

1 Title: **Overcoming challenges of harvest quota allocation in spatially structured populations**

2 Running Title: Harvest allocations for spatially structured populations

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25

26 **ABSTRACT**

27 Ignoring spatial population structure in the development of fisheries management advice can affect
28 population resilience and yield. However, the resources required to develop spatial stock assessment
29 models that match the spatial scale of management are often unavailable. As a result, quota
30 recommendations from spatially aggregated assessment models are commonly divided among
31 management areas based on empirical methods. We developed a spatially explicit simulation model to
32 1) explore how variation in population structure influences the spatial distribution of harvest that
33 produces maximum system yield, and 2) contrast the performance of empirical quota allocation methods
34 in approximating ideal spatial harvest strategies. Spatial scenarios that included post-recruitment
35 movement resulted in a broader range of spatial management options (e.g., setting regional total
36 allowable catch) that achieved near maximum system yield compared to scenarios without movement.
37 Stochastic projections showed that using the proportion of total survey biomass in each management
38 area to spatially allocate quota performed best for maximizing system yield when the true spatial
39 structure was unknown, considerably outperforming equal allocation and allocation based on a
40 recruitment index. However, with all methods, area-specific harvest rates sometimes led to unintended
41 depletion within management units. Improved data and understanding of spatial stock dynamics can
42 reduce the need for ad hoc approaches for spatial harvest allocation, allow for a greater range of
43 management options, and increase the efficacy of spatial management procedures.

44 **Keywords:** Stock Assessment, Spatial Management, Connectivity, Population Structure, Catch
45 Allocation, Harvest Rate

46 **1. Introduction**

47 Fish populations often exhibit spatial variability in biological characteristics (e.g.,
48 growth, maturity, fecundity, natural mortality, and movement) that arise from interactions with
49 ecological and environmental processes, which influence population dynamics and create
50 challenges for the development of sustainable fisheries management strategies (Ricker 1958;
51 Jackson et al., 2010; Hanselman et al., 2015; Vincenzi et al., 2016; Kerr et al., 2017b). Yet,
52 fishery management procedures commonly ignore spatial variability by assuming average
53 population demographics (homogeneity) within or across management units. Management units
54 are often conveniently defined (e.g., political boundaries) rather than aligning with known
55 biological characteristics of the resource, which can create additional spatial heterogeneity
56 through regulatory measures (Riess et al. 2009; Cope and Punt, 2011; Kerr et al., 2014;
57 Hanselman et al., 2015). Recent advances in the understanding of spatial population structure
58 and movement patterns (e.g., see Berger et al., 2017c) indicate a need to address spatial
59 heterogeneity when providing management advice, such as defining biological reference points
60 and associated catch quotas (Thouzeau et al., 1991; Rätz and Lloret, 2003; Melville-Smith and
61 de Lestang, 2006; Jackson et al., 2010; Williams et al., 2012; Hanselman et al., 2015; Vincenzi et
62 al., 2016). Additionally, it may be necessary to define regional-scale management procedures
63 due to jurisdictional boundaries for shared stocks (e.g., regional management agencies, state, or
64 international), fleet dynamics (van der Lee et al., 2014), socioeconomic considerations (e.g., cost
65 of travel to fishing grounds; Thiault et al., 2017); resource distribution (Hanselman et al. 2016),
66 and/or the existence of biological structure (Kerr et al., 2017a).

67 Population components defined by spatially varying life history characteristics can have
68 differential responses to management actions, and not accounting for this variability may inhibit
69 the ability to meet desired management objectives. For example, because long-lived, slow-
70 growing fish generally have a lower reproductive output compared to short-lived, fast-growing
71 fish, they cannot sustain high harvest levels (Musick, 1999). Additionally, connectivity dynamics
72 can confound the efficacy of management actions depending on the timing of those actions and
73 the scale at which they are applied in relation to fish movement (McGilliard et al., 2015).
74 Harvest rate differences among management units can differentially impact the size and age
75 classes that move compared to those that remain resident within a single fishing mortality regime
76 (Guan et al., 2013; Lee et al., 2017). These challenges demonstrate the need to understand and
77 account for the interactions among movement dynamics and biological variability when
78 considering spatial management procedures, such as TAC specifications (Kerr et al., 2014;
79 Goethel et al., 2016; Goethel and Berger, 2017).

80 The increasing availability and quality of spatially resolved information regarding
81 population structure, connectivity, and demographics has led to the development of population
82 models which better represent the complex spatiotemporal nature of a fishery resource (Berger et
83 al., 2017b, Goethel and Berger, 2017; Kerr et al., 2017a; Punt et al., 2017; Thorson et al., 2017;
84 Truesdell et al., 2017). Various simulation studies have explored the impact of alternative spatial
85 population processes on the estimation of population parameters used for setting management
86 advice, including movement (Hulson et al., 2011; Goethel et al., 2015; Vincent et al., 2017),
87 mortality (Johnson et al., 2015), growth (Punt, 2003), and recruitment (Hulson et al., 2013;

88 Denson et al., 2017). These theoretical studies have elucidated the importance of understanding
89 spatial variability when identifying biological reference points (Ying et al., 2011; Goethel and
90 Berger, 2017) and also highlighted the management implications of ignoring or misidentifying
91 spatial population structure (Kerr et al., 2014; Goethel et al., 2016). For example, Goethel and
92 Berger (2017) demonstrated that spatially explicit harvest strategies that maximize system yield
93 were highly dependent on the combination of spatial population structure, connectivity patterns,
94 movement rates, and productivity. Misdiagnosing either movement patterns or population
95 structure led to depletion within management units and an overall loss of system-wide yield.
96 Similarly, ignoring fleet dynamics (e.g., effort aggregation) has been shown to be as detrimental
97 to the resource as ignoring resource distribution and connectivity dynamics (Fu and Fanning,
98 2004; Goethel and Berger, 2017).

99 Although spatial population structure has increasingly been acknowledged in fishery
100 stock assessment frameworks over the last two decades (Fournier et al., 1998; Cope and Punt,
101 2011; Taylor et al., 2011; Berger et al., 2012; Methot and Wentzel, 2013; Goethel et al., 2015; Li
102 et al., 2015; Punt et al., 2015; Vincent et al., 2017), relatively few spatially explicit stock
103 assessments have been implemented for setting harvest limits (Berger et al., 2017a; Punt, 2017).
104 Spatially explicit assessments require high quality, spatially informed data as well as rates and
105 patterns of connectivity (Fournier et al., 1998; Taylor et al., 2011; Goethel et al., 2011, Taillebios
106 et al., 2017), but these data are often limited or not available for many populations (Berger et al.,
107 2017b). Given the limited number of applied spatial assessment models, spatial management
108 procedures are often implemented without estimates of population parameters (e.g., spawning

109 stock biomass or fishing mortality) at the scale of desired management actions (Cope and Punt,
110 2011; Goethel et al., 2016; Kerr et al., 2017b). The resulting mismatch across the assessment-
111 management interface often leads to *ad hoc* approaches for spatially allocating catch quotas,
112 because catch projections are based on the broader management domain (e.g. assessment area)
113 which creates the need for a method to sufficiently allocate catch to the smaller management
114 units (Goethel et al., 2016; Berger et al., 2017b). Spatial catch allocation methods typically
115 ignore inherent variation in biological processes of the managed resource and often rely on
116 empirical approaches for dividing quotas across management units (e.g., allocations based on
117 regional survey abundance; Hanselman et al., 2016). Despite the wide application of quota
118 allocation methods, there has been limited exploration into whether these methods are able to
119 ensure sustainable harvests when a fishery resource exhibits spatial heterogeneity in demography
120 and complex population structure.

121 We used stochastic projection models to quantify how spatial heterogeneity and
122 connectivity among population components influenced management quantities (e.g. maximum
123 sustainable yield reference points) for marine fish. We also evaluated whether selected empirical
124 or *ad hoc* spatial quota allocation methods could approximate the distribution of catch that
125 achieved the maximum sustainable harvest when the true spatial dynamics were assumed to be
126 unknown. Specifically, the objectives were to, 1) compare optimal spatial harvest strategies
127 across alternative population spatial structures and demographic parameterizations, and 2) assess
128 the performance of several empirical quota allocation methods using common data sources for
129 allocating system-level quotas to smaller spatial management units. Collectively, the study

130 objectives aim to offer guidance on whether a particular method for spatial quota allocation
131 performs best when information on the underlying spatial dynamics is limited.

132

133 **2. Methods**

134 Research objectives were evaluated using stochastic projection models extended from
135 spatially explicit modeling framework presented by Goethel and Berger (2017). The study design
136 consisted of two distinct modeling components, one for each of our two primary objectives.
137 Simulation models were developed loosely based Pacific hake and Alaskan sablefish, which
138 represent different species with distinct life history characteristics. A ‘hake-like’ model was
139 developed to mimic a mid-water semi-pelagic species of intermediate longevity and a ‘sablefish-
140 like’ model was designed to mimic a longer-lived groundfish species. These two species
141 (hereafter referred to as ‘hake’ and ‘sablefish’) provide a basis for examining two-area (hake)
142 and three-area (sablefish) models with spatial differences in natural mortality, recruitment,
143 growth, maturity, and movement based on either empirical data or hypothesized processes. An
144 important distinction between the two example species was how the stock recruitment-
145 relationships were parameterized. The model assumptions mimicked those applied the most
146 recent stock assessment such that the hake example assumed a Beverton-Holt stock-recruitment
147 relationship (steepness value = 0.814), and sablefish assumed no density dependence in the stock
148 recruit relationship (constant recruitment with annual deviations). In the sablefish example,

149 recruitment is de-coupled from the spawning stock biomass, removing any effect of area-specific
150 differences in maturity or fecundity.

151 Connectivity for the hake model applied a largely unidirectional ontogenetic movement
152 pattern, while the sablefish model applied a multi-directional movement pattern. Both simulation
153 models were conditioned with input parameters available from recent stock assessments. If input
154 parameters were not directly available, hypothesized values were used based on ongoing
155 research. The results from these models should be interpreted relative to each other in order to
156 gain comparative insight and not to inform management actions. A detailed description of model
157 inputs is provided in Appendix A.

158 Throughout this paper, definitions pertaining to spatial structure and movement follow
159 those defined in Goethel and Berger (2017). The ‘biological domain’ of a system was defined as
160 the entire spatial extent of the biological resource (Fig. 1). Spatial structure of the resource was
161 specified within the biological domain, which may consist of multiple biological populations
162 and/or areas. A ‘population’ represented a single reproductive unit within which all fish are able
163 to reproductively mix and recruitment dynamics were modeled using a single stock-recruit
164 function. A population may reside in a single homogeneous area or be distributed across multiple
165 areas with variable life history traits or fishery processes among the different areas. An ‘area’
166 represented the geographic extent over which a biological or fishery process is homogeneous.
167 Movement could occur among areas (assuming a Markovian process) and once a fish moved it
168 assumed the life history and reproductive dynamics of that area or population. Following these
169 definitions, we modeled three alternative types of spatial structure: panmictic, spatial

170 heterogeneity, and metapopulation. The panmictic structure was modeled as a single population
171 occupying a single area where all fish were assumed to be homogeneously distributed across
172 space (Fig 1a). Spatial heterogeneity was modeled assuming a single population that resided
173 across two or more areas (Fig. 1b). A metapopulation consisted of multiple, demographically
174 distinct populations connected through movement. Each population within a metapopulation
175 occurred in a single area and maintained a unique stock-recruit function, while reproductive
176 mixing was assumed to occur only with fish of the current resident population (Fig. 1c). Once
177 fish moved into a new population, they adopted the reproductive traits for that population. For
178 simplicity, we assumed that the spatial extent of the management units aligned with the spatial
179 extent of the biological units (populations or areas) defined in the biological domain.

180 The terms ‘apportionment’ and ‘allocation’ are often used interchangeably, however, in
181 this study we apply each term to describe a separate process in our modeling framework.
182 ‘Apportionment’ is defined as the partitioning of population-level recruitment across areas
183 (specifically when spatial heterogeneity is modeled) and ‘allocation’ refers to the process of
184 partitioning system-wide quota among individual management units.

185

186 *2.1. Influence of spatial heterogeneity on spatial harvest strategies*

187 To determine how differing population spatial structures and demographic
188 parameterizations influence the spatial distribution of harvest that maximized equilibrium system
189 yield (i.e., spatial harvest strategy, analogous to system-wide maximum sustainable yield, MSY),
190 we conducted a suite of simulations across a range of underlying assumptions regarding spatial

191 structure and connectivity. Scenarios were developed that explored plausible demographic
192 configurations and were parameterized for both example species using stock assessment outputs
193 and/or the current best understanding of each species' biology (see Appendix A). Model
194 outcomes were compared relative to a reference scenario parameterized as a single population
195 with spatial heterogeneity (*Spatial*; Table 1) which represented the most likely population
196 structure and demography for the example species. Model comparisons focused on four primary
197 aspects; 1) specification of population structure, 2) spatial biological or fishery heterogeneity, 3)
198 spatial recruitment dynamics, and 4) connectivity patterns (Table 1). Metrics used to compare
199 model scenarios included the area- and population-specific equilibrium values for yield, harvest
200 rate (u : yield/biomass), and depletion (terminal spawning biomass/unfished equilibrium
201 spawning biomass for each spatial unit). The area-specific yield that collectively achieved the
202 overall maximum system yield ('spatial harvest strategy') was the primary metric for model
203 comparisons.

204 Maximum system yield was found using a grid search across combinations of area-
205 specific fishing mortality rates ranging from 0 to 7.0 in increments of 0.025 and 0.050 (Goethel
206 and Berger, 2017) for hake and sablefish, respectively. All simulated population trajectories
207 began at unfished equilibrium abundance levels and the population dynamics for each scenario
208 were simulated for 200 years, which was sufficient to reach equilibrium. Simulations were
209 conducted using AD Model Builder (Fournier et al., 2012) and R (R core team 2016) statistical
210 computing software programs. Models can be found at
211 (https://github.com/KatelynBosley/SPASAM/tree/master/Spatial_BRP_project).

212

213 *2.1.1 Spatial MSY Scenarios*214 *Population Structure*

215 Three population structures were compared to determine the impact of varying
216 population structure on spatial harvest strategies (Table 1). Model types included spatial
217 heterogeneity (*Spatial*), metapopulation (*Metapop*), and the panmictic (*Panmictic*) structures.
218 The panmictic structure consisted of only one population with one area, therefore area-specific
219 input parameters from the *Spatial* scenario were aggregated for the *Panmictic* scenario. For the
220 *Metapop* scenario, each population maintained an identical steepness value, but area-specific
221 virgin recruitment (R_0) was scaled to provide population-specific recruitment matching area-
222 specific recruitment specified in the *Spatial* scenario. No additional changes to the
223 metapopulation models were made relative to the *Spatial* scenario.

224

225 *Biological and Fishery Heterogeneity*

226 Alternative selectivity (*Alt_Selectivity*) and maturity (*Alt_Maturity*) scenarios were
227 developed to examine how different parameterizations influenced spatial harvest strategies. The
228 *Alt_Selectivity* scenario assumed constant selectivity for sablefish (verses spatially-varying
229 selectivity in the *Spatial* scenario) and spatially varying selectivity for hake (verses constant
230 selectivity in the hake *Spatial* scenario). These scenarios allowed comparison of both spatially
231 varying and constant selectivity assumptions across the two life-history types (see Fig. S1 and S2
232 for the alternate selectivity ogives). An *Alt_Maturity* scenario was developed for hake that

233 assumed constant maturity across areas as opposed to spatially varying maturity specified in the
234 *Spatial* scenario (see Fig. S3 for alternate maturity ogives). The comparison of these two
235 maturity scenarios for hake allowed exploration of how the population dynamics were influenced
236 by spatial patterns in maturity.

237

238 *Recruitment Dynamics*

239 Alternative recruitment scenarios were explored by specifying different recruitment
240 apportionment values (*Alt_Apport*) to simulate a change to the distribution of recruits across
241 space. The alternate apportionment values for the hake model provided a less skewed division of
242 recruits among the two areas relative to the *Spatial* model (Table S1). For the sablefish model,
243 alternate apportionment values were obtained by reversing values for Areas 1 and 3 (Table S1).

244

245 *Movement*

246 Examination of alternative movement parameterizations included scenarios that induced
247 a higher residency rate relative to that of the *Spatial* model (*Hi_Residency*; Tables S3 and S4)
248 and another that did not include movement among areas (*Spatial_NM*). Additionally, scenarios
249 were specified without movement for the alternate selectivity (*Alt_Selectivity_NM*) and alternate
250 maturity models (*Alt_Maturity_NM*) to explore the interaction of spatially varying demographics
251 when connectivity did not exist among areas.

252

253 **2.2. Spatial allocation of quota using empirical methods**

254 For our second modeling component, we compared several methods for spatially
 255 allocating system-level catch to smaller management units. The purpose of these explorations
 256 was to mimic approaches to spatial quota allocation where spatially explicit assessment models
 257 are untenable, but spatial quota management may be needed to account for observed spatial
 258 structure in the population or socioeconomic factors that necessitate sub-dividing harvest across
 259 the species range. Performance of each allocation method was based on how well the method
 260 could approximate the expected spatial distribution of catch and biomass (based on the spatial
 261 harvest strategy identified for a given population structure as described in Section 2.1).

262 For all total allowable catch (TAC) allocation scenarios, the population dynamics were
 263 simulated for 200 years in order to reach equilibrium conditions and area-specific catch levels
 264 were determined by the allocation of a system-wide (S) catch. The system quota for an assumed
 265 population structure was calculated by multiplying the system-level harvest rate (aggregated
 266 catch divided by aggregated biomass across all areas) that maximized system yield (u_{S,max_Y} ;
 267 based on the value from the associated run in Section 2.1.1) by the system-level biomass (B_S) in
 268 the current year of the simulation. This approach assured that quotas did not exceed system-wide
 269 biomass, which would cause overall population extinction. An area-specific TAC was then
 270 calculated based on the system yield and a management unit (i) allocation factor ($Alloc_Bi$) given
 271 by:

$$272 \quad , \quad 273 \quad = u_{S,max_Y} * B_S * lloc_B , \quad (1)$$

274 The allocation factor could either be determined from observed data (e.g., the ratio of
 275 area-specific biomass to total population biomass) or input as a fixed proportion (e.g., equal
 276 allocation among areas). The allocation fraction was calculated as the relative ratio of the
 277 observed index (Obs_I) for the given management unit to the observed index for the entire
 278 system.

279

$$280 \quad lloc_B = Obs_I / Obs_{I_S} \quad (2)$$

281

282 The three different catch allocation methods were evaluated based on their ability to
 283 replicate optimal TAC allocations (using Eq. 1). All allocation methods were evaluated by
 284 applying system-level yield from the *Spatial* and *Spatial_NM* scenarios (determined in Section
 285 2.1) for both example species. The resulting area-specific yield and biomass from the TAC
 286 allocation scenarios were then compared to the values associated with the spatial harvest
 287 strategies derived in Section 2.1. The single population with spatial heterogeneity model
 288 configuration was applied because it represents the most common population structure modeled
 289 for marine fishes. The three TAC allocation methods we applied were 1) the use of an observed
 290 survey biomass index ($Alloc_Survey$ and $Alloc_Survey_NM$), 2) an observed recruitment index
 291 ($Alloc_Rec_Index$, $Alloc_Rec_Index_NM$) and, 3) equal allocation ($Alloc_Equal$,
 292 $Alloc_Equal_NM$). The survey biomass index was calculated as the area-specific biomass scaled
 293 by the input catchability parameter (q) with measurement error ($CV = 0.2$) assuming a lognormal
 294 error structure. The biomass index was simulated to occur mid-year such that the TAC allocation

295 factor ($lloc_B$) applied each year was based on the abundance index from the previous year
296 ($y-1$; i.e. a one year lag for the implementation of the spatial harvest allocation). The observed
297 recruitment index was determined as the number of area-specific recruits with applied lognormal
298 measurement error ($CV = 0.5$).

299 To demonstrate the impact of incorrect specification of population structure, TAC
300 allocation based on the survey biomass index was applied using system-level harvest values
301 (u_{S,max_Y}) from the panmictic model (*Alloc_Survey_Panmictic*) and the metapopulation model
302 (*Alloc_Survey_Metapop*) when the true dynamics were simulated as a single population with
303 spatial heterogeneity. A final comparative scenario applied TAC allocation based on survey
304 biomass when the true population structure was a metapopulation, but the population structure
305 was misdiagnosed as a single population with spatial heterogeneity (i.e., using the incorrectly
306 specified system-level harvest rates from the *Spatial* models described in Section 2.1;
307 *Sim_Survey_Metapop*).

308 For each scenario, the Newton-Raphson method was used to iteratively tune the model
309 until the spatially explicit fishing mortality rates for each year (y) corresponded to the area-
310 specific TAC values within a 0.1% error threshold (see Goethel and Berger, 2017). Scenarios
311 were comprised of 100 independent model runs to encapsulate random variation in indices. The
312 performance of each allocation method was then assessed by comparing the relative percent
313 difference (RPD) in area-specific management quantities (i.e., harvest rate and depletion)
314 between models that applied the TAC allocation methods (i.e. observed) and the comparable
315 scenario that maximized system yield from objective 1 (i.e. true). The TAC allocation methods

316 were evaluated based on whether the observed data sources could be used to approximate the
317 spatial harvest strategies derived from objective 1.

318

319 **3. RESULTS**

320 *3.1 Impact of spatial heterogeneity on spatial harvest strategies*

321 Differences in population dynamics, demographics, selectivity, and movement led to
322 vastly different approaches to system harvest for both species. The *Spatial* model for the hake
323 example, which assumed a unidirectional ontogenetic movement pattern, suggested that Area 1
324 (nursery) should not be fished and Area 2 should have high fishing pressure (Fig. 2). The
325 sablefish *Spatial* model allowed greater mixing among areas and results indicated that a spatially
326 balanced harvest strategy was optimal. In general, system-wide harvest rates and depletion levels
327 associated with maximum system yield were similar across scenarios, but the area-specific
328 harvest rates required to achieve them differed substantially due to the underlying heterogeneity
329 in spatial processes (Fig. 2).

330

331 *Population Structure*

332 System-wide harvest rate and depletion for the hake single-area *Panmictic* model were
333 not substantially different from the *Spatial* model (Table 3, Fig. 2). The spatial harvest rates from
334 the *Metapop* model were elevated relative to those for the *Spatial* model (Table 3), which
335 resulted in lower area-specific and system-wide depletion values (i.e. fewer fish). Specification
336 of population-specific stock-recruit relationships was a major factor influencing the difference

337 between the *Spatial* and *Metapop* scenarios. For the hake example, maturity ogives differed
338 between the populations with the age at 50% maturity lower for one population relative to the
339 other (Fig S3). This difference led to a 14% reduction in terminal system-level spawning stock
340 biomass for the *Metapop* scenario relative to the *Spatial* scenario. The sablefish example
341 produced results similar to hake when comparing the *Panmictic* scenario to the *Spatial*, but it
342 was not sensitive to the metapopulation assumption (*Metapop* model outputs were almost
343 identical to the *Spatial* model).

344

345 *Biological and Fishery Heterogeneity*

346 Changing maturity from spatially varying (*Spatial*) to constant across areas
347 (*Alt_Maturity*) for the hake reduced both system-wide and area-specific harvest rates and
348 depletion levels (Fig. 2). This resulted from an 8.2% reduction in system-wide spawning biomass
349 when using the Area 2 maturity ogive (Fig. S3) in both areas, which produced fewer mature,
350 younger fish.

351 Assuming constant selectivity across areas in the sablefish model (*Alt_Selectivity*)
352 resulted in a sharp change in the spatial harvest strategy that maximized yield with essentially no
353 fishing in Area 2 and an increase in harvest rate for Area 1 (Area 1 $u_{,max,Y}$ was 0.10 and 0.23
354 for the *Spatial* and *Alt_Selectivity* scenarios, respectively; Fig. 2c). Despite no fishing in Area 2,
355 depletion levels remained consistent across all areas (~0.25). Similarly, adding spatial
356 heterogeneity in selectivity for hake resulted in a marked shift in the spatial harvest strategy

357 relative to the *Spatial* scenario. Shifting selectivity in Area 2 so that fish are selected at older
358 ages, produced a spatial harvest strategy with significantly lower area-specific and system-level
359 depletion levels (Fig. 2).

360

361 *Recruitment Dynamics*

362 The *Alt_Apport* scenario for the hake example showed little influence on system-wide
363 and area-specific depletion (Fig 2). Altering recruitment apportionment caused a slight reduction
364 in the system-level harvest rate (u_{S,max_Y} was 0.2 and 0.25 in the *Alt_apport* and *Spatial*
365 scenarios, respectively; Fig. 2) and the harvest rate in area 2 was reduced by 9% relative to the
366 *Spatial* model. Altering recruitment apportionment for sablefish produced a more spatially
367 balanced harvest strategy resulting in depletion levels that were relatively uniform across the
368 three areas (~ 0.25 ; Fig. 2).

369

370 *Movement*

371 Simulations of both example species showed area-specific harvest rates and depletion
372 levels were approximately uniform when movement did not occur among areas (*Spatial_NM*;
373 Table 3, Fig. 2). Modeling movement in the *Spatial* scenarios led to harvest rates that varied
374 widely by area causing spatial variation in depletion levels (Table 3, Fig. 2). In the hake
375 example, unequal recruitment apportionment combined with a strong unidirectional, ontogenetic
376 movement pattern created a situation where fish recruited to Area 1 and then migrated to Area 2
377 as they matured. For sablefish, recruitment apportionment and movement in the *Spatial* scenario

378 were more similar across areas resulting in a more spatially uniform harvest strategy relative to
379 the hake example (Table 3). As expected, the high residency (*Hi_Residency*) models for both
380 example species resulted in less spatial variation of in harvest levels compared to the *Spatial*
381 scenario, with outcomes similar to scenarios not including movement (Fig. 2). Despite less
382 spatial variation in harvest rates, depletion levels were similar to those from the *Spatial* scenario
383 indicating the importance of other sources of heterogeneity (i.e. maturity and selectivity) in
384 deriving spatial harvest strategies.

385 Comparison of yield vs. harvest rate isopleths for the *Spatial* and *Spatial_NM* scenarios
386 showed conspicuous differences in the shape of the yield surface (Fig. 3). Modeling movement
387 among areas resulted in a broader, plateau-like surface indicating many combinations of spatial
388 harvest can produce in yields close to the maximum. Yield isopleths from scenarios that did not
389 model movement showed fewer combinations that achieved near maximum yield (Fig. 3). For
390 example, the *Spatial_NM* scenario for hake produced a steep surface (with small areal peak)
391 indicating that the harvest rate in Area 1 would need to remain near 0.3 and greater than 0.15 in
392 Area 2 achieve near maximum yield (Fig. 3a). The addition of movement resulted in a diagonal
393 plateau of harvest rate combinations across the two areas (Fig. 3b), where 68.5% of the harvest
394 rate combinations produced $\leq 90\%$ of the maximum yield compared to 46.9% without
395 movement. Similarly, the sablefish example produced an essentially flat-topped yield surface
396 over which the maximum system yield was realized through a broad range of area-specific
397 harvest combinations across the three areas when movement was modeled (Fig. 3d). This result

398 differed from the well-defined peak and a smaller range of harvest rates (around 0.2 for all areas;
399 Fig 3c) that achieved near maximum yield without movement.

400

401 ***3.2. Allocation of harvest quota to spatial management units***

402 Spatial allocation of quota based on empirical methods performed well, often resulting in
403 area-specific depletion levels that were within 25% of the ideal level. Overall, results across
404 allocation methods were similar between example species, which allowed generalizations to be
405 made across the two life-history types we examined.

406 None of the methods we tested for allocating catches were able to exactly reproduce the
407 spatial harvest strategy that maximized system-level yield, but most approaches were able to
408 approximate harvest rates within a 50% difference from expected without causing high levels of
409 area-specific depletion (Fig. 4; Tables S4-S7). Spatially allocating TACs based on relative
410 survey biomass (*Alloc_Survey*, *Alloc_Survey_NM*) performed the best, particularly when no
411 movement occurred among areas (median RPD <60% in all areas, Fig. 4). When the underlying
412 population dynamics included movement, the equal apportionment method (*Alloc_Equal*)
413 performed as well as using the survey biomass (median RPD <112% in all areas, Fig. 4).
414 However, applying an equal harvest allocation to the parameterizations without movement
415 (*Alloc_Equal_NM*) led to substantial differences in harvest rates and caused area-specific
416 depletion. Interestingly, the simulated dynamics when movement did not occur caused some
417 area-specific quotas to be greater than the available biomass (Table 4), ultimately driving one
418 management area (hake; Area 2) or two management areas (sablefish; Areas 2 and 3) to collapse.

419 The lack of available biomass resulted in overall underutilization of the resource with only 91%
420 and 82% of the expected system-wide TAC harvested for hake and sablefish, respectively.
421 Allocating the TAC using a recruitment index (*Alloc_Rec_Index*, *Alloc_Rec_Index_NM*)
422 performed poorly for both example species and exhibited the largest range of area-specific
423 differences for both harvest rate and depletion (Tables S4-S7, Fig. 4).

424 For both example species, applying the harvest rate for a panmictic population when
425 simulating spatial heterogeneity (*Alloc_Survey_Pan*) resulted in a slightly more conservative
426 management approach and lower depletion levels (as indicated by the positive RPD in Fig. 4).
427 The hake example was more sensitive to incorrectly assuming metapopulation structure
428 (*Alloc_Survey_Met*), which caused more fish to be removed from the system and resulted in
429 higher system-level depletion (Fig. 4). When applying population-level harvest rates to a model
430 that simulated metapopulation dynamics (*Sim_Survey_Metapop*), slight loss of yield caused
431 stock status to increase (population became less depleted). Because the sablefish example did not
432 assume a stock-recruit relationship, outcomes from the metapopulation scenarios were identical
433 to the models that assumed a single population with spatial heterogeneity (*Spatial*).

434

435 **4. Discussion**

436 The development and application of spatially explicit assessment models has been driven
437 by the need to provide management advice at finer spatial scales. Unfortunately, the data are
438 often not available or lack sufficient resolution to apply these spatially explicit modeling
439 approaches when providing management advice. We employed a suite of stochastic projection

440 models to demonstrate the importance of accounting for connectivity and spatial heterogeneity
441 when deriving spatial harvest strategies that achieve maximum sustainable resource utilization.
442 This work builds on the findings of Goethel and Berger (2017) by incorporating spatial variation
443 in fishery selectivity and demographics using example species that exhibit different life history
444 types. We also evaluated the consequences of applying empirical methods for spatial quota
445 allocation over a range of assumptions regarding the spatial complexity of a biological resource.

446 Previous simulation studies have shown that subtle differences in the shape of the
447 selection curve can have large impacts on maximum sustainable yield for panmictic populations
448 (Scott and Sampson, 2011; Goethel and Berger, 2017). Thus, it was not surprising that spatial
449 heterogeneity in selectivity or life-history parameters influenced spatial harvest strategies.
450 Results from *Alt_Selectivity* scenarios for both example species demonstrated that relatively
451 small changes in selectivity can have a large impact on management quantities, especially when
452 movement occurs. We also found that interactions between maturity rate and selectivity pattern
453 can have a strong influence on the population dynamics, resulting in spatial harvest strategies
454 that are not intuitive. Connectivity among management units can further complicate the
455 determination of harvest strategies derived from yield-based management metrics. Model
456 projections applied over the two life history types provided an example of these challenges,
457 showing that the combination of area-specific harvest rates that achieved maximum equilibrium
458 system yield were largely influenced by movement and less by the underlying form of spatial
459 population structure (e.g., panmictic, spatial heterogeneity, or metapopulation). Collectively,
460 these results indicate that specifying the correct form of spatial population structure may not be

461 as critical as understanding movement patterns and spatial heterogeneity in the fishery (e.g.,
462 selectivity curves) and other demographic parameters (e.g., maturity) when developing spatial
463 reference points for management advice.

464 A unique and important finding of our study showed that connectivity among
465 management units results in numerous spatial harvest rate combinations that nearly achieve
466 maximum system yield with similar levels of overall depletion. Unlike the scenarios without
467 movement, yield isopleths showing spatial harvest combinations for models that incorporated
468 connectivity generally had a moderate slope with a broad plateau instead of a single well-defined
469 peak characteristic of maximum equilibrium system yield curves. The movement of fish across
470 areas leads to the effective dispersal of fishing effort over the model domain, which causes
471 correlation among area-specific harvest strategies (Guan et al., 2013; Kerr et al., 2014; Goethel
472 and Berger, 2017). The plateau-like yield surfaces from our simulations showed a range of
473 harvest strategies with similar overall management outcomes, elucidating the potential for
474 greater flexibility in the distribution of fishing effort across space when developing management
475 plans. When movement exists among populations or areas, it may be possible to define a range
476 of area-specific harvest rates that are able to achieve the same overall goals (i.e., maintaining a
477 system-level target population size, MSY). In some cases, it may be more important to weigh
478 socioeconomic considerations (e.g., regional equality in TAC allocations, annual stability in the
479 allowable biological catch, costs of travel to the fishing grounds) in the evaluation of alternative
480 spatial management decisions. Our results suggest that the interaction between ontogenetic
481 movement patterns, recruitment dynamics, spatial variation in demographics, and fishery

482 selectivity can lead to spatial harvest strategies that may not meet management objectives,
483 particularly when applying strict MSY-based, area-specific harvest limits. This is demonstrated
484 by scenarios from the hake example that recommend exploitation predominantly in one area.
485 When connectivity dynamics are assumed, the application of spatial models can facilitate the
486 development of optimal management strategies by incorporating both ecological and economic
487 considerations.

488 Spatial harvest strategies produced by the hake example illustrated some of the
489 challenges associated with attempting to allocate system-level TACs to smaller spatial
490 management units. It is a common approach to use a relative index of abundance for defining
491 catch allocations across management units. However, when a population displays ontogenetic
492 movement patterns that interact with maturity and fishery selectivity, some portion of the
493 biomass will remain in areas that, from a maximum system yield perspective, should not be
494 harvested. This implies that allocation methods ignoring age structure may not be appropriate for
495 populations with complex age-based movement patterns and it may be necessary to explicitly
496 account for age-specific abundance when evaluating management goals. Similarly, the allocation
497 scenarios showed that Area 1 in the sablefish example was consistently overharvested due to the
498 low harvest rate required to maximize system yield. Despite the tendency to overharvest certain
499 areas regardless of the allocation method, system-level depletion was not strongly biased. This
500 result suggests that system-wide spawning stock biomass and population trajectories may not be
501 significantly impacted unless the overfished area contains a large portion of the total mature
502 biomass.

503 Evaluation of catch allocation methods showed that incorrect specification of area-
504 specific catch limits did not result in significant depletion regardless of underlying population
505 structure. Given this general result, the survey index allocation method is likely to perform
506 sufficiently for developing management advice when it is impossible to directly account for
507 spatial population structure in stock assessments, a conclusion that is also supported by Hintzen
508 et al. (2015). If high quality and reliable surveys are not available or residency rates are known to
509 be low, then the equal or 'fixed' allocation method may be preferable. In general, the equal
510 allocation method performed nearly as well as the survey index allocation method and provides
511 an appealing alternative because it requires a lower investment in resources. However, the equal
512 allocation method can be more risk-prone in terms of local depletion when connectivity among
513 areas (or populations) is limited. Application of equal allocation to scenarios without
514 connectivity led to overfishing in at least one area for both example species. As a result, area-
515 specific TACs derived from equal allocation methods may be too high when a population
516 exhibits spatial heterogeneity, potentially causing an overall loss of yield and/or unbalanced
517 harvest of population components thereby inhibiting management goals and reducing population
518 resiliency (Kell et al., 2009). Overall, our results illustrate some of the challenges that can arise
519 from the implementation of a constant catch or fixed-ratio strategy if the spatial dynamics of a
520 resource are unknown. When applying any allocation method, it is advisable to consider the
521 spatial differences that may result from the interaction between age-specific movement and
522 fishery selectivity (i.e., availability).

523 Our study evaluated TAC allocation approaches that represent either currently applied
524 methods or theoretical alternatives for overcoming the challenge of spatial TAC allocation.
525 Division of quota based on survey index has been applied to as an *ad hoc* approach designed to
526 match spatial and temporal variation productivity with fishery harvest (e.g. sablefish, Hanselman
527 et al., 2016) whereas fixed-ratio allocation has been applied to facilitate resource distribution
528 across political boundaries (e.g. Pacific Hake, Berger et al. 2017a). Although recruitment indices
529 have not yet been used to spatially allocate catch, there is increasing interest in using juvenile
530 survey data to better estimate population productivity and inform stock assessment models
531 (Schweigert et al., 2009; Field et al. 2010; Buchheister et al., 2016). Our results showed that
532 TAC allocation based on a recruitment index performed poorly, but both our example species
533 displayed a high degree of connectivity among areas and they were intermediate to long-lived. It
534 is possible that a juvenile survey with sufficient spatial and temporal resolution may perform
535 better for species that exhibit greater within-area residency and that are shorter-lived (e.g.
536 herring). Future work should examine alternative TAC allocation approaches, including the
537 recruitment index, given different life history types to determine if longevity plays a role in how
538 these methods perform.

539 There are several caveats and limitations to our modeling approach for evaluating the
540 performance of TAC allocation methods. Generally, the population dynamics and catch
541 allocation simulations we applied were a simplification of most real-world catch allocation
542 situations. For example, the TAC allocation equations included an estimate of biomass from the
543 same year in which the quota allocation procedure is applied. In practice, estimates of biomass

544 may not available for the same year that a management procedure is put into effect.
545 Implementation of our approach would then need to apply biomass parameters with a greater
546 time-lag to derive TAC allocation fractions for a given year or input a projected biomass
547 estimate. We did not explore how timing differences between data availability and the
548 implementation of spatial management can influence TAC allocation performance; however,
549 future work could refine our approach by taking into consideration the timeframe in which
550 empirical data is available and processed relative to when spatial management procedures are
551 enacted. Additionally, our approach to spatial quota allocation assumed that the exploitation rate
552 and biomass are known perfectly, without error, which would be impossible to know in a real-
553 world application. Not considering these important sources of error in our modeling framework
554 produces ‘best case’ scenarios which may not encompass the full range of plausible outcomes.

555 Finally, there is the inherent difficulty associated with including spatially varying
556 biological parameters such as growth, maturity, and fecundity when concomitantly modeling
557 Eulerian or box-transfer movement. In some cases, a flux of fish that transition from the
558 biological characteristics of one area to another in a given time step results in unrealistic
559 biological changes (e.g., going from mature to immature or an instantaneous reduction in size),
560 and the range of impacts these assumptions have on management performance is yet to be fully
561 understood (Goethel and Berger, 2017). These challenges are not unique to our study as the
562 Eulerian approach to modeling movement is quite common. Lagrangian approaches such as
563 individual-based modeling are a more flexible alternative but tend to be data-intensive (Turchin,
564 1998; Kerr and Goethel, 2014; Goethel et al., 2016). Despite these simplifications in our

565 modeling approach, our results broadly indicate that understanding the spatial structure and
566 connectivity of fishery resources is important for achieving successful spatial management of
567 fisheries, even under best-case circumstances.

568 This study provides insight into the performance of different catch allocation schemes
569 under a range of spatial population and fishery regimes, but a comprehensive analysis using
570 closed-loop feedback simulations, such as a management strategy evaluation (MSE; Smith,
571 1994; Smith et al., 1999; Butterworth and Punt, 1999; Punt et al., 2001), is needed to adequately
572 provide specific management advice that is robust to system uncertainties. In an MSE, objectives
573 are predefined and the consideration of trade-offs are made explicit, which allows the choice of
574 management options while acknowledging trade-offs and risk (Kell et al., 2005; Mapstone et al.,
575 2008). Exploring these methods within an MSE or simulation-estimation framework would
576 provide a more complete examination of how spatial processes and simplified stock assessment
577 assumptions (e.g. panmictic) influence management performance for a given stock, and would
578 highlight whether the applied harvest allocation method is able to achieve the overall
579 management goals (e.g., resource and fishery sustainability). Moreover, the integration of
580 spatially complex simulation models into an MSE framework could provide feedback on how
581 socioeconomic information could be incorporated to supplement biological information for
582 setting spatial TAC allocations.

583 The increasing use of species distribution models along with demographically structured
584 population and fleet dynamic models are providing improved ways to incorporate spatial
585 complexities into management advice (Berger et al., 2017b). As spatially resolved data becomes

586 more available, and statistical research and computing power continue to advance, the ability to
587 incorporate spatial processes throughout the assessment-management framework will reduce the
588 need to rely on *ad hoc* approaches to harvest allocation.

589

590 **5. Conclusions**

591 Spatial assessment-management frameworks can improve management performance
592 (Punt et al., 2015; Goethel and Berger, 2017; Punt, 2017; Punt et al., 2017), but implementation
593 often demands reliable spatial data to inform models and management decision making. Given
594 the limited application of spatial stock assessments for providing management advice (Berger et
595 al., 2017b), there remains a need to identify robust approaches to TAC allocation (Kerr et al.,
596 2014; Goethel et al., 2016). Our results demonstrate that with high levels of movement among
597 population components of a biological resource, it may not be critical to determine an ideal
598 spatial harvest strategy for the desired reference point. Because of this flexibility, the spatial
599 allocation methods that we evaluated did not negatively impact resource sustainability. When
600 yield curves are well-defined and peaked, the empirical approaches to TAC allocation may be
601 more risk-prone. In these circumstances, it may be prudent to evaluate the performance of
602 alternative approaches, such as adaptive management or application of precautionary catch
603 buffers, within a dynamic modeling framework.

604 We recommend that future simulation work evaluate how TAC allocation methods
605 perform over a range of harvest levels and spatial population dynamics while also including
606 additional sources of error (both process and measurement error) expected from true fishery data.

607 Generally, the application of stochastic projection models can provide insights into how robust
608 TAC allocation methods are to variability in spatial processes and can highlight best approaches
609 for how they can be applied within a fishery management framework.

610

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618

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806 **Table 1:** Description of scenarios used to determine the management implications of
 807 misdiagnosing spatial processes. Each scenario was evaluated for both hake and sablefish unless
 808 otherwise noted. The *Spatial* model was applied as the reference model for model comparisons
 809 because it represented the most likely population dynamics for the example species.

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Scenario	Description
Includes movement	
<i>Panmictic</i>	Panmictic structure
<i>Spatial</i>	Single population with spatial heterogeneity (reference model)
<i>Metapop</i>	Metapopulation structure
<i>Alt_Selectivity</i>	Alternate selectivity
<i>Alt_Maturity</i>	Alternate maturity (hake only)
<i>Alt_Apport</i>	Alternate recruitment apportionment
<i>Hi_Residency</i>	High residency
No movement	
<i>Spatial_NM</i>	Spatial Model without movement
<i>Alt_Select_NM</i>	Alternate selectivity without movement
<i>Alt_Maturity_NM</i>	Alternate maturity without movement (hake only)

812 **Table 2.** Description of TAC allocation scenarios. *Population Structure* indicates population structure assumed in the stochastic
 813 projection. u_{max_Y} describes the scale of harvest rate applied to the management area. *TAC Allocation Method* describes the approach
 814 used to allocate the proportion of the system wide TAC to the smaller spatial management units within the system.

Scenario	Description	Population Structure	u_{max_Y}	TAC Allocation Method
<i>Alloc_Survey</i>	Survey Allocation	Spatial	Population	Survey Biomass
<i>Alloc_Survey_NM</i>	Survey Allocation - No Movement	Spatial	Population	Survey Biomass
<i>Alloc_Rec_Index</i>	Rec Index Allocation	Spatial	Population	Recruit Index
<i>Alloc_Rec_Index_NM</i>	Rec Index Allocation – No Movement	Spatial	Population	Recruit Index
<i>Alloc_Equal</i>	Equal Allocation	Spatial	Population	Equal Distribution
<i>Alloc_Equal_NM</i>	Equal Allocation - No Movement	Spatial	Population	Equal Distribution
<i>Alloc_Survey_Panmictic</i>	Panmictic u_{S,max_Y}	Spatial	Panmictic	Survey Biomass
<i>Alloc_Survey_Metapop</i>	Metapopulation u_{S,max_Y}	Spatial	System Metapop	Survey Biomass
<i>Sim_Survey_Metapop</i>	Spatial Heterogeneity u_{S,max_Y}	Metapopulation	Population	Survey Biomass

815 **Table 3.** Spatial harvest rates that achieve maximum system yield (u_{max_Y}) and associated
 816 depletion levels for hake and sablefish scenarios with and without movement for alternative
 817 population structures.

Hake		Movement		No Movement	
Model Scenario	Area	$u_{m \ x_Y}$	Depletion	$u_{m \ x_Y}$	Depletion

818

Panmictic (<i>Panmictic</i>)	-	-	-	0.23	0.32
	1	0.00	0.53	0.25	0.31
Spatial Heterogeneity (<i>Spatial & Spatial_NM</i>)	2	0.53	0.21	0.25	0.30
	Total	0.25	0.31	0.25	0.31
	1	0.00	0.50	-	-
Metapopulation (<i>Metapop</i>)	2	0.58	0.20	-	-
	Total	0.27	0.29	-	-

Sablefish Model Scenario	Area	Movement		No Movement	
		u_m	Depletion	u_m	Depletion
Panmictic (<i>Panmictic</i>)	-	-	-	0.18	0.24
	1	0.10	0.29	0.20	0.23
Spatial Heterogeneity (<i>Spatial & Spatial_NM</i>)	2	0.17	0.24	0.20	0.24
	3	0.33	0.21	0.21	0.24
	Total	0.20	0.24	0.20	0.23
	1	0.10	0.29	-	-
Metapopulation (<i>Metapop</i>)	2	0.17	0.24	-	-
	3	0.33	0.21	-	-
	Total	0.20	0.24	-	-

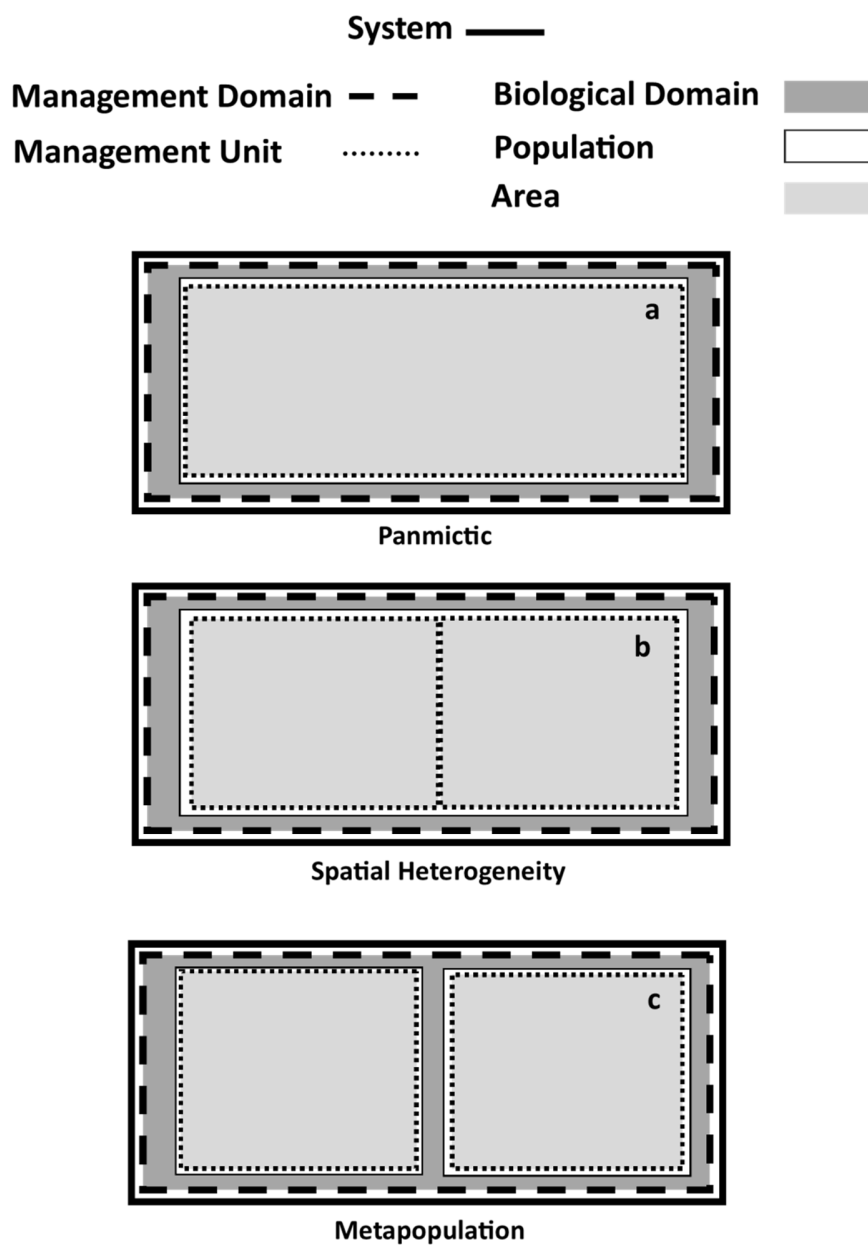
820 **Table 4:** Spatial harvest rates (u) and proportional TAC allocations for scenarios that maximize system yield (based on results from
 821 the *Spatial* and *Spatial_NM* scenarios) compared to TAC allocation scenarios that spatially distribute catch according to the survey
 822 biomass index (Survey) and equivalent (Equal) catch allocation methods. *Prop_TAC* represents the true proportion of catch derived
 823 from each scenario. Values from the equal apportionment scenario without movement (*) caused collapse in at least one area due to
 824 the allocated quota exceeding available biomass. Under the equal allocation scenario, values in parenthesis indicate the terminal area-
 825 specific depletion levels.

826

Species	Maximum System Yield				Survey [†]				Equal			
	Movement		No Movement		Movement		No Movement		Movement		No Movement*	
	u	TAC proportion	u	TAC proportion	u	TAC proportion	u	TAC proportion	u	TAC proportion	u	TAC proportion
Hake												
Area 1	0.00	0.00	0.25	0.80	0.21	0.41	0.25	0.80	0.26	0.50	0.13	0.76* (0.49)
Area 2	0.53	1.00	0.25	0.20	0.28	0.59	0.24	0.20	0.24	0.50	0.46	0.24* (0.19)
System	0.25		0.25		0.25		0.25		0.25		0.16	
Sablefish												
Area 1	0.10	0.18	0.20	0.42	0.19	0.31	0.20	0.42	0.20	0.33	0.08	0.43* (0.63)
Area 2	0.17	0.25	0.20	0.30	0.19	0.29	0.19	0.30	0.23	0.33	0.44	0.28* (0.09)
Area 3	0.33	0.57	0.21	0.28	0.20	0.39	0.20	0.27	0.17	0.33	0.37	0.29* (0.08)
System	0.20		0.20		0.20		0.20		0.20		0.15	

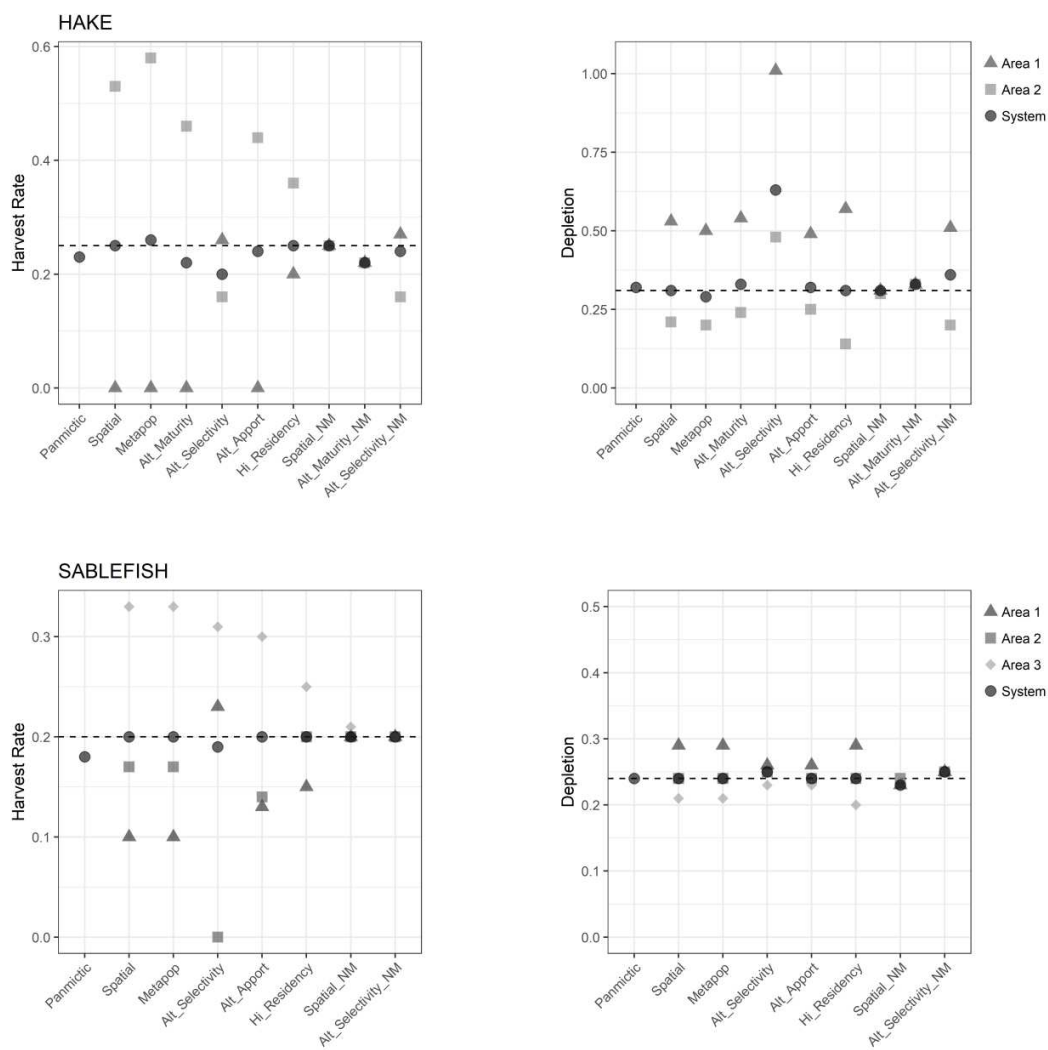
[†] median values

827 **Figure 1.** Schematic showing the hierarchical structure of the biological and management
 828 components within the system for the three population structures (a-c) that were modeled. For
 829 simplicity, the management and biological spatial components are aligned in the current study.
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832 **Figure 2.** Scenarios comparing spatial harvest rates (a,c) and depletion (b,d) levels across
 833 alternative model parameterizations (see Table 1 for descriptions). Scenarios are presented
 834 relative to the *Spatial* population structure assumption (dashed line).

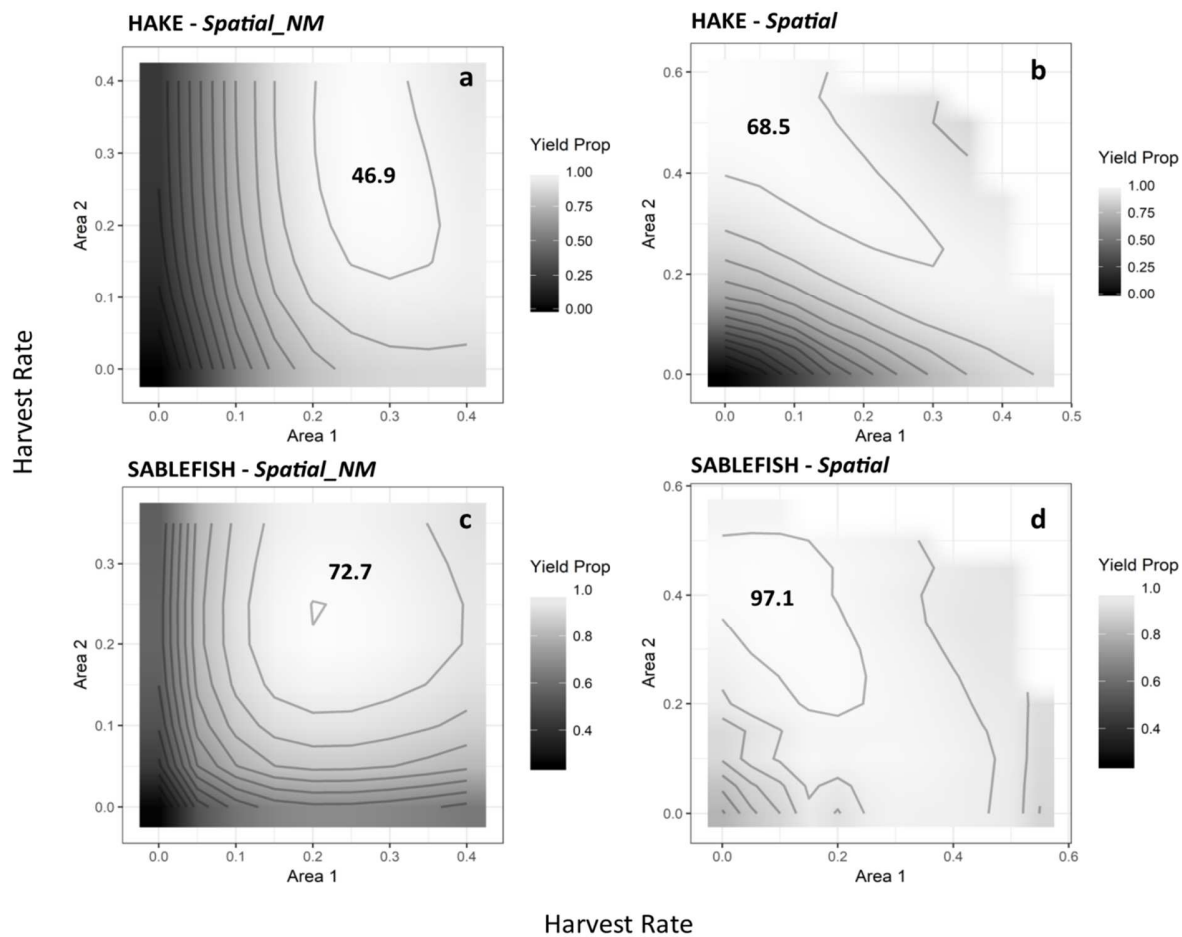


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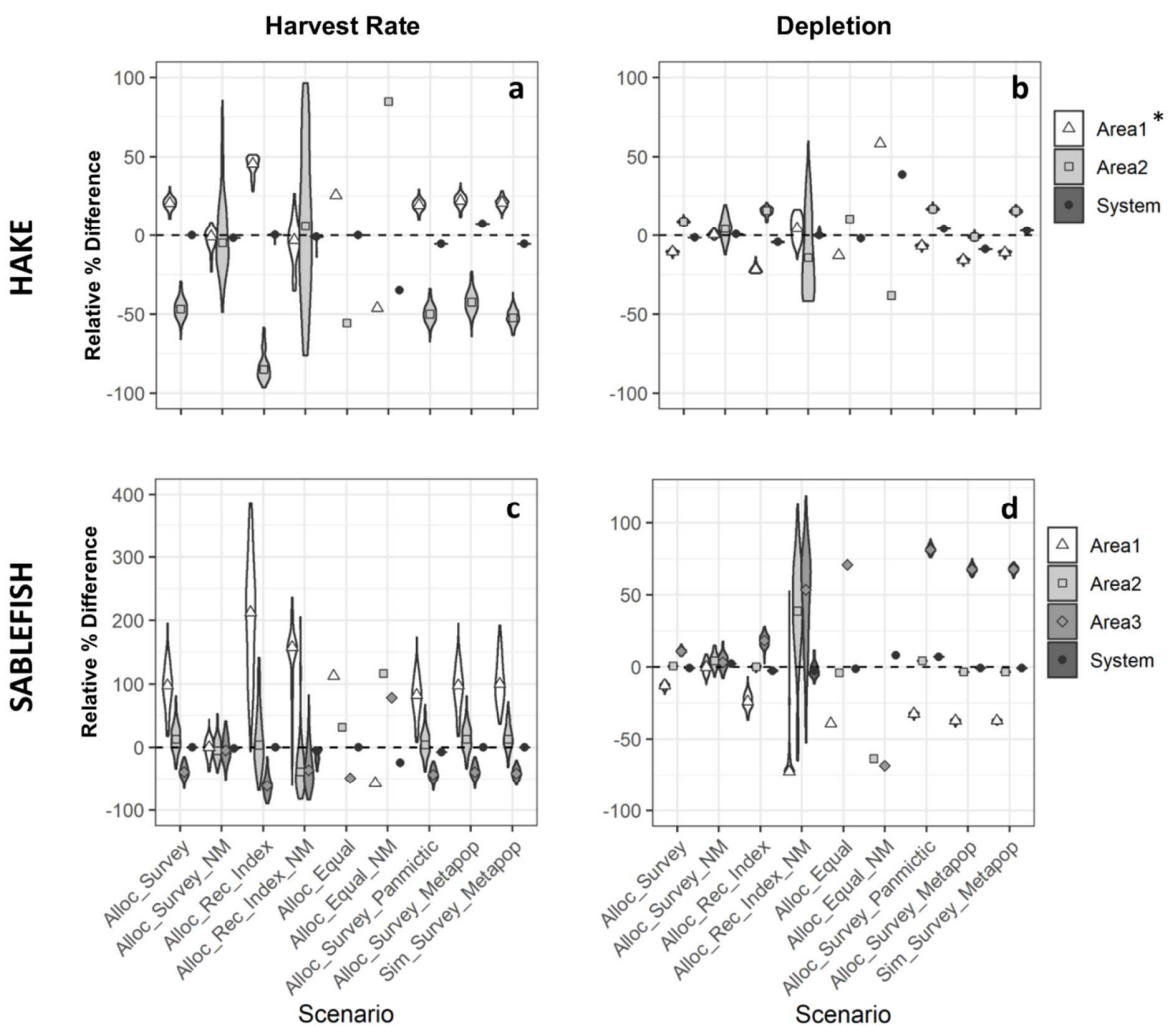
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837 **Figure 3.** Isopleths representing a 3-dimensional yield surface as a proportion of the system-
838 wide maximum given spatial harvest rate combinations for *Spatial_NM* (a,c) and *Spatial* (b,d)
839 scenarios. For the three-area sablefish model, the two spatial dimensions that best illustrate the
840 primary findings are shown (Areas 1 & 2). Isopleths showing yield surfaces across alternate
841 spatial dimensions are shown in Fig. S8. The plot area shows fishing mortalities less than
842 7.0. Inset values indicate the proportion of spatial harvest rate combinations that achieved
843 $\geq 90\%$ of system-wide maximum yield.

844



846 **Figure 4.** The relative percent difference (RPD) in harvest rate (a,c) and depletion (b,d)
847 comparing results from TAC allocation method scenarios to values that achieve maximum
848 system yield as derived in objective 1. For the hake example, Area 1 values for *Spatial* model
849 comparisons represent the true harvest rates (*e.g.* $20 = 0.2$), because u_{max_Y} was zero and
850 therefore the calculation of RPD for Area 1 was undefined. The scenarios that do not include
851 movement are shown relative to the *Spatial_NM* model. The metapopulation scenarios are shown
852 relative to the *Metapop* model. A full description of model scenarios are provided in Table 2.
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Appendix A: Description of Species Used for Model Scenarios

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Hake

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For this study, we identified two species that have spatially varying life history characteristics and where management advice relies on spatial allocation of catch quotas, Pacific hake (*Merluccius productus*), and sablefish (*Anoplopoma fimbria*) in Alaskan waters, which represent intermediate and long-lived species, respectively. The two species show potential to have spatial variability in natural mortality, recruitment, growth, maturity, and ontogenetic movement, which may impact population dynamics, productivity, and thus spatial harvest strategies. The models for both species were conditioned with input parameters that were available directly from the most recent stock assessment and further structured using hypotheses and ongoing research regarding the spatial population dynamics of the species. All results presented in this study should be interpreted relative to each other to gain comparative insight and not used directly to inform management for either species.

Pacific hake (or Pacific whiting) is a semi-pelagic, schooling, migrating species that ranges from southern Baja California to southern Alaska (Hamel et al., 2015; Berger et al., 2017a). The spatial distribution of Pacific hake is largely defined by ontogenetic movement, where larger (older) adults tend to migrate further north than smaller (younger) individuals. The most recent stock assessment assumed a single panmictic (homogeneous) population, with time-varying fishery selectivity to capture annual differences in the availability of fish by age that results from high recruitment variation and ontogenetic movement (Taylor et al., 2014; Berger et

882 al., 2017a). Catch advice is provided based on projections from the panmictic assessment model,
883 and quotas are then allocated to Canada and the United States (northern and southern
884 management units) based on a fixed ratio derived from historical catches and specified by the
885 Pacific Whiting Treaty (2004). Given the ontogenetic movement of fish along a general north-
886 south gradient, the impact of fishing differentially affects the population depending upon where
887 the majority of the harvest is occurring, the time of year that it occurs, and the distribution of
888 age-classes in a specific year.

889 Our reference model for hake (*Spatial*: see Table 1 in the main text) was structured as a
890 single population with spatial heterogeneity with the population distributed across two areas
891 (United States, Area 1, and Canada, Area 2; see Fig. A1). The model was age-structured (15 age
892 classes with the last as a plus group) and incorporated ontogenetic migrations with age-specific
893 movement rates. Age-based movement rates were hypothesized using available acoustic survey
894 and fishery-dependent catch-at-age data by area because formal tagging or other animal tracking
895 experiments have not been conducted for this species. A single Beverton-Holt stock-recruitment
896 function was applied using population-wide spawning stock biomass to inform future
897 recruitment, which was subsequently apportioned to each area (80% to the United States and
898 20% to Canada). Recruitment apportionment values were consistent with the spatial distribution
899 of age-1 observations in the acoustic survey (J. Clemons, NW Fisheries Science Center, NOAA,
900 pers. comm.) and evidence that spawning predominantly occurs further south (Area 1; Ressler et
901 al., 2007). Area-specific maturity ogives were also specified in the model and were based on
902 previous spatial estimates (Taylor et al., 2014). All remaining parameters were spatially and
903 temporally invariant and were obtained directly from the most recent stock assessment (Berger et

904 al., 2017a). These include natural mortality ($M = 0.226$), stock-recruitment steepness ($h = 0.814$),
905 average virgin recruitment ($R_0 = 3.13$ billion), and fishery and survey selectivity ogives (Fig.
906 A2), and survey catchability ($q = 1$).

907

908 *Sablefish*

909 Sablefish are bottom-dwelling groundfish capable of long-distance migrations along the
910 west coast of the United States and Canada. Movement rates within Alaskan federal waters and
911 between Alaska state and federal waters are well characterized for the species (Wolotira et al.,
912 1993; Hanselman et al., 2015). Sablefish exhibit an ontogenetic movement pattern where
913 younger fish inhabit shallower nearshore habitats and move to deeper offshore waters as they
914 age. Currently, Alaskan federal waters are assessed as a panmictic stock using a single area
915 assessment model (Hanselman et al., 2016). Catch projections based on the results of the
916 panmictic stock assessment have traditionally been used to set the total catch for the entirety of
917 Alaskan federal waters. Allocation to each of six management units was then determined using a
918 5-year exponential weighting scheme of relative survey and fishery indices of abundance, where
919 older surveys carry less weight. However, high variability in yearly allocations was problematic
920 which lead to the establishment of fixed allocation ratios beginning in 2013.

921 The reference model constructed for the sablefish (*Spatial*: see Table 1 in the main text)
922 assumed a single population distributed across three spatial areas (West, Area 1; Central, Area 2;
923 East, Area 3; see Fig. A3) matching those specified in a spatially explicit stock assessment model
924 currently in development (K. Fenske, AK Fisheries Science Center, NOAA, per. comm.). The
925 West area combines the Bering Sea, Aleutian Islands, and Western Gulf of Alaska; the Central

926 area is the Central Gulf of Alaska, and the East area combines the West Yakutat and East
927 Yakutat/Southeast management areas (Fig. A3). The model was age-structured (31 age classes
928 with the last as a plus group) and included movement rates derived from the Hanselman et al.
929 (2015) tagging analysis of age 2+ sablefish, which was simplified to develop a single age- and
930 time-invariant movement matrix and standardized to exclude movement out of Alaskan federal
931 management areas. A stock-recruitment function is not specified in the Alaskan sablefish
932 assessment because some of the largest recruitment events have come from periods of low stock
933 biomass (Hanselman et al., 2016). Therefore, the simulation model follows the current
934 assessment where annual recruitment was fixed as an overall population-level mean ($R_0 = 15.54$
935 million). Recruitment was then apportioned based on the proportion of age-2 fish that were
936 estimated to be in each of the three areas (44% to Area 1, 30% to Area 2, and 26% to Area 3).
937 Biological parameters for the sablefish model were derived from data collected during longline
938 surveys and from outputs of the spatially explicit stock assessment model (K. Fenske, AK
939 Fisheries Science Center, NOAA, per. comm.). Fishery selectivity ogives represented the
940 average of male and female selectivity-at-age for each area (Fig. A4). Survey selectivity-at-age
941 (Fig. A4) and catchability ($q = 8.70$) parameters were from the current sablefish assessment
942 (Hanselman et al., 2015). Spatial estimates for the proportion of mature females-at-age were
943 derived using visual observations from a longline survey (Sasaki, 1985; Fig. A4). Natural
944 mortality was assumed to be constant across space, time, and age ($M = 0.1$).

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946 **Literature Cited**

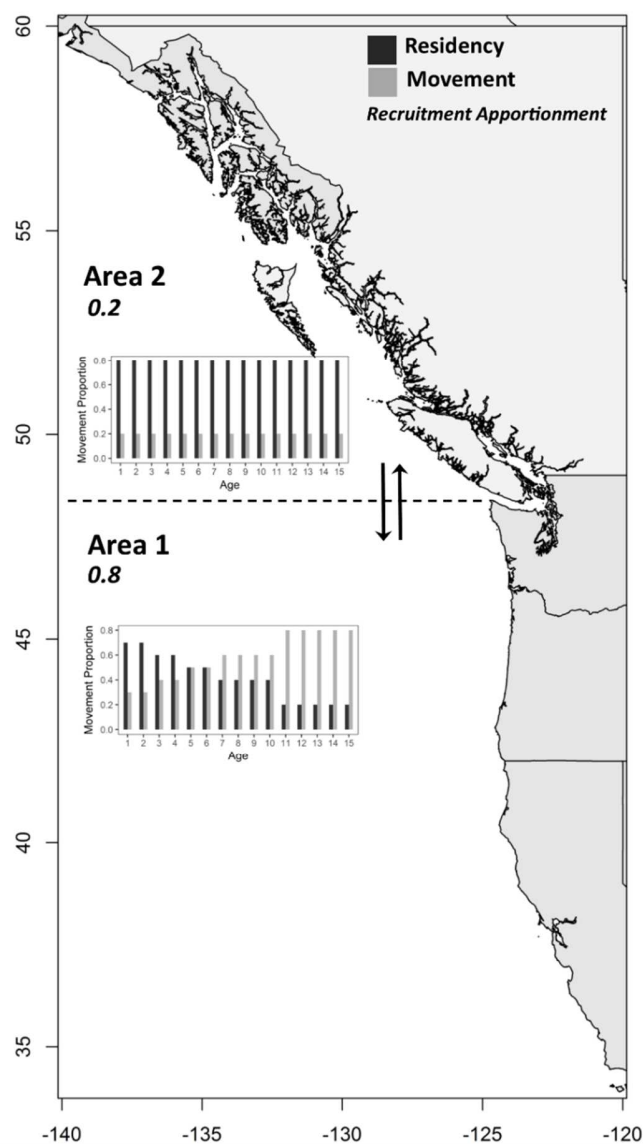
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984 **Figure A1.** Map of the Northeastern Pacific showing hypothesized hake age-dependent
985 movement rates and recruitment apportionment by area. Area 1 corresponds to waters off the
986 continental United States and Area 2 encompasses the waters off British Columbia, Canada.

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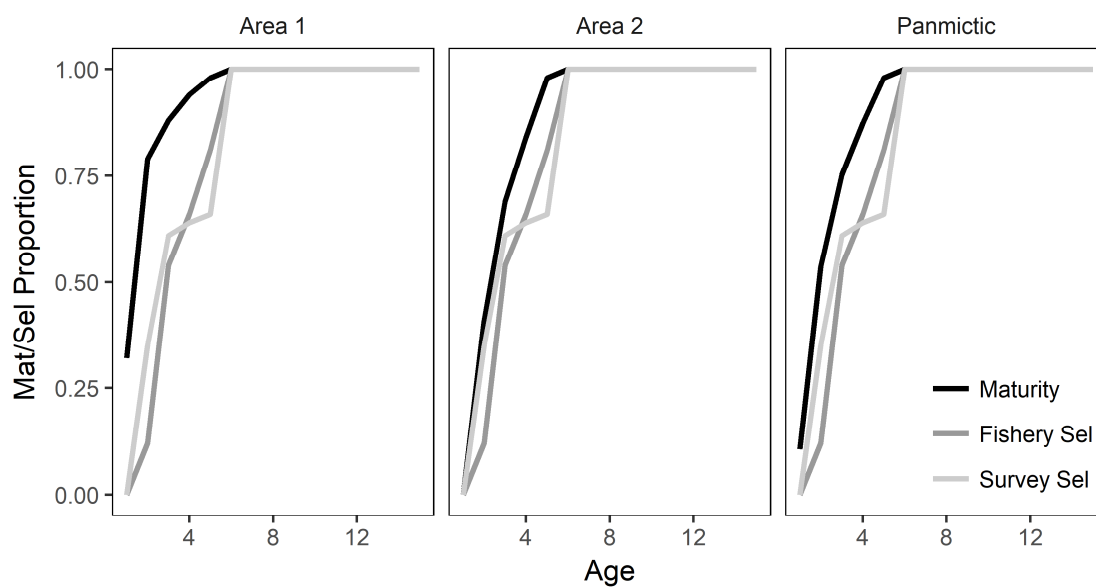
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989 **Figure A2.** Maturity and selectivity ogives for hake *Spatial* (Area 1 and Area 2) and *Panmictic*
990 model structures. The maturity ogive varied by area in the hake *Spatial* model while both survey
991 and fishery selectivity were spatially consistent throughout the system.

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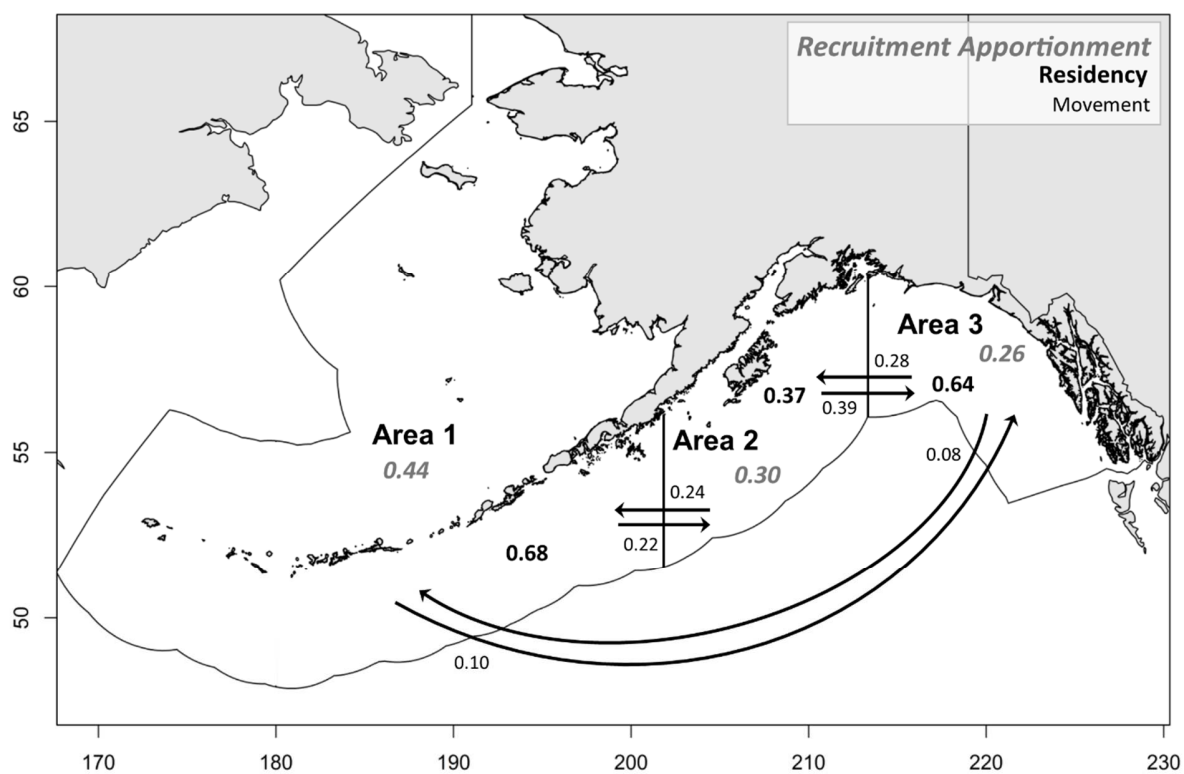
1006 **Figure A3.** Map showing sablefish movement rates and recruitment apportionment rates by area.

1007 Area 1 includes the Bering Sea, Aleutian Islands, and western Gulf of Alaska; Area 2 is the

1008 central Gulf of Alaska; and Area 3 includes the West Yakutat and East Yakutat/Southeast sub-

1009 areas.

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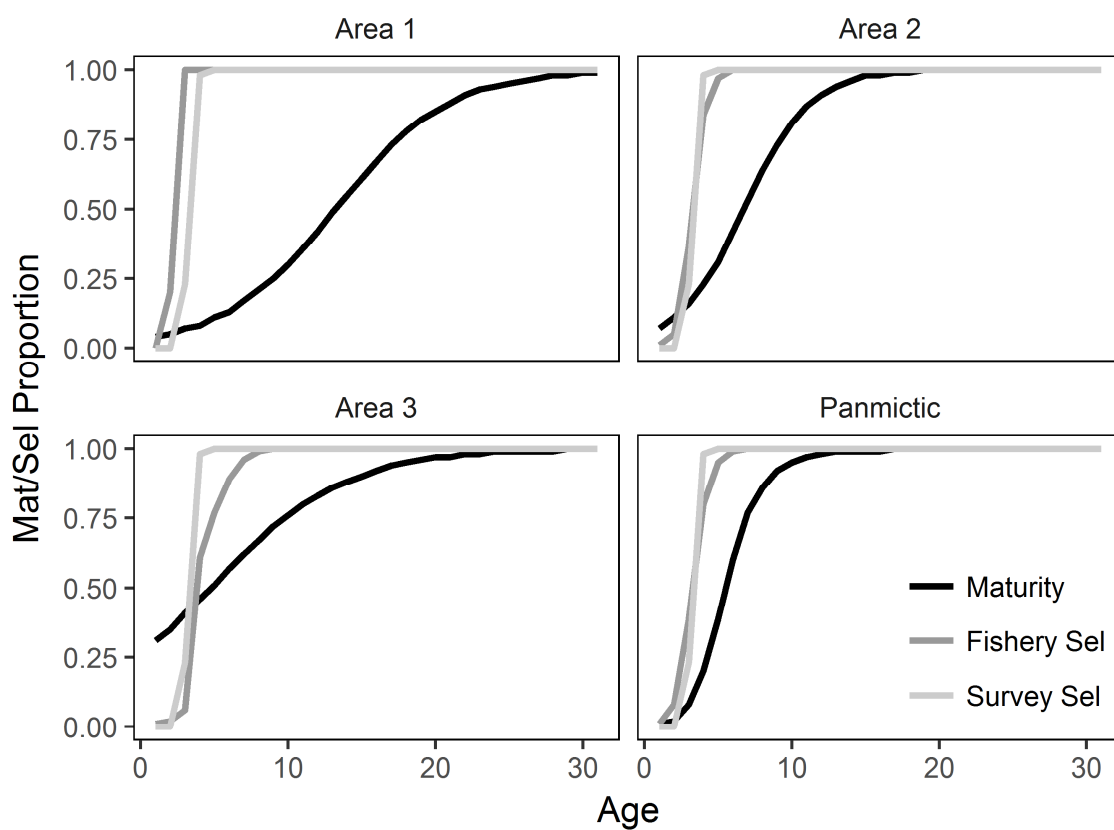
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1016 **Figure A4.** Maturity and selectivity ogives for sablefish *Spatial* (Areas 1, 2, and 3) and
1017 *Panmictic* model structures. The maturity and fishery selectivity ogives varied by area in the
1018 *Spatial* sablefish model while survey selectivity remained spatially consistent throughout the
1019 system.

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