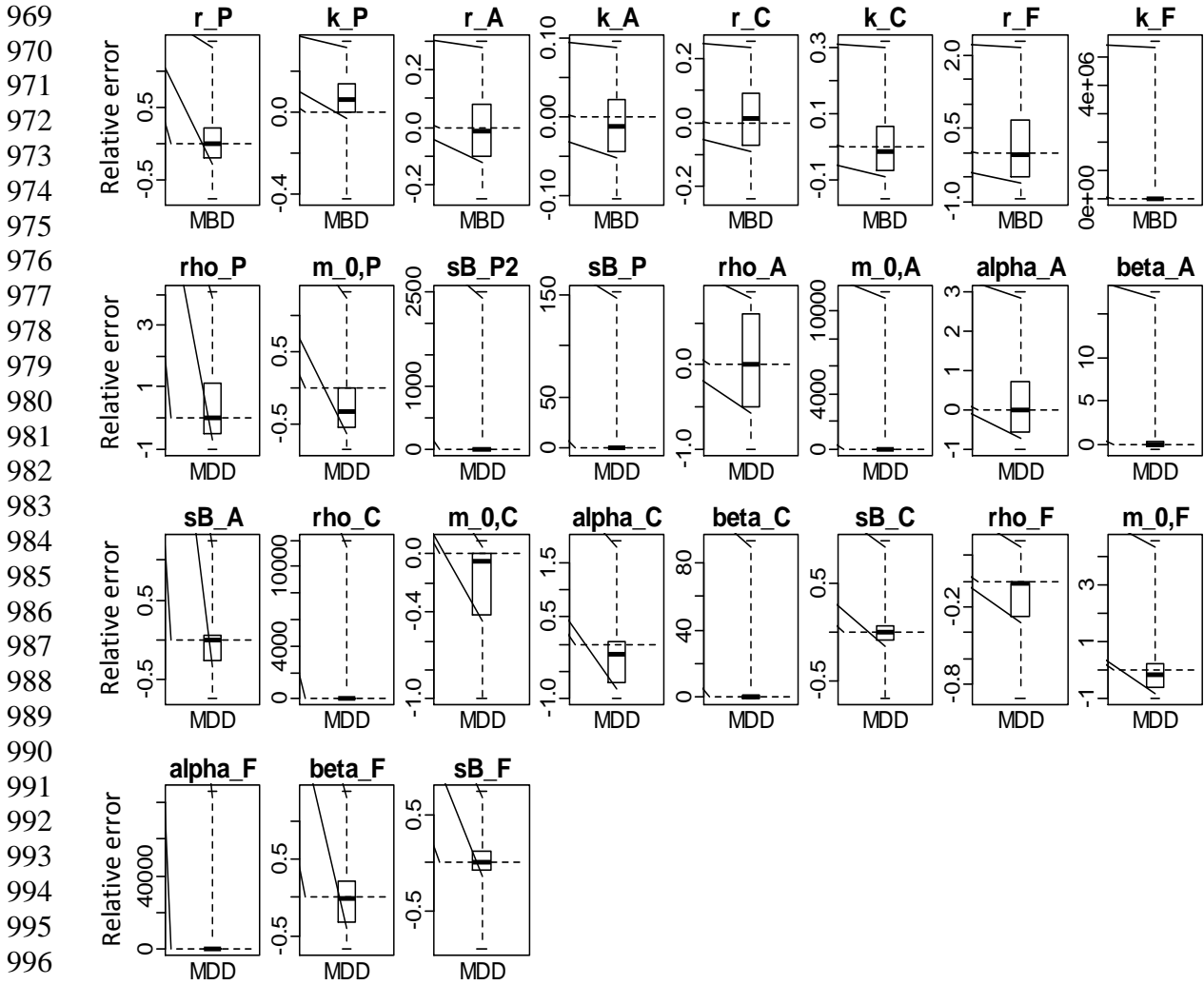


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 959 Figure 6. Scatterplots of parameter estimates by the MBD models for pairs of selected predation
 960 parameters that are strongly positively correlated. See Table 1 for parameter definitions. Both x and y
 961 axes are on natural log scale.

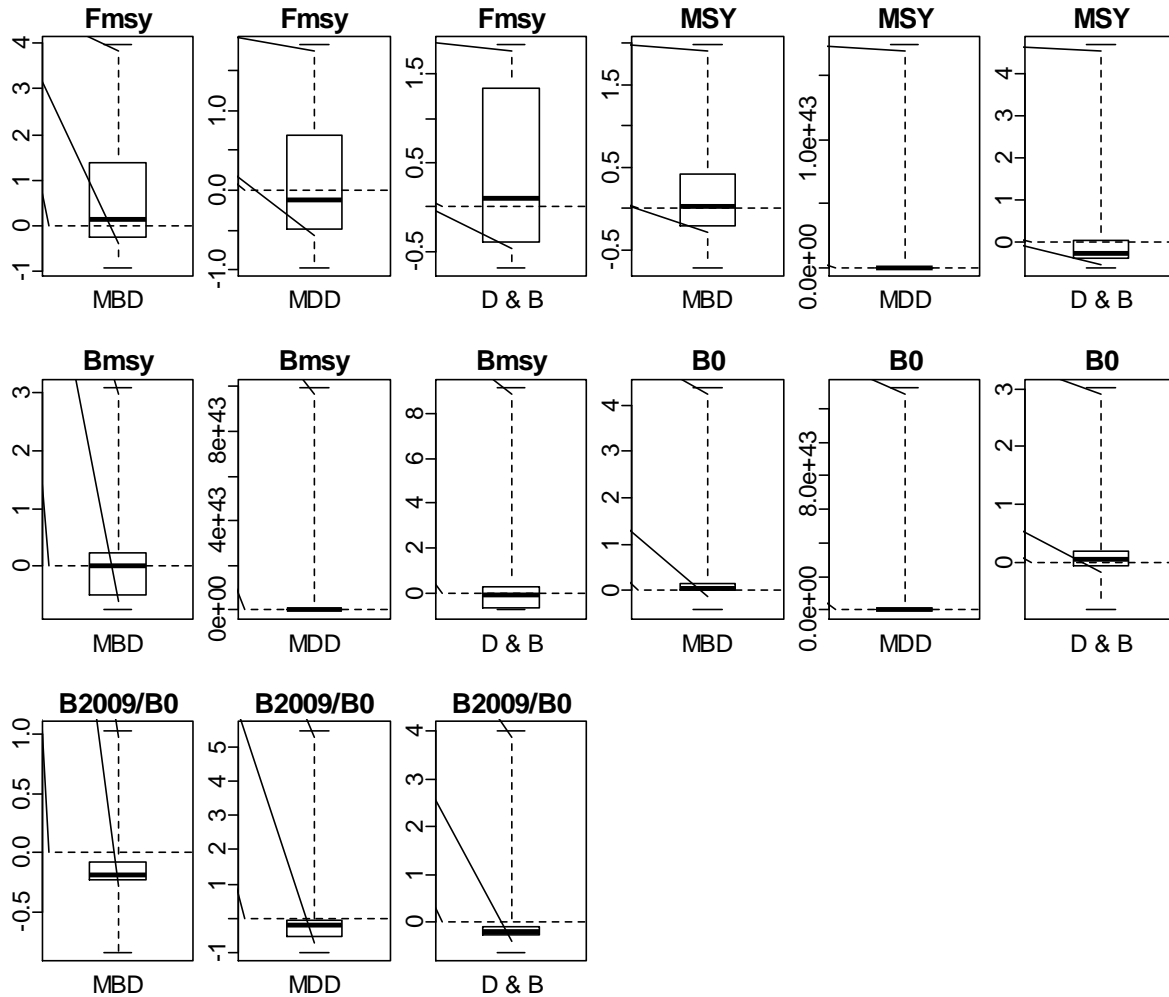
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 965 Figure 7. Scatter plots of parameter estimates by the MDD models for pairs of selected predation
 966 parameters that show strong positive correlation. Definitions of the parameters are found in Table 1. Both
 967 x and y axes are on natural log scale.
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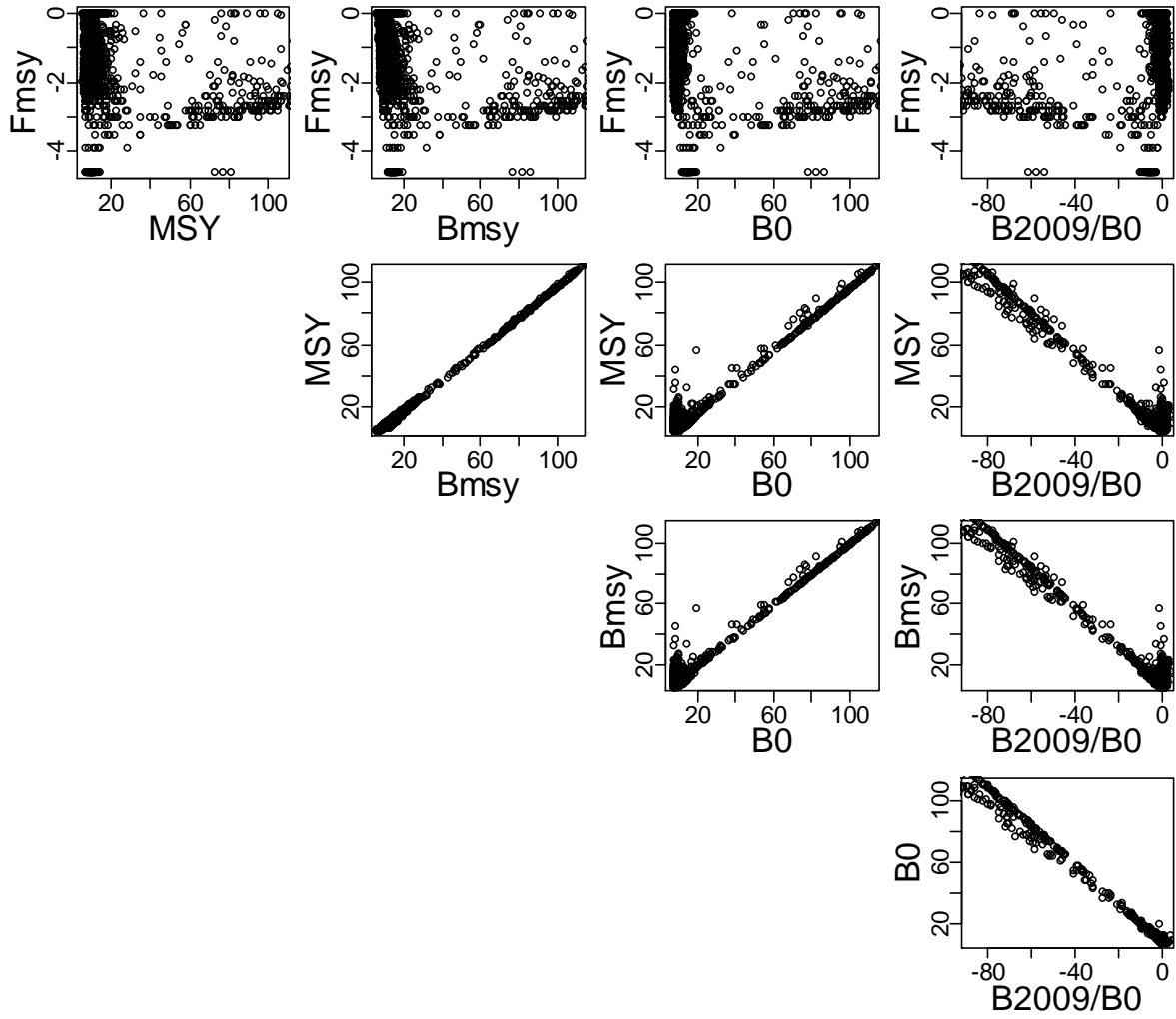


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 998 Figure 8. Boxplots of relative errors in parameter estimates from Monte Carlo simulations, i.e., true
 999 parameters are at 0 (dotted horizontal lines). See Table 1 for parameter definitions. Lower and upper
 1000 bounds of the boxes indicate 25th and 75th percentiles, respectively. Thick horizontal lines inside the boxes
 1001 indicate median errors. Whiskers indicate 2.5th and 97.5th percentiles. These parameters are unique to
 1002 either the MBD or the MDD model.
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 1005 Figure 9. Boxplots of relative errors for estimated biological reference points from Monte Carlo
 1006 simulations, i.e., true parameters are at 0 (dotted horizontal lines). Lower and upper bounds of the boxes
 1007 indicate 25th and 75th percentiles, respectively. Thick horizontal lines inside the boxes indicate median
 1008 errors. Whiskers indicate 2.5th and 97.5th percentiles. Both data generation and parameter estimation were
 1009 done using the MBD or the MDD models, for the plots labeled “MBD” and “MDD”, respectively. For the
 1010 plots labeled “D & B”, the MDD model was used to simulate data, then the MBD model was used to
 1011 estimate management quantities.

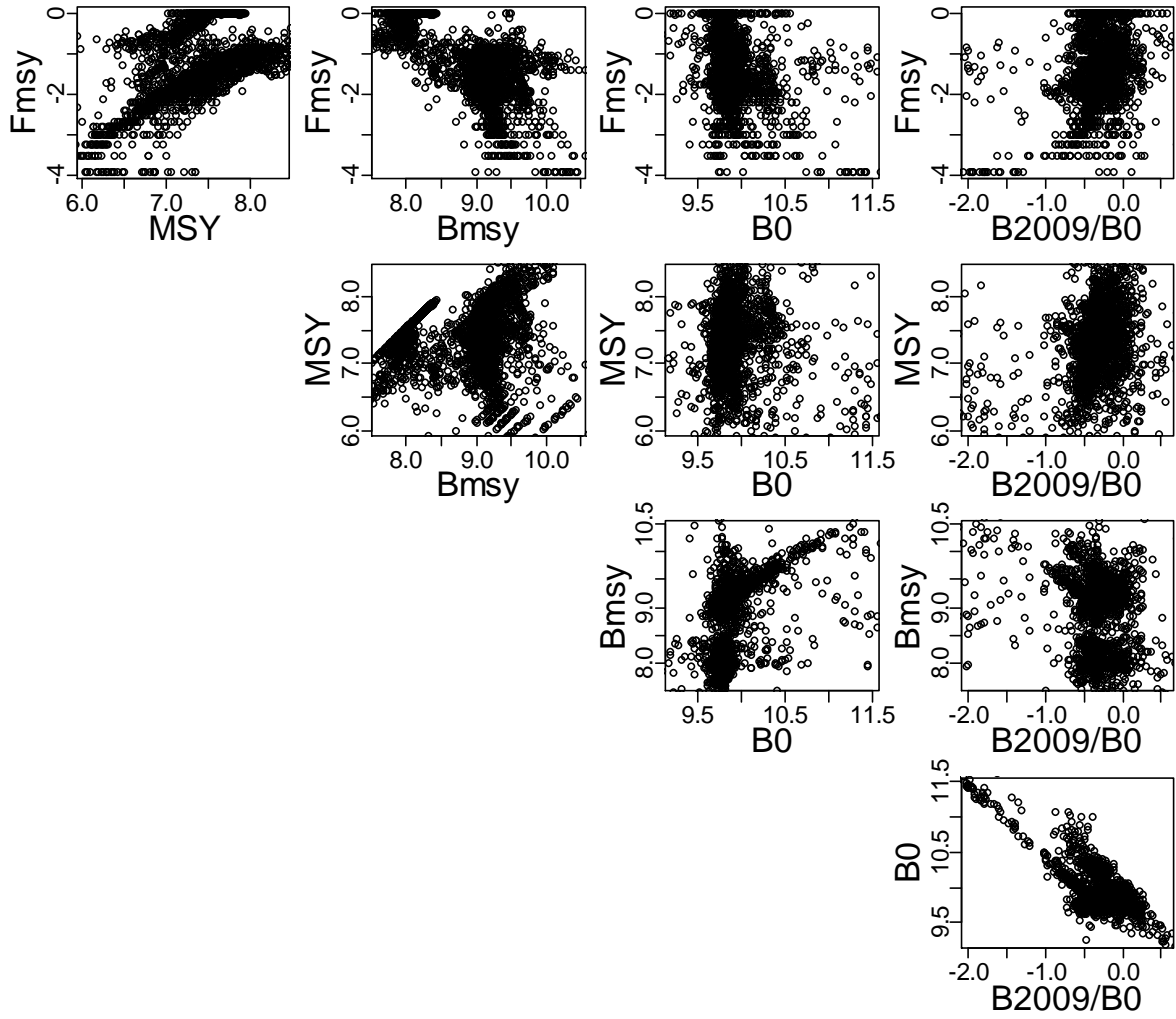
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1014 Figure 10. Scatterplots of biological reference points estimated by the MDD models. Both x and y axes

1015 are on a natural log scale.

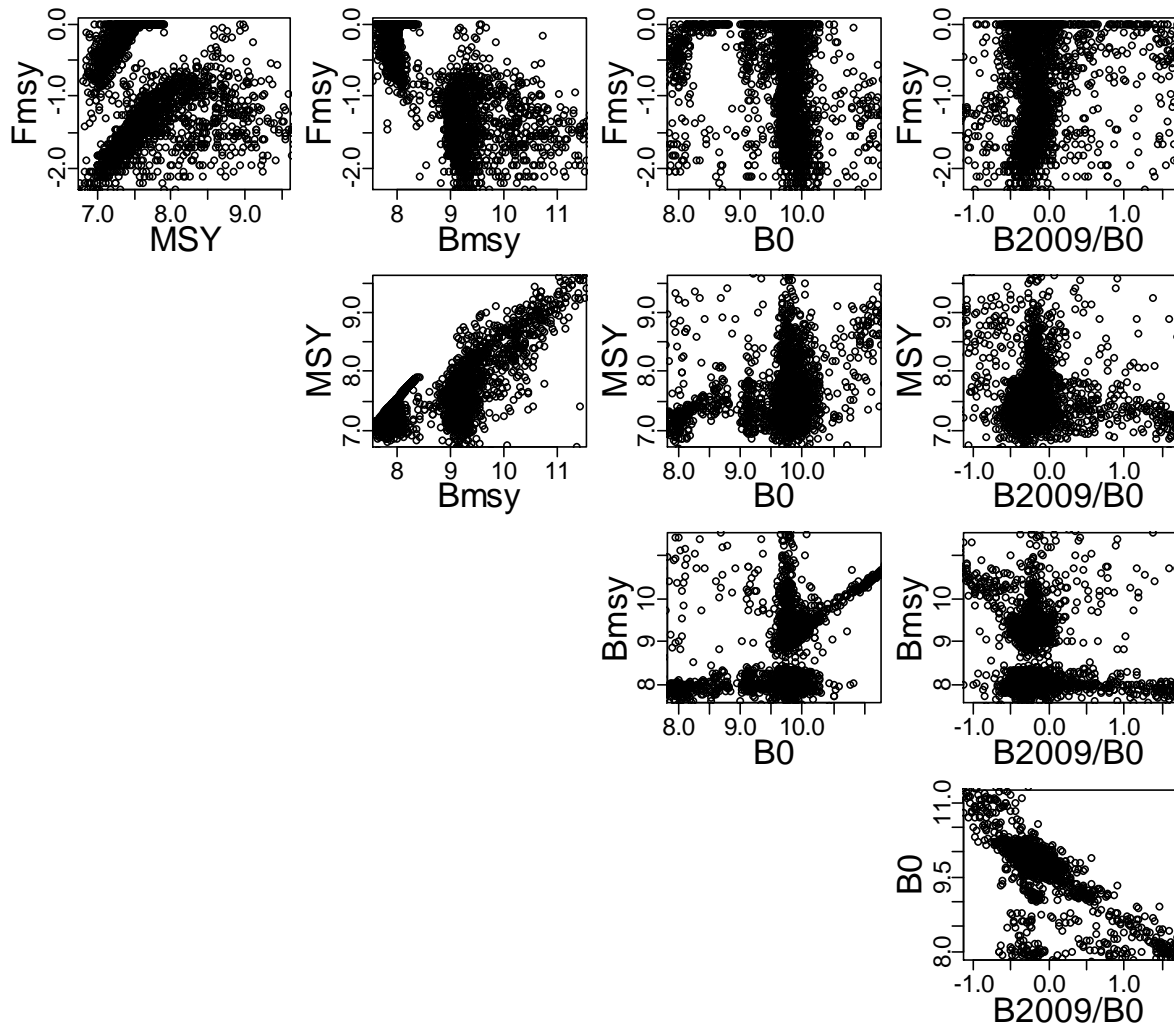


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1017 Figure 11. Scatterplots of biological reference points estimated by the MBD models. Both x and y axes

1018 are on a natural log scale.

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Figure 12. Scatterplots of biological reference points estimated by the MBD models based on biomass

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projections using the MDD models. Both x and y axes are on a natural log scale.

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1024 **Chapter 2: Multispecies Biomass Dynamics Models Reveal Effects of Ocean Temperatures on**
1025 **Predation of Juvenile Pollock in the Eastern Bering Sea**

1026

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1031

1032 **Abstract**

1033 Walleye pollock is the most abundant and commercially valuable groundfish species in the eastern Bering
1034 Sea (EBS). However, poor recruitment between 2001 and 2005, a period of warm ocean temperatures, led
1035 to a sharp decline in the EBS pollock stock from 2003 to 2009 and a ~40% reduction in catch relative to
1036 the previous decade. Juvenile pollock are important forage fish in the EBS ecosystem, often representing
1037 the largest fraction in the diets of major Bering Sea piscivores, including arrowtooth flounder, flathead
1038 sole, Pacific cod, and adult walleye pollock. Predation on juvenile pollock, including cannibalism by adult
1039 pollock, plays an important role in determining pollock recruitment strength. Some studies have
1040 suggested that a pool of cold water on the EBS shelf provides a thermal refuge for juvenile pollock from
1041 their predators, and that the recent warming trend may have caused an increase in predation on juvenile
1042 pollock. We constructed multispecies biomass dynamics models of walleye pollock, Pacific cod,
1043 arrowtooth flounder, and three other flatfish species, including their trophic interactions, to quantify the
1044 magnitude of predation. Using model selection criterion, we tested a hypothesis that reduction in the
1045 extent of the cold pool (indicated by an increase in annual mean bottom water temperature) intensifies
1046 predation on juvenile pollock. We found that warmer temperatures increase cannibalism and predation on
1047 age-1 pollock by adult pollock (age 3+) and arrowtooth flounder, respectively, and decreases cannibalism
1048 on age-0 pollock by adult pollock. The opposite effect of water temperature on age-0 and age-1 pollock
1049 likely reflects different distributions of these pollock age classes in relation to the cold pool. The model
1050 developed in this study can be used to examine effects of climate change on inter-specific interactions
1051 within the groundfish community and their implications on ecosystem structure and productivity.

1052 **Keywords:**

1053 Bering Sea ecosystem, the cold pool, multispecies model, biomass dynamics model, predator-prey
1054 interaction

1055 **Prepared for submission to:**

1056 Canadian Journal of Fisheries and Aquatic Sciences

1057 **Introduction**

1058 Walleye pollock (*Gadus chalcogrammus*) is the most abundant and commercially important groundfish
1059 species in the Bering Sea. Pollock represent 56% of exploitable groundfish biomass in the Bering Sea and
1060 Aleutian Islands management area (NPFMC 2010), and pollock catches averaged 76% of the total
1061 groundfish catch by weight from 1990 to 2009 (NPFMC 2009). Commercial fisheries for pollock
1062 represent over 40% of the global whitefish production. However, the eastern Bering Sea (EBS) pollock
1063 stock declined more than 60% from a high of 12.2 million t in 2003 (age 3+ biomass) to a low of 4.6
1064 million t in 2008, before increasing again in more recent years (Ianelli et al. 2013). This decline in
1065 biomass was also reflected in reduced harvests. In 2009 and 2010, annual EBS pollock catch dropped to
1066 0.81 million tons, roughly a 40% reduction from the average catch (1.28 million tons) over the previous 9
1067 years (Ianelli et al. 2010). Changes in stock biomass are primarily due to the effect of year class
1068 variability and the sharp decline since 2003 has been attributed to poor recruitment between 2001 and
1069 2005 (Ianelli et al. 2010, Coyle et al. 2011). The mechanisms controlling pollock recruitment are complex
1070 and poorly understood, but likely involve both physical and biological factors, as well as interactions
1071 among them (Jurado-Molina and Livingston 2002, Mueter et al. 2006).

1072 Pollock, especially juveniles, are important forage fish in the EBS ecosystem. Juvenile pollock often
1073 represent the largest fraction in the diets of major Bering Sea piscivores, including arrowtooth flounder
1074 (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), and adult walleye pollock (Aydin et al.
1075 2007, Coyle et al. 2011). Cannibalism by adult pollock has been estimated to cause 40% of juvenile
1076 pollock mortality (Aydin et al. 2007) and plays an important role in determining the pollock recruitment
1077 strength (Wespestad and Quinn 1996). Arrowtooth flounder are a major predator of both juvenile and
1078 adult pollock, raising serious concerns about the effects of an increasing arrowtooth flounder population
1079 in the Bering Sea on future pollock recruitment.

1080 Physical oceanographic conditions also affect pollock recruitment, either by affecting food production
1081 (bottom-up) or by affecting predation intensity (top-down). It was hypothesized that warm spring
1082 conditions and early sea ice retreat on the EBS shelf reduces the availability of large zooplankton prey for
1083 age-0 pollock, resulting in weak age-1 recruitment the following year (Hunt et al. 2011). Low abundance
1084 of large zooplankton in warm years may reduce pollock recruitment further as fish predators turn to age-0
1085 pollock as an alternative prey. In warm years, strong northward advection transports juvenile pollock
1086 inshore and away from adults. Spatial separation between juvenile and adults may in turn reduce
1087 cannibalism and enhance recruitment the following year (Wespestad et al. 2000, Mueter et al. 2006)

1088 The presence of the so-called “cold pool” is one of the unique features of the EBS shelf. The cold pool is
1089 a body of cold bottom water generally $< 2^{\circ}\text{C}$, which persists on the middle shelf (50-100 m) throughout
1090 summer. The cold pool forms when sea ice freezes in the winter, and the size of the cold pool in summer
1091 depends on the extent of sea ice during the previous winter. Many subarctic fish species avoid the cold
1092 pool (Mueter and Litzow 2008) and are therefore excluded from much of the shelf when the cold pool is
1093 extensive, concentrating fish in the outer shelf and slope regions (Figure 1a, Spencer 2008). It has been
1094 hypothesized that an extensive cold pool increases encounter rates between prey and predators and results
1095 in higher predation rates on forage fishes (Wyllie-Echeverria and Ohtani 1999, Wespestad et al. 2000).
1096 On the other hand, there is some evidence that young pollock, in particular age-1 fish, can tolerate cold
1097 temperatures better than older fish and thus are able to seek refuge in the cold pool to avoid predation
1098 (Francis and Bailey 1983, Bailey 1989, Wyllie-Echeverria and Wooster 1998). If that were the case, then
1099 predation on juvenile pollock is expected to be lower in cold years with an extensive cold pool (Figure
1100 1b).

1101 In this study we use a multi-species modeling approach to examine the effects of variability in the cold
1102 pool on predation of juvenile pollock. Specifically, we test the hypothesis that the extent of the cold pool
1103 is related to the predation rate on juvenile pollock by their major predators, including adult pollock.

1104 **Methods**

1105 Overview

1106 We quantified predation on juvenile pollock by modeling the biomass dynamics of six EBS groundfish
1107 species – walleye pollock, arrowtooth flounder, Pacific cod (*Gadus macrocephalus*), yellowfin sole
1108 (*Limanda aspera*), northern rock sole (*Lepidopsetta polyxystra*), and flathead sole – and predatory
1109 interactions among them (Figure 2). We aggregated all flatfish species except arrowtooth flounder into a

1110 ‘small-mouth flatfish’ group because of similar decadal trends in stock biomass and similar trophic and
1111 ecological roles in the ecosystem. Walleye pollock was divided into two age groups, juveniles (age 0, 1,
1112 and 2) and adults (age 3+) to explicitly model cannibalism of juveniles by adult pollock. Model details are
1113 provided in Appendix 1. The model provides a good fit to the data and captures the major biomass
1114 dynamics and apparent interactions among the species groups [Uchiyama et al., in prep].

1115 To test for the effects of variability in the cold pool on predation we included temperature-dependent
1116 predation rates in the model as described below. The model was fit to survey biomass data, catch data,
1117 and mean bottom water temperature as a proxy for the cold pool extent. Several alternative models that
1118 each included temperature-dependence for one selected predator-prey interaction were considered and a
1119 multi-model approach was used to quantify the evidence for different temperature-dependent predation
1120 terms.

1121 Data

1122 Survey biomass estimates of the study species, commercial catch statistics, and estimated biomass lost to
1123 predation used in this study are described in Appendix 1. In addition, estimates of summer bottom
1124 temperature (T_B) were obtained from the Alaska Fisheries Science Center
1125 (http://www.afsc.noaa.gov/RACE/groundfish/survey_data/ebswater.htm).

1126 Apportionment of pollock predation into age classes

1127 Estimated biomass lost to predation reported in the Alaska Fisheries Science Center’s groundfish food
1128 habits reports represent aggregated biomass of all prey age classes. To fit model predicted predation on
1129 pollock by age class, reported predation estimates were assigned to pollock age classes 0 through 3+
1130 using the methods described below. The length distribution of pollock prey consumed by their predators
1131 was obtained from the Alaska Fisheries Science Center (Kerim Aydin, NMFS, personal communication).
1132 These pollock prey length data were subdivided into four sampling quarters (January – March, April –
1133 June, July – September, October – December). Based on visual examination, we assumed that pollock
1134 prey in each quarter consisted of four distinct cohorts and that body length of individual prey in each
1135 cohort followed a normal distribution around a mean. The smallest cohort in the first sampling quarter
1136 was assumed to be age-1 because the mean body length of this cohort was as large as that of the second
1137 smallest cohort in the second quarter, and because pollock spawning peaks in early April in the EBS
1138 (Wespestad et al. 2000). For the second, third, and fourth sampling quarters, the smallest cohort was
1139 assumed to be age-0. Parameters of cohort body length distributions (i.e., means and variances) were

1140 estimated using the R package ‘mixtools’ (Benaglia et al. 2009). Based on the quarter-specific cohort
1141 body length distributions, the probability that prey of a given size in a given quarter belongs to a
1142 particular cohort was calculated to assign individual pollock prey to one of four age classes (0, 1, 2, and
1143 3+). Body weights of individual prey were estimated from their body length and the length-weight
1144 relationship in Kooka (2012). Individual prey weights were summed by prey age class, predator, and
1145 sampling year. The proportion by weight of each prey age class was then calculated for each predator and
1146 year. The biomass of each pollock age class lost to predation was then calculated by multiplying total
1147 pollock biomass lost to predation by the age class proportions calculated above.

1148 Models

1149 Previously, we developed two alternative multispecies models for focal EBS groundfish species – a
1150 biomass dynamics model and a delay difference model (Uchiyama et al., in prep.). Although each model
1151 has advantages and disadvantages, we selected the multispecies biomass dynamics model as the preferred
1152 model, largely because small changes in parameter values often led to unrealistic or chaotic behaviors of
1153 biomass trajectories for the multispecies delay difference model. Therefore, in this study, biomass
1154 dynamics of adult walleye pollock (age 3+), arrowtooth flounder (age 1+), Pacific cod (age 1+), and
1155 small-mouth flatfish group (age 1+) were modeled using the multispecies biomass dynamics model
1156 described in Uchiyama et al. (in prep), modified to include temperature-dependent predation rates.

1157 To examine the effects of bottom temperature on juvenile pollock predation we modeled predation rates
1158 (d in Appendix 1) in the biomass dynamics model as a linear function of summer bottom temperature
1159 anomalies (T_B):

$$1160 \quad d_{za} = \bar{d}_{za} + e_{za} * T_B,$$

1161 where d_{za} is the predation rate for predator z and prey (juvenile age class) a , \bar{d}_{za} is the mean predation rate
1162 at $T_B = 0$, and e_{za} is the slope parameter for the linear relationship between predation rate and temperature.
1163 Models were constructed to test for the effects of temperature on one predator-prey pair at a time by
1164 estimating the parameter e_{za} for the predator-prey combination of interest and fixing e_{za} at zero for all
1165 other predator-prey combinations. Thus, each model corresponds to the hypothesis that the per-capita
1166 predation rate of predator z on juvenile age class a increases ($e_{za} > 0$) or decreases ($e_{za} < 0$) with changes
1167 in bottom temperature. A total of thirteen models were tested, including all combinations of three pollock
1168 age classes and four predators, plus a model with no effect of bottom temperature. Model parameters were
1169 estimated using the maximum likelihood method. The likelihood function is described in Appendix 1.

1170 Model selection

1171 We quantified the evidence for different temperature-dependent predation rates using the Akaike
1172 Information Criterion and Akaike weights. For each of the 13 model configurations, the Akaike
1173 Information Criterion corrected for small sample size (AIC_C) was calculated following Burnham &
1174 Anderson (2002):

$$1175 \quad AIC_C = -2\ln(L) + 2k + \frac{2k(k+1)}{n-k-1},$$

1176 where L = likelihood

1177 k = number of parameters.

1178 n = number of observations.

1179 Akaike weights (w_i) were calculated for each model by the following equation;

$$1180 \quad w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{i=1}^R \exp\left(-\frac{1}{2}\Delta_i\right)},$$

1181 where $\Delta_i = AIC_{C,i} - AIC_{C,minimum}$

1182 R = number of models compared.

1183 Akaike weights, w_i , reflect the weight of evidence in favor of model i being the best model among the
1184 models considered. To reduce the bias related to model selection uncertainty, parameter estimates were
1185 averaged over the entire set of models following Burnham & Anderson (2002):

$$1186 \quad \hat{\theta}_j = \sum_{i=1}^R w_i \hat{\theta}_{j,i},$$

1187 where $\hat{\theta}_j$ = model-averaged estimate of j^{th} parameter.

1188 $\hat{\theta}_{j,i}$ = estimator of the j^{th} parameter in model i .

1189 Model-averaged predictions for biomass and biomass lost to predation by year were computed similarly:

1190
$$\hat{B}_y = \sum_{i=1}^R w_i \hat{B}_{y,i},$$

1191 where \hat{B}_y = model-averaged prediction of biomass or biomass lost to predation in year y .

1192 $\hat{B}_{y,i}$ = the model-averaged estimated biomass or biomass lost to predation in year y

1193 for model i .

1194 **Results**

1195 The model that included an effect of bottom temperature on predation of age-1 pollock by arrowtooth
1196 flounder was most strongly supported by the data (Table 1). Three other models (bottom temperature
1197 effect on cannibalism of age-0 and age-1 pollock by adult pollock, and predation of age-0 pollock by
1198 Pacific cod) had better support than the null model (i.e., no bottom temperature effect) although the
1199 difference in AIC_c was small. Bottom temperature had a positive effect (i.e., predation increased with
1200 increasing temperature) in seven of the 12 models, including pollock predation on age-1 pollock,
1201 arrowtooth predation on juvenile pollock of all ages, cod predation on age-0 pollock, and flatfish
1202 predation on age-0 and age-1 pollock. In contrast, warmer bottom temperature was estimated to cause a
1203 decrease in cannibalism of age-0 and age-2 pollock by adult pollock, predation of age-1 and age-2 pollock
1204 by cod, and predation of age-2 pollock by flatfish.

1205 Model-averaged predictions suggest that a large portion of the biomass of age-0 and age-1 pollock was
1206 lost to predation, but predation was relatively small for age-2 pollock, adult pollock (age 3+), arrowtooth
1207 flounder, Pacific cod, and small-mouth flatfish (Table 2, Figure 3).

1208 Temperature had the largest relative effect on age-1 predation by arrowtooth flounder, with predation
1209 rates varying $\pm 25\%$ relative to the estimated predation rate at the mean temperature of 2.25 °C (Figure 4).
1210 Temperature effects on predation of age-0 and age-2 pollock were largest for Pacific cod ($\pm 10\%$, Figure
1211 4), although the absolute predation rates were small (Figure 3). For age-0 and age-2 pollock, predation by
1212 adult pollock, arrowtooth flounder, and small-mouth flatfish changed by less than $\pm 3\%$ relative to

1213 predation at the mean temperature. Predation on age-1 pollock by adult pollock increased with
1214 temperature by 8%, while predation by cod decreased and predation by flatfish increased with
1215 temperature by less than 1%. Predation on age-2 pollock decreased with increasing temperature for all
1216 predators except arrowtooth flounder. However, the change in arrowtooth predation was small (<1%), as
1217 was the change in flatfish predation.

1218 Compared to the effect of changes in predator biomass on predation, the effects of changing bottom
1219 temperature on predation rates are negligible, except in three cases (cod predation on age-0 and age-2,
1220 arrowtooth predation on age-1).

1221 **Discussion**

1222 Our results suggest that variability in the extent of the cold pool on the EBS shelf affects important
1223 predator-prey interactions. In particular, warmer temperatures are associated with enhanced predation on
1224 juvenile pollock (age-1) by arrowtooth flounder and, to a lesser extent, by adult pollock. These results are
1225 consistent with the hypothesis that an extensive cold pool provides a refuge for age-1 pollock from these
1226 predators (Figure 1b).

1227 Other lines of evidence also suggest that changes in water temperature affect predation on juvenile
1228 pollock. Walleye pollock migrate from their spawning ground to the feeding ground on the shelf in
1229 spring. Pollock migrate further inshore when the bottom temperature is high (Kotwicky et al. 2005);
1230 increased cannibalism of age-1 pollock is associated with spatial overlap between age-1 and adult
1231 pollock. Arrowtooth flounder are more widely distributed on the shelf when the cold pool is smaller
1232 (Spencer 2008, Ciannelli et al. 2012). The overlap between distribution of juvenile pollock and that of
1233 arrowtooth flounder on the shelf increases in warm years, and pollock recruitment is negatively correlated
1234 with the magnitude of the overlap (Hunsicker et al. 2013).

1235 Our results imply that increasing abundances of arrowtooth flounder, in combination with anticipated
1236 decreases in ice extent and duration, may increase predation on age-1 pollock. Decreases in ice extent and
1237 enhanced summer temperatures have previously been shown to reduce the overwinter survival and
1238 subsequent recruitment of young-of-year pollock due to reduced prey availability (Hunt et al 2011, Heintz
1239 et al 2013). This study suggests that recruitment may be further reduced in warm years because of
1240 increased predation mortality on age-1 pollock. Therefore, anticipated declines in the future recruitment
1241 and abundance of walleye pollock in a warming climate may be even more pronounced than predicted

1242 (Mueter et al 2011). While Mueter et al. (2011) included scenarios with increasing arrowtooth flounder
1243 abundances in projections, the effect of increasing temperatures on predation was not considered.

1244 Our results suggest that bottom temperature affects predator-prey interactions differently among different
1245 age classes of pollock prey. While predations on age-1 pollock were predicted to increase with increasing
1246 bottom temperature, predation on age-0 pollock by adult pollock was predicted to decrease with
1247 increasing temperature. The difference in predicted temperature effect may reflect different distributions
1248 of juvenile age classes in relation to the cold pool. Age-1 pollock can tolerate wider range of water
1249 temperature than age-0 pollock and are found more often near the bottom (Bailey 1989, Duffy-Anderson
1250 et al. 2003, Hollowed et al. 2012), while age-0 pollock are typically distributed above the thermocline
1251 during summer (Olla et al. 1996). If age-0 pollock are excluded from the cold pool as are many of their
1252 predators, but age-1 pollock are not, reduction of the size of the cold pool may have opposite effects on
1253 predation of age-0 and age-1 pollock.

1254 We identify some caveats in our approach. Although our results suggest that bottom temperature affects
1255 predator-prey interactions among the EBS groundfish species, estimated effects were highly uncertain and
1256 mostly weak (except ATF on age-1), hence these may not be ecologically important relationships. In the
1257 current study, estimated temperature effects on predation rates were assumed to be linear for simplicity.
1258 Results may change if fish respond to change in temperature in a non-linear fashion. For example,
1259 predation rates might increase up to some optimum temperature and decrease thereafter. Effect of bottom
1260 temperature on each of the predator-prey interaction was assumed independent of one another. However,
1261 change in one interaction may affect others, as it changes proportions of available prey to predators.

1262 In the current study, we examine effects of bottom temperature on predator-prey interactions in the EBS
1263 groundfish community using multispecies biomass dynamics model. The model developed in this study
1264 could be used to examine effects of other covariates on inter-specific interactions, to help explain
1265 observed changes in the fish community, and to understand implications of climate change on an
1266 ecosystem and its productivity.

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- 1364

1365 Table 1. Comparison of estimated model parameters: AIC_C , ΔAIC_C , w_i .

Predator	Prey age class	Parameter estimate (model-averaged)	ΔAIC_C	w_i
Arrowtooth	1	60.424	0	0.798
Pollock	1	0.049	4.96	0.067
Pollock	0	-0.051	6.98	0.024
Cod	1	-0.255	7.08	0.023
NA	NA	NA	7.55	0.018
Arrowtooth	0	0.058	7.76	0.016
Cod	2	-0.577	8.34	0.012
Flatfish	1	1.116	8.54	0.011
Cod	0	0.474	9.16	0.008
Arrowtooth	2	0.014	9.22	0.008
Pollock	2	-8.7E-05	9.38	0.007
Flatfish	0	0.519	9.98	0.005
Flatfish	2	-4.8E-12	22.18	0.000

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1367 Table 2. Percentage of prey biomass consumed by each predator, averaged over 1982 – 2009.

Prey	Predator	pollock	cod	ATF	flatfish	Total
age-0 pollock		42.96%	0.01%	0.07%	0.25%	43.29%
age-1 pollock		63.61%	0.92%	9.44%	3.30%	77.27%
age-2 pollock		0.78%	0.35%	1.80%	0.00%	2.93%
adult pollock			1.23%	0.15%		1.38%
cod		0.02%				0.02%
ATF		0.00%	0.09%			0.09%
flatfish		0.01%	0.36%	0.19%		0.56%

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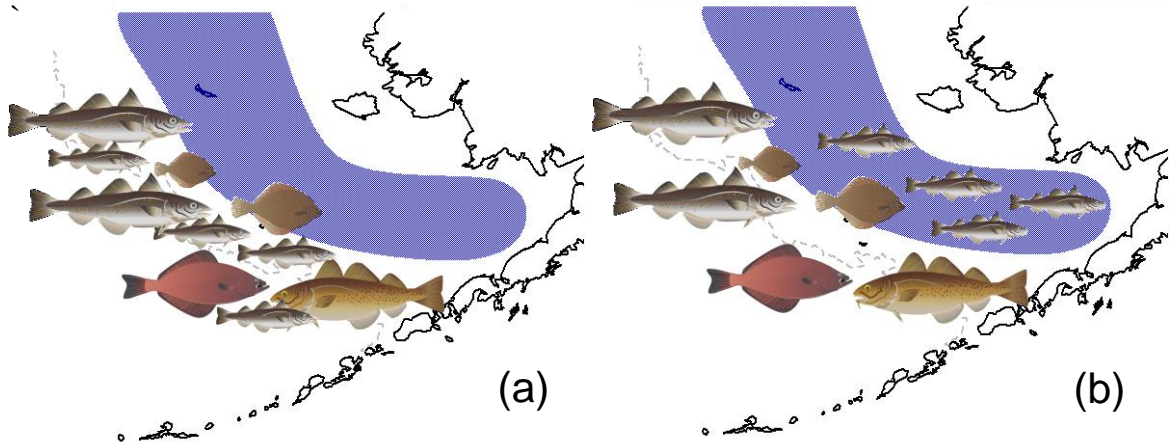


Figure 1. Schematic diagrams showing alternative hypotheses on how the cold pool may affect predation on juvenile pollock. The cold pool (a) excludes young pollock from the shelf, exposing them to predators on the slope; or (b) protects young pollock from predators if they can tolerate the cold temperature.

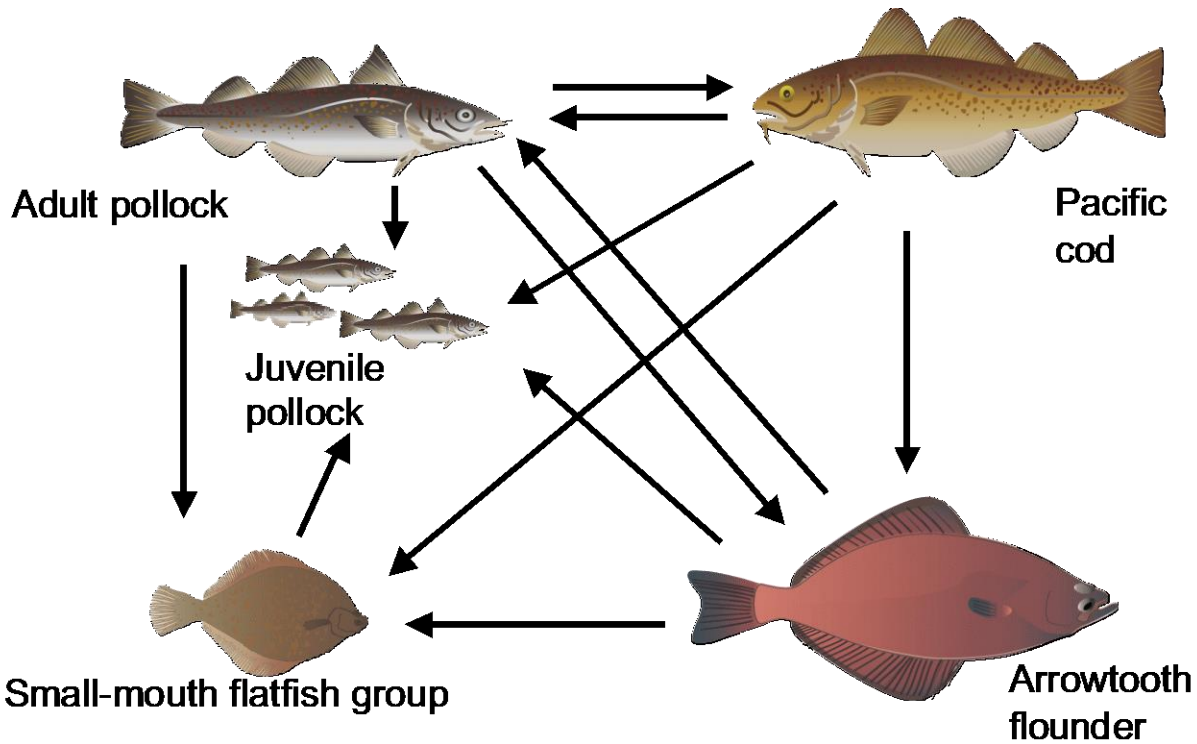
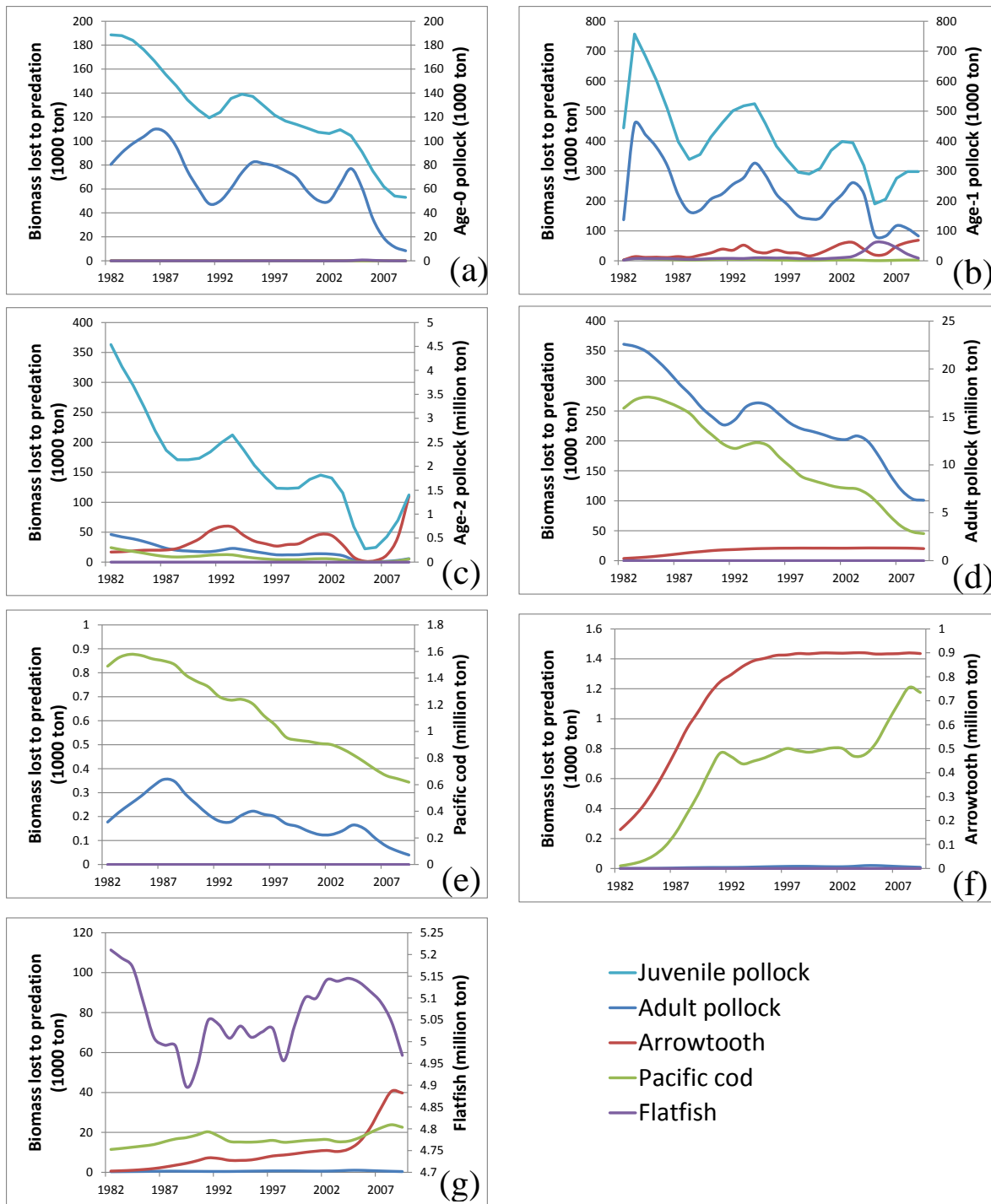
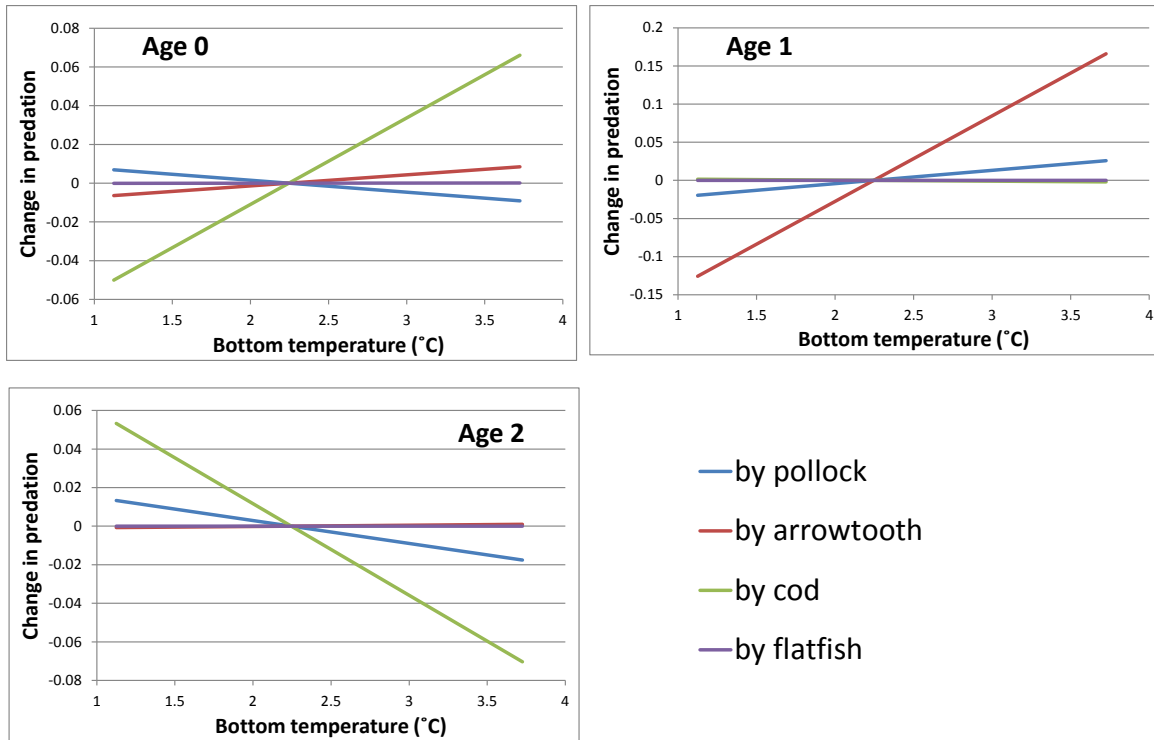


Figure 2. Predator-prey relationships among EBS fish species modeled in this study. Arrows represent the directions of predator to prey.



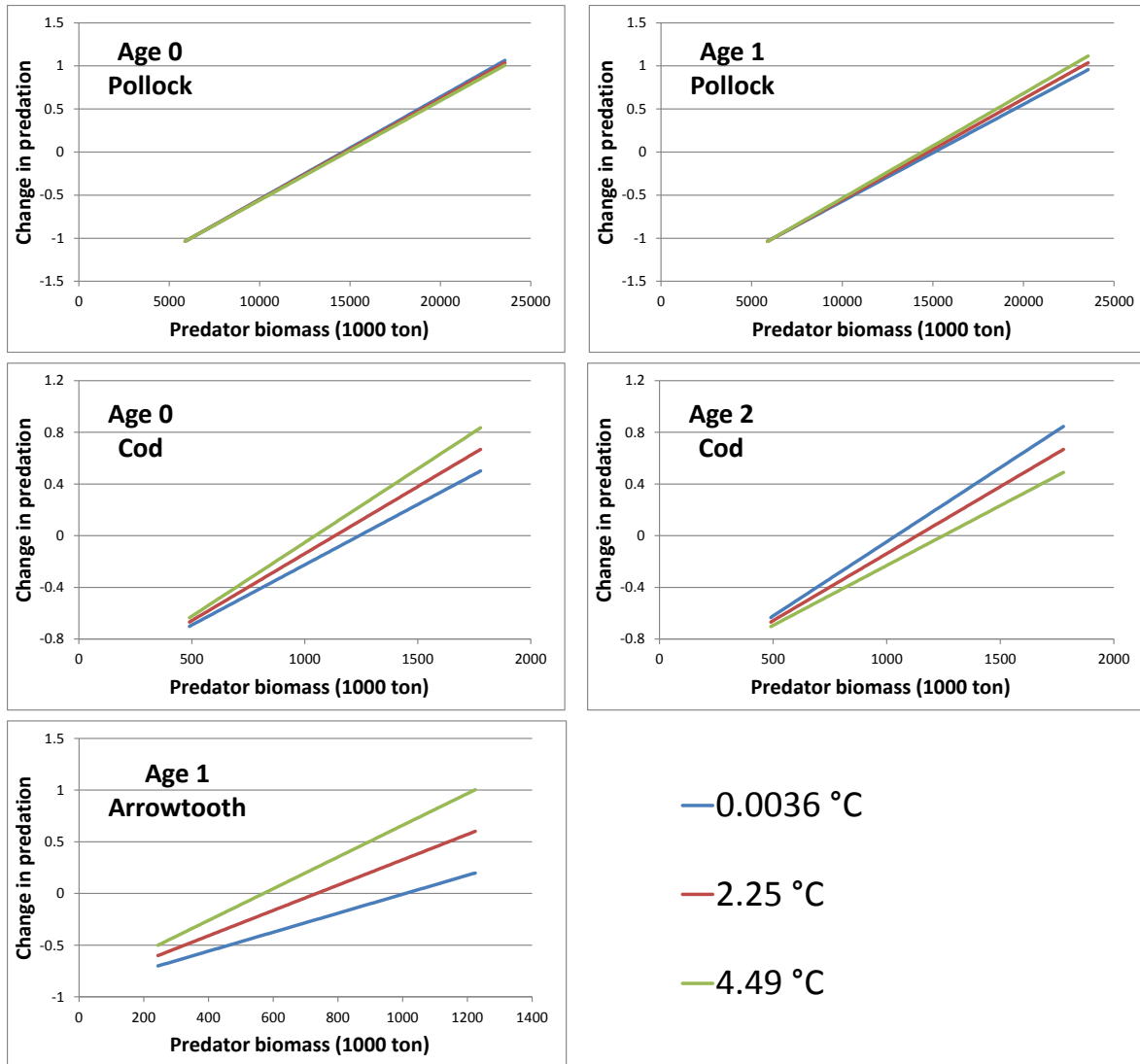
1413
 1414 Figure 3. Model-averaged predicted biomass and biomass lost to predation by predator for (a) age-0
 1415 pollock, (b) age-1 pollock, (c) age-2 pollock, (d) adult pollock, (e) Pacific cod, (f) arrowtooth flounder,
 1416 and (g) small-mouth flatfish.



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1419 Figure 4. Relative effects of bottom temperature on predation on juvenile pollock by their predators. The
1420 y axes show predicted biomass of juvenile pollock lost to predation for the range of observed temperature,
1421 expressed in proportion to the biomass lost to predation at the mean bottom temperature (2.25°C).

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Figure 5. Predicted changes in predation on juvenile pollock age classes by their predators over a range of predator biomasses at three different bottom temperatures. The y-axes show changes in juvenile pollock biomass lost to predation in proportion to the amount at the mean predator biomass. Prey biomasses were fixed at their respective mean values. Predator biomasses were varied from mean biomass – 2SD to mean biomass + 2SD. Each line represents predation amount at 0.004, 2.245, and 4.490 °C.

1431 **Conclusions**

1432 We successfully developed multispecies simulation models of pollock, cod, and flatfish in the eastern
1433 Bering Sea. Not only did these models allow us to reproduce observed changes in populations of pollock,
1434 cod, and flatfish in the eastern Bering Sea since the 1980s, but the models captured known predator-prey
1435 relationships as revealed by groundfish diet data. Both model formulations, the multispecies biomass
1436 dynamics (MBD) model and a multispecies delay difference (MDD) model, yielded good fits to the data.
1437 Also, both models predicted the multispecies B_0 , MSY , and F_{MSY} to be lower than the sum of the estimates
1438 from single-species assessment models, consistent with multispecies dynamics models developed for
1439 other ecosystems. Although the MDD model fit survey biomass estimates better than the MBD model, the
1440 MDD model and its maximum likelihood parameters produced biologically unrealistic biomass
1441 projections at values of $F > 0.14$. More realistically, under the MBD model, when high values of F was
1442 exerted on all species, the biomass of Pacific cod and arrowtooth flounder was depleted, which in turn
1443 reduced predation on juvenile pollock, resulting in a rapid increase in pollock biomass. Thus, we feel that
1444 we have satisfactorily achieved objectives 1 and 2. Nevertheless, results must be interpreted with caution,
1445 given strong positive correlations among many of the predation parameters that resulted in large relative
1446 errors.

1447 Using the MBD model, we tested a hypothesis that reduction in the extent of the cold pool intensifies
1448 predation on juvenile pollock. We found that warmer temperatures increase cannibalism and predation on
1449 age-1 pollock by adult pollock (age 3+) and arrowtooth flounder, respectively, and decreases cannibalism
1450 on age-0 pollock by adult pollock. The opposite effect of water temperature on age-0 and age-1 pollock
1451 likely reflects different distributions of these pollock age classes in relation to the cold pool. These results
1452 are consistent with the hypothesis that an extensive cold pool provides a refuge for age-1 pollock from
1453 these predators. Decreases in ice extent and enhanced summer temperatures have previously been shown
1454 to reduce the overwinter survival and subsequent recruitment of young-of-year pollock due to reduced
1455 prey availability (Hunt et al. 2011, Heintz et al. 2013). Our study suggests that recruitment may be further
1456 reduced in warm years because of increased predation mortality on age-1 pollock. Therefore, anticipated
1457 declines in the future recruitment and abundance of walleye pollock in a warming climate may be even
1458 more pronounced than predicted by Mueter et al. (2011). This enhanced understanding of the effects of
1459 temperature on pollock through predation achieves objective 3 of our study. Future studies should
1460 continue to explore ways that environmental conditions alter these relationships, and to evaluate their
1461 implications on fishery management and expected future fishery yields.

1462 **Management or Policy Implications**

1463 The groundfish species that we studied support valuable fisheries that are managed under a federal
1464 Fishery Management Plan under the auspices of the North Pacific Fishery Management Council. The
1465 Council’s policy for groundfish fisheries includes the adoption of ecosystem-based fishery management
1466 principles, including the incorporation of ecosystem considerations into its management decisions
1467 (NPFMC 2010). Thus, the Council recognizes that “potential changes in productivity may be caused by
1468 fluctuations in natural oceanographic conditions, fisheries, and other, non-fishing activities” and intends
1469 to “protect managed species from overfishing, and where appropriate and practicable, increase habitat
1470 protection and bycatch constraints.” Central to ecosystem-based fishery management is the need to
1471 account for ecological interactions among species. Multispecies models, informed by routinely collected
1472 assessment and ecological data, may provide a practical tool to bring multispecies considerations into the
1473 annual fishery management process.

1474 Although multispecies models, such as ours, are unlikely to replace single-species models for annual
1475 stock assessment and management over the near term, they can lead to improvements in single-species
1476 models. As one specific example, multispecies models typically demonstrate that the lack of separate
1477 accounting of predation mortality in single-species models often results in natural mortality estimates that
1478 are biased low. Such errors can lead to misspecification of harvest control rules used to manage the
1479 fishery. Thus, estimates of natural mortality, and hence harvest control rules, in single species models can
1480 be informed by improved mortality estimates estimated by multispecies models.

1481 In addition, multispecies models can be used to provide tactical management advice. For instance,
1482 multispecies models can be used to evaluate the implications of single-species harvest strategies on
1483 expected biomass of their predators and prey so that these ecosystem considerations can be taken into
1484 account during the annual harvest specification process. We explored the consequences of one particular
1485 harvest strategy, in which total sustainable yield of the multi-species system was maximized. However,
1486 simulations of other harvest strategies with different management objectives, such as maximizing
1487 economic values of catches or rebuilding depleted stocks, are also possible and worth exploring.

1488 Finally, because they incorporate these trophic interactions, multispecies models can be used to estimate
1489 the effects of environmental conditions (e.g., temperature) on predation rate, thus providing a tool to
1490 forecast responses of the groundfish community to future climate changes. Thus, another fruitful applied
1491 area of research would be to incorporate effects of climate change on trophic interactions and to study
1492 how these effects may affect management decisions on these important fishery resources.

1493 **Publications**

1494 Uchiyama, T., G.H. Kruse, and F.J. Mueter. 2014. Correlative biomass dynamics model. North Pacific
1495 Research Board Final Report B75, 79 p.

1496 Uchiyama, T., G.H. Kruse, and F.J. Mueter. In prep. A multi-species biomass dynamics model for
1497 investigating predator-prey interactions in the Bering Sea groundfish community. Prepared for
1498 submission to Deep Sea Research Part II: Topics Studies in Oceanography.

1499 Uchiyama, T., F.J. Mueter, and G.H. Kruse. In prep. Multispecies biomass dynamics models reveal
1500 effects of ocean temperatures on predation of juvenile pollock in the eastern Bering Sea. Prepared
1501 for the Canadian Journal of Fisheries and Aquatic Sciences.

1502 **Outreach**

1503 Exhibits/Displays/Demonstrations Developed

1504 None.

1505 Community Meetings

- 1506 • August 12/13, 2008: Franz Mueter provided testimony on the impacts of climate change on fish and
1507 fisheries to a panel convened by the Aspen Institute in Fairbanks. A copy of the presentation was
1508 provided to Nora Deans, NPRB.
- 1509 • In August 2011, Gordon Kruse testified in Dutch Harbor at a hearing on the Arctic by the Alaska
1510 State Legislature's Joint Alaska Northern Waters Task Force. He summarized fisheries research being
1511 conducted by UAF in the Bering, Chukchi and Beaufort Seas. The presentation included an overview
1512 of the BSIERP program in general, with more detail on those BSIERP projects involving UAF
1513 scientists, including the current project.
- 1514 • Gordon Kruse participated in the Alaska Young Fishermen's Summit, sponsored by the University of
1515 Alaska Marine Advisory Program, and held in Juneau, Alaska on February 13, 2012. Gordon spoke to
1516 51 young Alaskan fishers about the role of science in state and federal fisheries management of
1517 groundfish and other species groups.
- 1518 • On May 29, 2012, Mueter presented a public outreach seminar to the community of Nome as part of
1519 the " Strait Science Series" on "Limits to the northward movement of fishes in the eastern Bering
1520 Sea", Nome, AK.

1521 Presentations at Festivals/Events

1522 None.

1523 Workshop Presentations

- 1524 • August 2008: Several earlier workshops sponsored by PICES and NPRB resulted in PICES Scientific
1525 Report #34 “[Forecasting Climate Impacts on Future Production of Commercially Exploited Fish and](#)
1526 [Shellfish](#)”. Kruse prepared a section for the report on status of knowledge and proposed mechanisms
1527 linking climate change to the production of red king crab, Tanner crab and snow crab.
- 1528 • September 13-16, 2008: Mueter participated in the ESSAS (Ecosystem Studies of the Sub Arctic
1529 Seas) Annual Meeting in Halifax, Nova Scotia, including a workshop on climate variability in
1530 subarctic seas.
- 1531 • On June 18, 2009, Franz Mueter co-chaired (with Earl Dawe, DFO, St. Johns, Newfoundland) a
1532 workshop on gadid-crustacean interactions in subarctic ecosystems at the ESSAS Annual Meeting in
1533 Seattle. He presented an overview (with Siddeek Shareef and Jie Zheng) of gadid and crustacean
1534 fisheries and dynamics in the Gulf of Alaska and eastern Bering Sea.
- 1535 • On September 9, 2009, Gordon Kruse was invited to give an invited presentation on Climate Change
1536 and Marine Protected Areas: A Fisheries Perspective from Alaska to the Marine Protected Areas
1537 Federal Advisory Committee (FAC). Kruse also served on a panel of experts to field questions from
1538 the MPA FAC for two hours. This was reported on the evening news on KTUU (Anchorage) on
1539 September 9, 2009. Kruse reported on climate change effects on groundfish, crabs, herring, and other
1540 marine species and their implications to the design of marine protected areas.
- 1541 • November 16-18, 2009: Mueter gave an invited presentation by videoconference to the Alaska
1542 Community-Based Climate Change Adaptation Outreach Program Development Workshop on
1543 "Climate change impacts on fisheries".
- 1544 • Gordon Kruse participated as a member of a panel to address the question: What will our fisheries
1545 and oceans look like in 20 years? The panel was convened during the Alaska Young Fishermen’s
1546 Summit hosted by the Alaska Marine Advisory Program in Anchorage on December 8, 2009.
- 1547 • April 24, 2010. Mueter participated in a workshop on "Networking across global marine "hotspots",
1548 held in conjunction with the international symposium on "Climate change effects on fish and
1549 fisheries: Forecasting impacts, assessing ecosystem responses, and evaluating management
1550 strategies." in Sendai, Japan. As part of the workshop he gave an invited presentation on "Biological
1551 responses to recent climate variability on the eastern Bering Sea shelf".

- 1552 • May 10-14, 2010: Mueter participated in an International Stock Production Modeling Workshop at
1553 Woods Hole, MA, contributing biological and physical time series of variability in the Bering Sea and
1554 Gulf of Alaska for analysis at the workshop.
- 1555 • August 30 – September 1, 2010. Mueter and M.S. student Laurinda Marcello participated in the
1556 Ecosystem Studies of the Subarctic Seas (ESSAS) Annual Meeting in Reykjavik, Iceland, which
1557 featured a workshop on effects of climate variability in subarctic ecosystems and a workshop on
1558 gadid-crustacean interactions in subarctic seas. Mueter gave a invited presentation (co-authored with
1559 Mike Litzow) on linking climate and fish in the Northeast Pacific as part of the first workshop and
1560 Marcello presented results from her retrospective work on snow crab recruitment in the Eastern
1561 Bering Sea.
- 1562 • On April 7-8, 2011, Franz Mueter participated in a workshop on stock-specific indicators at the
1563 Alaska Fisheries Science Center in Seattle and gave a presentation on forecasting pollock recruitment
1564 and growth.
- 1565 • Mueter helped organize a half-day workshop and a scientific session on gadid-crustacean interactions
1566 at the ESSAS Open Science Meeting in May 2011. MS student Laurinda Marcello presented her work
1567 on snow crab (partially supported by BSIERP) at the meeting and submitted an associated
1568 manuscript.
- 1569 • On October 27-28, 2011, Franz Mueter participated via WebEx in a workshop on Management
1570 Strategy Evaluations held at the Alaska Fisheries Science Center in Seattle.
- 1571 • On February 6-9, 2012, Franz Mueter participated in a BEST Synthesis workshop in Bermuda.
- 1572 • On April 4-5, 2012, Franz Mueter participated in a workshop on Workshop on Assessment and
1573 Management Issues Related to Recruitment at the Alaska Fisheries Science Center in Seattle and gave
1574 a presentation on environmental forcing of recruitment in the Bering Sea and Gulf of Alaska and its
1575 use in stock assessments and stock projections.
- 1576 • In May 2012, Mueter participated in a full-day workshop on "Climate change and range shifts in the
1577 ocean" at the 2nd International Symposium on the effects of climate change on the World's Oceans in
1578 Yeosu, South Korea.
- 1579 • Mueter participated in a full-day workshop on interactions between the subarctic and Arctic at the
1580 PICES Annual Meeting in Hiroshima, Japan, in October 2012 and presented a paper on the spatial
1581 dynamics of fish stocks in the eastern Bering Sea.
- 1582 • On February 26-28, 2013, Franz Mueter participated in a BEST Synthesis workshop in Friday
1583 Harbor, WA.

1584 Presentations in Schools (K-12, Undergraduate)

1585 None.

1586 Press Articles (Newspaper/Journal/Newsletter)

- 1587 • May 2008: An article on climate change and Alaska’s fisheries, written by Kruse, appeared in the
1588 Periodical "Alaska Seas and Coasts", published by Alaska Sea Grant and the Marine Advisory
1589 Program of the University of Alaska Fairbanks.
- 1590 • July 13, 2008: Kruse was interviewed and quoted in a newspaper article in the Fairbanks Daily News
1591 Miner on the effects of climate change on marine ecosystems of Alaska.
- 1592 • October 2008: Mueter was interviewed about responses of fish populations in the Bering Sea to
1593 climate variability by Ken Weiss from the LA Times for an article on climate warming and marine
1594 fishes Los Angeles Times, October 19, 2008: "[Migrating Alaskan pollock are creating the potential
1595 for a new dispute with Russia](#)"
- 1596 • February 4, 2009. Dr. Kruse was interviewed by reporter Tom Kazzia for an article on the effects of
1597 climate change on Tanner crabs and other species in Alaska. The article “Crab comeback in
1598 Kachemak Bay” appeared in Anchorage Daily News on 2/21/2009. Kruse was quoted twice in the
1599 article.
- 1600 • November 23, 2009: Franz Mueter was interviewed by Lu Snyder for an article on the effects of
1601 climate change on fishes that was published in the December 2009 edition of FISHRAP, the
1602 newsletter of the Northern Southeast Regional Aquaculture Association (Vol. 27, no. 2, p. 1).
- 1603 • September 2, 2011: Mueter gave a phone interview on changes in arrowtooth flounder abundance to
1604 Craig Medred of the Alaska Dispatch.
- 1605 • On September 9, 2012, Gordon Kruse was interviewed on camera for two hours by Luke Griswold-
1606 Tergis for a future PBS documentary on fisheries management in Alaska. It is a story about the
1607 evolution of fisheries management and current issues in Alaska. Mr. Griswold-Tergis produced a
1608 recent movie, Smokin’ Fish (<http://smokinfishmovie.com/>), featuring Juneau’s Cory Mann, which
1609 brings to light the epic art of being and remaining an American Indian in the 20th Century. The film
1610 played on PBS and was screened at many events, including film festivals, libraries, and schools both
1611 nationally and internationally. A one-hour film is intended for the current film production with similar
1612 distribution.
- 1613 • In May 2011 Gordon Kruse was interviewed for a UAF Aurora Magazine article that was published
1614 in fall 2011. He was heavily quoted concerning the collapse of many of Alaska’s king crab stocks,

1615 their failure to recover, and broader ecosystem changes in the GOA and EBS (see
1616 <http://www.uaf.edu/aurora/>).

1617 Factsheets Produced

1618 Uchimaya, T., G.H. Kruse, and F.J. Mueter. 2014. Understanding Bering Sea groundfish populations:
1619 Using models to shed light on patterns and trends. BEST-BSIERP project headlines. BEST-BSIERP
1620 Bering Sea Project.

1621 Video or Film Produced

1622 None.

1623 Radio/Television Interviews

1624 • On August 13, 2009, both Kruse and Mueter were interviewed by Marc Kagan, video director and
1625 producer for NOAA, for a film on climate change and its effects on fish, crabs and other species in
1626 the marine ecosystems of Alaska. Gordon spoke about work related to this project, as well as other
1627 NPFB-funded research projects, such as Pacific herring. Franz spoke about changes in distribution of
1628 fish and shellfish in the eastern Bering Sea and other climate effects on the Bering Sea ecosystem,
1629 based in part on results from the retrospective analyses.

1630 • On March 27, 2010, Mueter was interviewed by Anne Hillman from KUCB, Dutch Harbor, on the
1631 effects of climate variability on walleye pollock. The interview aired on the local public radio station
1632 and is available [online](#).

1633 • On September 9, 2012, Gordon Kruse was interviewed on camera for two hours by Luke Griswold-
1634 Tergis for a future PBS documentary on fisheries management in Alaska. It is a story about the
1635 evolution of fisheries management and current issues in Alaska. The interview included discussion of
1636 some of the issues associated with the Bering Sea groundfish fishery and research resulting from the
1637 BSIERP project.

1638 • On January 24, 2013, Franz Mueter was interviewed by Jaqueline Estes (APRN) on the potential
1639 effects of climate change on fish communities in the Arctic and Subarctic. The story aired on APRN
1640 on the following days.

1641 • On January 24, 2013, Franz Mueter was also interviewed by Lauren Rosenthal from KUCB (Dutch
1642 Harbor), which led to an online article and a story on KUCB, largely focusing on the Arctic
1643 (<http://www.alaskapublic.org/2013/01/24/chukchi-trawl-survey-sheds-light-on-unexplored-waters/>).

1644 • Gordon Kruse was interviewed by Jay Barrett of KMXT in Kodiak for a radio report on the 29th
1645 Lowell Wakefield Fisheries Symposium on Fisheries Bycatch: Global Issues and Creative Solutions.
1646 The report aired on KMXT on 10/31/13 and an expanded version on 11/4/13. The report was also
1647 aired during the Alaska Fisheries Report on 11/7/13. Gordon is the chair of the Scientific Steering
1648 Committee for this international symposium to be held during May 13-16, 2014.

1649 Podcast and Blogs

1650 None.

1651 Web Page or Site Developed

1652 None.

1653 Conference Presentations (Chronological order)

1654 Mueter, F.J., K. Coyle. (Oral presentation) "From physics to humans: Climate effects on Bering Sea food
1655 webs and fisheries. PICES 27th Annual Meeting, Dalian, China, October 30, 2008.

1656 Mueter, F.J. (Invited Seminar). Climate effects on Bering Sea food webs and fisheries. Juneau Center,
1657 School of Fisheries and Ocean Sciences, University of Alaska Fairbanks. Juneau, Alaska, January
1658 23, 2009.

1659 Mueter, F.J. (Invited seminar). Environmental and Ecological Indicators for the Eastern Bering Sea.
1660 NOAA, NMFS, Ted Stevens Marine Research Institute. May 4, 2009.

1661 Mueter, F.J., Siddeek Shareef, Jie Zheng (Oral presentation). Gadid-crustacean interactions in the eastern
1662 Bering Sea and Gulf of Alaska. Ecosystem Studies of Subarctic Seas (ESSAS) Annual Meeting.
1663 June 18, 2009.

1664 Mueter, F.J. (Invited Seminar). Climate effects on Bering Sea food webs and fisheries. University of
1665 Alaska Fairbanks, Fairbanks, AK. September 30, 2009. A copy of the presentation was submitted
1666 with the semi-annual report on October 1, 2009.

1667 Mueter, F.J. and M.A. Litzow (Invited Presentation). The spatial footprint of biological re-organization in
1668 a demersal community. PICES 28th Annual Meeting Science Board Symposium, Cheju Island,
1669 Korea, October 26, 2009.

- 1670 Mueter, F.J., Gordon H. Kruse, Vernon Byrd, and Heather Renner (Poster). Covariation among major
 1671 fish, seabird, and mammal populations in the eastern Bering Sea. Alaska Marine Science
 1672 Symposium, January 20, 2010, Anchorage, AK.
- 1673 Mueter, F.J., Carol Ladd, Phyllis Stabeno, Ron Heintz, Ken Coyle, Gordon H. Kruse (Oral presentation).
 1674 Environmental controls of gadid year class strength in the eastern Bering Sea. Alaska Marine
 1675 Science Symposium, January 21, 2010, Anchorage, AK.
- 1676 Mueter, F.J. (Invited presentation). Climate variability on the eastern Bering Sea shelf: Effects on the
 1677 distribution and productivity of fish populations. Western Alaska Interdisciplinary Science
 1678 Conference (WAISC). 24 March 2010, Unalaska, AK.
- 1679 Mueter, F.J. (Invited presentation). Climate variability in the eastern Bering Sea. Western Alaska
 1680 Interdisciplinary Science Conference (WAISC). 24 March 2010, Unalaska, AK
- 1681 Mueter, F.J., Bond, N.A., and Ianelli, J.N. (Invited Presentation). Long-term forecasts of walleye pollock
 1682 dynamics in the eastern Bering Sea based on estimated responses of recruitment and growth to
 1683 climate variability. PICES 2010 Annual Meeting, Tuesday, October 26, 2010.
- 1684 Mueter, F.J. (Oral Presentation). Spatial dynamics of Bering Sea groundfish: Effects of temperature and
 1685 density. Alaska Chapter, American Fisheries Society, Annual Meeting. November 4, 2010.
- 1686 Kruse, G.H., and Mueter, F.J. (Invited keynote presentation). Climate change and the future of Alaska's
 1687 fisheries. Alaska Chapter, American Fisheries Society, Annual Meeting, Juneau, AK. November 3,
 1688 2010.
- 1689 Mueter, F.J. Effects of temperature and density on spatial dynamics of Bering Sea groundfishes. Alaska
 1690 Marine Science Symposium. January 20, 2011.
- 1691 Mueter, F.J. (Invited seminar) The Bering Sea ecosystem: From climate to plankton to fish. University of
 1692 Alaska Southeast. Biological Sciences seminar, Juneau, AK, April 13, 2011.
- 1693 Mueter, F.J. (Keynote) Groundfish in Hot Water: Challenges facing fish and fisheries in Alaska. Alaska
 1694 Department of Fish & Game. Statewide groundfish meeting in Anchorage, AK April 27, 2011.
- 1695 Mueter, F.J., Stepanenko, M.A., Smirnov, A.V., and Yamamura, O. (Invited). Comparing walleye pollock
 1696 dynamics across the Bering Sea and adjacent areas. International Symposium on "Comparative

- 1697 studies of climate effects on polar and sub-polar ocean ecosystems: progress in observation and
 1698 prediction” (ESSAS Open Science Meeting). Seattle, WA, May 23, 2011.
- 1699 Kruse, G.H. (Invited oral presentation). Overview of the BEST-BSIERP Program. Presented to Fishery
 1700 Science Committee, Annual Meeting of the North Pacific Marine Science Organization (PICES),
 1701 Khabarovsk, Russia. October 19, 2011.
- 1702 Mueter, F.J., Bohaboy, E.C., Bundy, A., Fu C., Hjermmann, D.O., Link, J.S. Common patterns, common
 1703 drivers: comparative analysis of aggregate surplus production across ecosystems. American
 1704 Fisheries Society 141st Annual Meeting, Seattle, WA, September 4-8, 2011.
- 1705 Uchiyama, T., Kruse, G.H., and Mueter, F.J. (Poster). Predator-prey interactions in the Eastern Bering
 1706 Sea Ecosystem: A Study Using Multispecies Biomass-dynamics Models. Alaska Marine Science
 1707 Symposium, Anchorage, AK. January 2012.
- 1708 Uchiyama, T., Kruse, G.H., and Mueter, F.J. (Poster). Warm Conditions in the Eastern Bering Sea
 1709 Increase Pollock Cannibalism: A Study Using Multispecies Biomass-dynamics Models.
 1710 BEST/BSIERP PI meeting, Anchorage, AK. March 2012.
- 1711 Mueter, F.J. Spatial dynamics of fish communities in subarctic and arctic seas under a changing climate.
 1712 PICES-ICES workshop on a "Global assessment of the implications of climate change on the spatial
 1713 distribution of fish and fisheries", St. Petersburg, Russia, May 22, 2013.
- 1714 Mueter, F.J., Litzow, M.A., Lauth, R.L., Danielson, S.L., and Spencer, P.D. Spatial dynamics of
 1715 groundfish: the roles of temperature, abundance and advection. Ecosystem Studies of the Subarctic
 1716 Seas (ESSAS) Annual Science Meeting, Hakodate, Japan, January 9, 2013.
- 1717 Mueter, F.J., Litzow, M.A., Lauth, R.L., Danielson, S.L., and Spencer, P.D. The roles of temperature,
 1718 abundance and advection in modifying the spatial dynamics of groundfish at the Subarctic-Arctic
 1719 boundary in the eastern Bering Sea. PICES 2012 Annual Meeting, Hiroshima, Japan, October 12,
 1720 2012.
- 1721 Mueter, F.J. (Keynote). Ecosystems, complexity, and sustainability from global to regional to local scales.
 1722 American Fisheries Society, Alaska Chapter, Annual Meeting. Kodiak, Alaska, October 24, 2012.

1723 Conference Participation

- 1724 • September 2008: Kruse participated in the Annual Science Conference of the International Council
1725 for the Exploration of the Sea (ICES).
- 1726 • October 2008: Kruse and Mueter participated in the Annual PICES meeting in Dalian. Kruse co-
1727 convened the Science Board Symposium on “Beyond observations to achieve understanding and
1728 forecasting in a changing North Pacific Ocean” and convened the Fisheries Contributed Paper
1729 Session.
- 1730 • Dr. Kruse chaired the Steering Committee for the 25th Lowell Wakefield Symposium on “Biology
1731 and Management of Exploited Crab Populations under Climate Change” held in Anchorage, AK,
1732 during March 10-13, 2009. The meeting was attended by approximately 80 participants from 6
1733 countries. Dr. Kruse was also lead editor for the symposium proceedings.
- 1734 • From March 24-27, 2010, Mueter participated in the Western Alaska Interdisciplinary Science
1735 Conference (WAISC) in Unalaska. In addition to giving two presentations related to the BSIERP
1736 project, he participated in discussions with the community on global warming and ocean acidification
1737 issues.
- 1738 • Mueter, with Laura Richards (DFO, Canada), John Field (NOAA, USA), and Sanae Chiba (Japan)
1739 organized a session at the 2010 PICES Annual Meeting in Portland, Oregon, entitled "Observations of
1740 ecosystem mixing under climate change" that featured an invited presentation by BEST/BSIERP PI
1741 Lorenzo Cianelli.
- 1742 • Kruse organized both a session and an international symposium that both highlighted BEST/BSIERP
1743 research at the 2010 PICES Annual Meeting in Portland, Oregon.
- 1744 • In November, 2010, Kruse chaired a scientific session titled, “Dynamics of Marine Ecosystems”, at
1745 the Annual Meeting of the Alaska Chapter, American Fisheries Society, in Juneau Alaska. This
1746 session included BSIERP-related talks, including a BEST/BSIERP overview talk by Mike Sigler.
- 1747 • In November 2010, Gordon Kruse organized and chaired the Steering Committee for the 26th Lowell
1748 Wakefield Symposium titled, “Ecosystems 2010: Global Progress on Ecosystem-based Fisheries
1749 Management.” The symposium attracted 108 participants from 19 countries. Talks included multiple
1750 BEST/BSIERP presentations, including those delivered by Mike Sigler, Ivonne Ortiz, Kerim Aydin
1751 and others.
- 1752 • In May 2011 both Mueter and Kruse participated in the ESSAS Open Science Meeting in Seattle,
1753 where Franz Mueter gave an invited BSIERP presentation on walleye pollock dynamics during the
1754 Bering Sea session and Gordon Kruse delivered a presentation on red king crab dynamics in the
1755 session on gadid-crustacean interactions.

- 1756 • Mueter attended the Annual Meeting of the American Fisheries Society in Seattle in September 2011
 1757 and presented in a session on increased variability in fish populations and in a session on surplus-
 1758 production models. Both drew on some retrospective data compiled as part of BSIERP.
- 1759 • Mueter participated in the 2nd International Symposium on the effects of climate change on the
 1760 World's Oceans in Yeosu, South Korea, participated in a workshop and co-authored three papers
 1761 partially supported by this project, presented by George Hunt, Paul Spencer, and Ting-Chun Kuo.
- 1762 • Both Mueter and Kruse participated in the PICES Annual Meeting in Hiroshima, Japan, in October
 1763 2012, participated in and helped organize workshops and scientific sessions, and co-authored several
 1764 papers presented at the meeting that were partially supported by this project.
- 1765 • Both Mueter and Kruse participated in the PICES Annual Meeting in Nanaimo, BC, in October 2013,
 1766 participating in workshops, committee meetings, and scientific sessions.

1767 Social Media (Facebook, Twitter, YouTube Channel, etc.)

1768 None.

1769 Teacher Workshops or Hosted Teacher-at-Sea

1770 None.

1771 Books

1772 None.

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