
Equilibrium reference point calculations for the next generation of spatial assessments

Kapur M. S. ^{1,*}, Siple M. C. ², Olmos Maxime ³, Privitera-Johnson K. M. ¹, Adams G. ¹, Best J. ⁴, Castillo-Jordan C. ⁵, Cronin-Fine L. ⁴, Havron A. M. ⁶, Lee Q. ¹, Methot R. D. ⁷, Punt Andre E. ¹

¹ School of Aquatic and Fisheries Sciences, University of Washington, Seattle, WA 98195, USA

² Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, 7600 Sand Point Way N.E., Seattle, WA 98115, USA

³ College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR 97330, USA

⁴ Quantitative Ecology and Resource Management, University of Washington, Ocean Teaching Building, Suite 300, Seattle, WA, Box 357941, 98195, USA

⁵ Oceanic Fisheries Programme, The Pacific Community (SPC), B.P. D5, 98848 Nouméa, New Caledonia

⁶ ECS Federal in Support of National Oceanic and Atmospheric Administration Office of Science & Technology, 1315 East-West Boulevard, Silver Spring, MD 20910, USA

⁷ National Marine Fisheries Service, Silver Spring, MD, USA

* Corresponding author : M. S. Kapur, email address : maia.kapur@noaa.gov

Abstract :

Fish populations with spatial structure inherently violate the assumption of a single well-mixed stock, necessitating the use of spatially-structured population dynamics models. Accounting for spatial structure accurately and easily is a major goal for the next generation of stock assessment software development. Reference points (e. g., limit or target harvest rates and their associated biomass) are inherent to stock assessments and are often calculated under equilibrium conditions. However, the calculation process can be challenging for spatiallystructured population dynamics models. We outline how to calculate equilibrium quantities within spatiallystructured models where density-dependence in recruitment is local. We compare those values to equivalent situations when density-dependence in recruitment is global, thereby extending the set of population dynamics models on which spatially-structured stock assessments could be based. Results suggest that our method for calculating reference points under the assumption of local density-dependence can be performed using a straightforward optimization routine, and provide clearer understanding of the effects of fishing on a spatiallystructured population. Finally, we address areas of research and development needed to integrate spatiallystructured population dynamics models within existing management systems.

Keywords : Fisheries assessment, Fisheries management, Recruitment, Spatial dynamics

35 **1. Introduction**

36 Fisheries scientists have long recognized the need to appropriately account for spatial
37 heterogeneity in stock assessments (e.g., Beverton and Holt, 1957; Schaefer, 1968). The
38 interaction of biological and environmental processes, and spatial exploitation patterns, can lead
39 demographic rates (i.e., growth, death, immigration, and emigration) to vary across space,
40 resulting in observable spatial patterns in fish populations and yields. Ignoring spatial structure in
41 assessments can lead to bias in estimated management quantities (Booth, 2000; Fay et al., 2011;
42 Punt, 2019a; see Online Supplementary Material for a discussion of the definition of “spatial
43 structure”). Accounting for spatial structure can provide a greater degree of biological realism
44 by 1) allowing for spatial variation in demographic parameters, 2) reducing the variance of fixed
45 effect parameter estimates, and 3) more accurately reflecting the spatial dynamics of the fishing
46 fleet(s), which may differ from those of fish population dynamics (Punt, 2019a). Spatially-
47 structured assessments can inform rules for setting catch limits that respond to local dynamics
48 (Bosley et al., 2019; McGarvey et al., 2017). They also can evaluate other types of spatial control
49 mechanisms for fisheries management such as spatial closures within management zones,
50 protected areas, and Territorial Use Rights for Fishing reserves (e.g., Kapur and Franklin, 2016;
51 McGilliard et al., 2015; Field et al., 2006).

52 Problems for sustainable management can arise from a mismatch between management
53 regions, which are often political, and the spatial extent of demographic population units, or
54 stocks¹. A stock can be defined by both its demography and the spatial area it inhabits. For
55 example, Atlantic bluefin tuna (*Thunnus thynnus*) are comprised of two demographically distinct
56 stocks inhabiting different areas with connectivity between them (National Research Council,
57 1994). Ignoring spatial structure in the assessment and management processes for such species
58 may lead to local depletion (Benson et al., 2015; Goethel and Berger, 2016). For example, Morse
59 et al., (2020) found that applying single-area models separately to each of two connected stocks
60 in a simulation framework (i.e., ignoring spatial mixing) resulted in biased estimates of
61 recruitment and spawning biomass for both stocks. Similarly, Ying et al., (2011) found that
62 assessing and managing three mixed stocks of small yellow croaker (*Larimichthys polyactis*) off
63 the coast of China as independent populations led to a high probability of overexploitation. As a
64 corollary, assessing yellow croaker as a single stock, with the assumption of global recruitment,
65 led to a high probability of local depletion. This echoes the findings from the previously
66 mentioned simulation studies, and suggests that assumptions regarding the timing and locality of
67 density dependence (recruitment) can influence the degree to which an assessment model
68 diverges from the spatially-structured reality (Cadrin et al., 2019).

69 **However, limited research has been undertaken to identify sustainable harvest rates**
70 **that account for spatial structure and dynamics in a manner that matches spatial**
71 **assessment assumptions. Reference points, which can be used to determine whether a stock**
72 **is above or below a desired threshold either in terms of biomass or the degree of**
73 **exploitation (which is ideally below a limit), bridge the assessment-management interface**
74 **and the associated models used to calculate them can be adapted to account for spatial**
75 **dynamics.**

76 A salient feature of the next generation of stock assessment **models** will be accommodation
77 of spatial heterogeneity **in mathematical representations of** fished populations and the fleets
78 that exploit them (spatially-structured assessments; Punt et al., 2020). **The process of**

¹ We use the term “stock” to refer to a demographically unique or independent sub-population.

79 performing a stock assessment can involve data collection, processing, model selection, and
80 the input of managers. Here, we are concerned with the functionality of stock assessment
81 modeling packages. This distinction means that assessment scientists are able to design and
82 run stock assessment model configurations that include various assumptions regarding the
83 spatial structure of recruitment; whether and how these configurations are incorporated
84 into the management process for a given stock is a decision left to the fishery management
85 system in question.

86 Reference points are the bridge between the population model-fitting exercise and
87 management implementation for many fisheries management agencies, including sovereign
88 governments and international Regional Fishery Management Organizations (RFMOs).
89 Reference points are quantities (most of which are based on the assumption that the population is
90 in equilibrium, i.e., time-invariant selectivity, growth and fishing mortality) derived from
91 population dynamics models. Common biomass reference points include unfished biomass, B_0 ,
92 and the biomass at which maximum sustainable yield (MSY) is attained (B_{MSY}). Fishing mortality
93 reference points include the fishing mortality rate at which MSY is attained (F_{MSY}), and the
94 fishing mortality rate that maximizes the average yield from each recruit for a given size at first
95 capture (F_{max}). Spawning biomass per recruit, SPR , can also be used as the basis for reference
96 points. Typical SPR -based reference points include $F_{x\%}$, the fishing mortality corresponding to a
97 $x\%$ reduction in SPR from unfished conditions and SPR_{MSY} the ratio of SPR when the population
98 is fished at F_{MSY} to the SPR of the unfished population (Caddy and Mahon, 1995; Mangel et al.,
99 2013).

100 Several of the generic stock assessment packages used worldwide include features to specify
101 spatial population structure, and compute reference points (Table 1). However, in most cases,
102 equilibrium yield-based reference points are defined by the assumption of spatially-aggregated
103 recruitment (Francis and McKenzie, 2015). Some stock assessment packages provide reference
104 points separately for each modelled area. **For example, CASAL/Casal2 (Table 1, Bull et al.**
105 **2012, Doonan et al., 2016) can account for natal homing and connectivity between different**
106 **areas; both can provide estimates of unfished biomass (B_0), while CASAL provides yield**
107 **estimates (MSY , B_{MSY}). In both cases, biomass can be calculated separately for the**
108 **specified areas (Francis and McKenzie, 2015, T. A'mar, pers. comm), or as population-wide**
109 **totals which are then allocated by area-specific fractions.**

110 Previous work has outlined the assumptions and decisions considered in spatial assessments
111 (Berger et al., 2017; Cadrin et al., 2020; Punt, 2019a), and highlighted the modeling challenges
112 posed by populations with varying demographics – or multiple stocks – inhabiting a managed
113 region (Cadrin et al., 2019; Punt et al., 2017). **A spatial management approach does not**
114 **require spatially explicit assessment or simulation models. Spatially structured modeling**
115 **frameworks, including models that incorporate space both implicitly and explicitly, can be**
116 **used directly to estimate reference points in a spatially explicit manner. They may also be**
117 **used as operating models in a management strategy evaluation framework to find reference**
118 **points that are not spatially defined, but are robust to uncertainty in spatial population**
119 **structure and/or dynamics (Fig. 1). Non-spatially structured models can only provide**
120 **reference point estimates that apply to the whole population, but those reference points**
121 **may still be used in spatial management though the implementation of protected areas or**
122 **spatial closures, or through the allocation of allowable catch in a spatially explicit manner.**
123 **Thus, there are many paths to spatial management and tools need not be explicitly spatial**
124 **to be useful in a spatial context.**

125 Spatially-structured assessments need to provide estimates of the reference points specific to
126 a region or the prevailing fisheries management paradigm. Current methods are unable to do so
127 accurately for certain spatial scenarios, specifically local productivity dynamics, which presents
128 a barrier when designing and implementing next-generation assessment software. **One software**
129 **package which approaches this issue is PRO-2BOX (Porch, 2018), which calculates MSY**
130 **by finding the F-vector that maximizes the combined long-term yield from the two**
131 **recruitment sources, which is subtly different from the combined long-term yield of each**
132 **stock. A chief limitation of that approach is that it does not allow fish to change their stock**
133 **affiliation (and thus movement characteristics) upon migration to another area. In the**
134 **present simulation study, we demonstrate how the assumption of changed affiliation**
135 **requires the use of an iterative optimization, and the implications of such an assumption on**
136 **equilibrium reference points.**

137 Calculation of F_{MSY} (and hence B_{MSY} and MSY)² involves (numerically) solving the
138 equation:

$$139 \quad \frac{\delta C(F)}{\delta F} \Big|_{F=F_{MSY}} = 0 \quad (1)$$

140 where $C(F)$ is the equilibrium yield when fully-selected fishing mortality is F . Equation 1 can
141 be solved by simulation, which involves running the model to equilibrium (e.g., Goethel and
142 Berger, 2016). Although simulation can be used to compute MSY-based reference points, this is
143 computationally intensive and not easily integrated into software that analytically computes the
144 uncertainty associated with reference points. It can be shown (see Section 2.1) that the
145 calculation of $C(F)$ is analytical when recruitment is a function of the total spawning biomass
146 (over all areas) and the proportion of the total recruitment that recruits to each area is
147 independent of fishing mortality (and hence independent of the spawning biomass in each area).
148 This “global” density-dependence assumption is the most common way recruitment is
149 represented in stock assessment models used for tactical management (Table 1). However,
150 another plausible way to represent the recruitment process is to assume that the recruitment to an
151 area is functionally related to the biomass in that area (“local recruitment”) (Cadriin et al., 2019;
152 Porch, 2018). The need for next-generation stock assessment methods to include “local” density
153 dependence in recruitment was highlighted by Punt (2019b) and Punt et al. (2020). We anticipate
154 that an approach that considers area-specific productivity will be more sensitive to depletion in
155 any linked area, and enable the identification of local depletion, which is a known problem with
156 models that assume global recruitment (Okamoto et al., 2018).

157 We show how MSY-based reference points can be calculated for populations that exhibit
158 local density-dependent recruitment. **The intention is to mathematically reconcile changes in**
159 **the biomass in one area caused by the exploitation of fish within that area and other area(s)**
160 **and by movement of biomass.** It is important to understand whether there are inherent
161 properties of local recruitment that would lead to different (from previous) values for system
162 wide MSY . We therefore develop a set of scenarios to compare the values for reference points
163 given “global” and “local” recruitment. Our goal is to illustrate the functionality and tradeoffs
164 associated with different assumptions about recruitment density dependence in spatial models, as
165 local recruitment is being considered for implementation in future versions of Stock Synthesis
166 (R. Methot, NOAA Fisheries, pers. comm). Finally, we describe the limitations posed by

² The focus here is on F_{MSY} , MSY and B_{MSY} because the other reference points outlined above are byproducts of their calculation.

167 existing management systems (both in the US and internationally) (Privitera-Johnson and Punt,
168 2020), and provide examples of how spatial reference points are implemented in management.

169 2. Methods

170 **In this section, we derive and describe the calculation of MSY (and related reference**
171 **points) under the common assumption that density dependence is global, and then**
172 **introduce the relevant changes to this calculation when that assumption is violated, i.e.,**
173 **when density dependence is instead local to each area.** This analysis compares the
174 conventional (“global”) assumption for calculating reference points such as F_{MSY} and B_{MSY} with
175 an assumption that allows for local recruitment. In both cases, equilibrium recruitment is solved
176 for as part of an optimization routine. **We then develop a simulation model to compare MSY**
177 **estimates using the global and local assumption.** We present a simple single-sex, age-
178 structured model with fishing throughout the year and two spatial areas (areas 1 and 2) to
179 illustrate how spatially-articulated reference points differ depending upon the recruitment
180 assumption used (Sections 2.1 and 2.2). In Equations 2-10, we use the letters ω and B to
181 represent two theoretical spatial areas, noting that these could be extended to include more than
182 two areas. The stock-recruitment relationship has the Beverton-Holt form, and fish are exploited
183 by two fleets, each targeting a single area (*sensu* Sampson and Scott, 2011). A survival equation
184 links age classes. Referring to the terminology introduced above, the analysis is comprised of
185 two stocks for the local density dependence case – though some demographic parameters may be
186 identical among areas, density-dependence can operate globally or locally within each area,
187 resulting in two demographic units. **Several sensitivity tests are presented for the two MSY**
188 **approaches by introducing systematic changes into the simulation model, such as in the**
189 **demographic parameters (stock-recruitment steepness, natural mortality, weight-at-age),**
190 **movement and fishery selectivity. The performance metrics used to compare the results**
191 **among the two assumptions include: area-specific F_{MSY} , total yield, total B_{MSY} and area-**
192 **specific depletion, the ratio of the biomass obtained at F_{MSY} to the unfished biomass**
193 **(B_{MSY}/B_0).**

194 2.1 MSY and its definition in age-structured models with global density-dependence in 195 recruitment

196 For the case in which the population dynamics model is spatial and the stock-recruitment
197 relationship operates globally³, $C(F)$ is calculated as:

$$198 \quad C(F) = R(F)\tilde{C}(F) \quad (2)$$

199 where $\tilde{C}(F)$ is system-wide yield-per-recruit as a function of F , and $R(F)$ is global equilibrium
200 recruitment when fully-selected fishing mortality is F . These quantities are defined as:

$$201 \quad \tilde{C}(F) = \sum_{\omega} \sum_a w_a \frac{S_a^{\omega} F^{\omega}}{Z_a^{\omega}} \tilde{N}_a^{\omega} (1 - e^{-Z_a^{\omega}}) \quad (3a)$$

$$202 \quad \tilde{N}_a^A = \begin{cases} \chi^{\omega} R(F) & \text{if } a = 0 \\ \tilde{N}_{a-1}^{\omega} e^{-Z_{a-1}^{\omega}} (1 - \sum_{A' \neq A} \phi_{a-1}^{\omega, \omega'}) + \sum_{A' \neq A} \phi_{a-1}^{\omega', \omega} \tilde{N}_{a-1}^{\omega'} e^{-Z_{a-1}^{\omega'}} & \text{otherwise} \end{cases} \quad (3b)$$

$$203 \quad Z_a^{\omega} = M + S_a^F F^{\omega} \quad (3c)$$

³ A single-area model is a special case of this model.

204
$$R(F) = \frac{R_0(4h\tilde{S}(F)-(1-h)\tilde{S}(0))}{(5h-1)\tilde{S}(F)} \quad (3d)$$

205
$$\tilde{S}(F) = \sum_{\omega} \sum_a f_a \tilde{N}_a^{\omega} \quad (3e)$$

206 where \tilde{N}_a^{ω} is the numbers-per-recruit in area ω of age a , Z_a^{ω} is the total mortality on animals of
 207 age a in area ω , S_a^{ω} is selectivity of animals of age a in area ω , F^{ω} is the fully-selected fishing
 208 mortality enacted in area ω , w_a is the weight of an animal of age a , M is an age- and time-
 209 invariant rate of natural mortality, \tilde{S} is the spawning biomass-per-recruit by area, $\phi_a^{\omega,\omega'}$ is the
 210 probability of animals of age a in area ω moving to area ω' (after mortality), χ^{ω} is the **time-**
 211 **invariant** proportion of global recruitment to area ω , f_a is the fecundity of animals of age a , h is
 212 steepness of the stock-recruitment relationship (the expected proportion of unfished recruitment
 213 at 20% of unfished spawning biomass), and R_0 is unfished recruitment. Equation 3d arises from
 214 the following reparameterization of the Beverton-Holt stock-recruitment relationship:

215
$$R(F) = \frac{4hR_0R(F)\tilde{S}(F)}{(1-h)R_0\tilde{S}(0)+(5h-1)R(F)\tilde{S}(F)} \quad (4)$$

216 Equations 3a-c can be generalized in several ways including 1) allowance for multiple fleets in
 217 each area, 2) weight-at-age that varies spatially, 3) different stock-recruitment relationships, 4)
 218 different time of movement vs mortality, etc. Nevertheless, all of these formulations lead to yield
 219 being an analytical function of fully-selected fishing mortality⁴. To find F_{MSY} and associated
 220 quantities given global density-dependence, the values of the elements of the vector F^{ω} are
 221 found that maximize the system-wide yield (sum of yields in each area, MSY, Eqn. 1). This
 222 requires specification of the putative proportion of total recruitment that recruits to each area
 223 (i.e., χ^{ω} for each area()), which always sum to 1, and Beverton-Holt steepness h .

224 2.2 MSY and its definition in age-structured models with local density-dependence in recruitment

225 The presence of local density-dependence (e.g., stock-recruitment curves that operate
 226 independently in each area) involves modifying Eqns 2, 3a and 3b to **explicitly track the area-**
 227 **specific yield which results from a single recruit in each spawning area. This adjustment**
 228 **enables the yield curve to be defined, and thus the responsiveness of the yield-per-recruit**
 229 **for an areas to the net effect of fishing mortality and movement within and outside of that**
 230 **area.**

231
 232
$$C(F) = \sum_B R^B(F) \sum_{\omega} \tilde{C}^{B,\omega}(F) \quad (5)$$

233
$$\tilde{C}^{B,\omega}(F) = \sum_a w_a \frac{S_a^{\omega} F^{\omega}}{Z_a^{\omega}} \tilde{N}_a^{B,\omega} (1 - e^{-Z_a^{\omega}}) \quad (6)$$

234
$$\tilde{N}_a^{B,\omega} = \begin{cases} 1 & \text{if } a = 0 \text{ and } \omega = B \\ 0 & \text{if } a = 0 \text{ and } \omega \neq B \\ \tilde{N}_{a-1}^{B,\omega} e^{-Z_{a-1}^{\omega}} (1 - \sum_{\omega' \neq \omega} \phi_{a-1}^{B,\omega,\omega'}) + \sum_{\omega' \neq \omega} \phi_{a-1}^{B,\omega,\omega'} \tilde{N}_{a-1}^{B,\omega'} e^{-Z_{a-1}^{\omega'}} & \text{otherwise} \end{cases} \quad (7)$$

235 where $\tilde{C}^{B,\omega}(F)$ is yield in area ω based on a single recruit to area B as a function of F , $R^B(F)$ is
 236 equilibrium recruitment to area B when fully-selected fishing mortality is F , $\tilde{N}_a^{B,\omega}$ is the numbers
 237

⁴ Solution of Equation 1 requires a numerical solution of a non-linear equation.

238 in area ω of age a that were produced by one recruit that settled (at age 0) in area B , $\phi_a^{B,\omega,\omega'}$ is
 239 the probability of animals that originally settled to area B and currently in area ω moving to area
 240 ω' at age a (after mortality). ω' is any area different from ω , thus this syntax enables the
 241 inclusion of migration among two or more areas; the simulation study presented here only
 242 considers two areas. Importantly, fish that migrate into a given area are assumed to be
 243 completely assimilated into the population they migrate into, which other models have attempted
 244 to approximate by tracking the fraction of global recruitment that remains in or leaves their natal
 245 area (e.g., PRO-2BOX, Porch, 2018). This simulation study does not explicitly consider the
 246 growth of individual fish through time, which would require the assignment of **specific growth**
 247 **patterns** to settled recruits; the identity of a fish's **growth pattern** would shift depending on the
 248 area in which the fish is at age a . Given the assumption of area-specific density dependence and
 249 a Beverton-Holt stock recruitment relationship, the stock-recruitment relationship for each area
 250 (here ω) is given by:

$$251 \quad R^\omega(F) = \frac{4h^\omega \chi^\omega R_0 \sum_B \tilde{S}^{B,\omega}(F) R^B(F)}{(1-h^\omega) \sum_B \tilde{S}^{B,\omega}(0) \chi^B R_0 + (5h^\omega - 1) \sum_B \tilde{S}^{B,\omega}(F) R^B(F)} \quad (8)$$

252 where χ^ω is the proportion of the total (global) recruitment (**which was set without loss of**
 253 **generality to 1**), to area ω in an unfished state, and

$$254 \quad \tilde{S}^{B,\omega}(F) = \sum_a f_a \tilde{N}_a^{B,\omega} \quad (9)$$

255 Equation 8 is non-linear in $R^B(F)$; which reflects the key difference between global and local
 256 recruitment. Equation 8 can be solved iteratively by reorganizing it as:

$$257 \quad 4h^\omega \chi^\omega R_0 \sum_B \tilde{S}^{B,\omega}(F) R^B(F) =$$

$$258 \quad [(1-h^\omega) \sum_B \tilde{S}^{B,\omega}(0) \chi^B R_0 + (5h^\omega - 1) \sum_B \tilde{S}^{B,\omega}(F) R^B(F)] R^\omega(F) = \mathbf{Y}_F^\omega \quad (10)$$

260 which is solved for $R(F)$ using the R (R Core Team, 2020) function *optim()*.

261 The process for calculating F_{MSY} in the case of local recruitment involves specifying the weight-
 262 at-age (perhaps by area), selectivity-at-age by fleet, natural mortality, steepness by area, R_0 and
 263 χ^ω , and then:

- 264 1. Using Equations 5-6, calculate the spawning biomass-per-recruit by area given no fishing
 265 in either area ($F=0$; i.e. $\tilde{S}^{B,\omega}(0)$).
- 266 2. Given a value for F , calculate spawning biomass- and yield-per-recruit by area (Equations
 267 9 and 5) and hence find the values for recruitment by area that satisfy Equation 10.
 268 Equation 1 can then be applied to calculate **equilibrium** catch given that F .
- 269 3. Repeat step 2 with different values for F until equation 1 is optimized.

270 2.3 Scenarios & Performance Metrics

271 Base Model

272 The reference points will differ depending on how recruitment is modelled (“global” vs “local”),
 273 with the effect depending on assumptions about growth, movement, fishery selectivity, natural
 274 mortality, and stock-recruitment steepness. Values for MSY-related quantities are therefore
 275 computed for “global” and “local” recruitment for a range of scenarios (Table 2). The unfished

276 biomass is the same for all scenarios and the remaining assumptions are the same for the two
277 recruitment assumptions (where possible).

278 In the base-case scenario, recruitment is divided evenly between areas; we conduct an
279 exploration of sensitivity to the proportion of recruitment to area 1 from 0.5 to 0.9. The
280 probability of moving from area 2 to area 1 is a piecewise linear function of age (0 at age 0
281 increasing to a pre-specified movement rate at age 9 and constant thereafter; Fig. 2A). The base-
282 case scenario assumes that area 1 is a sink area. The model specifies weight-at-age for each area.
283 Ages are modelled from 0 (recruits) to 100 yr⁵. Fish length is specified by the von Bertalanffy
284 growth curve, with an asymptotic length of 50 cm, an annual growth rate of 0.15 yr⁻¹ and an age
285 at length zero of 1, though results are insensitive asymptotic length. Weight is an allometric
286 function of length following $w_{age} = aL_{age}^b$, where $a = 0.63$ and $b = 1.81$; we conduct a
287 sensitivity to area-specific weights-at-age by increasing the age at length zero in area 1.
288 Selectivity is an increasing logistic function of age, specified by ages at 50%- and 95%-
289 selectivity, and can vary among areas. Fecundity-at-age is proportional to weight-at-age, with the
290 ages at 50%- and 95%-maturity specified by area (although they are **the same in our**
291 **simulations**). The probability of moving is zero for age-0 fish, increases linearly to a maximum
292 at age 9, after which all ages have the same movement rate. These movement rates vary between
293 areas and among scenarios. **Fishing is assumed to occur on an annual basis before movement.**

294 The simplicity of this example is to illustrate the differences between the global and local
295 density dependence. Therefore, the resulting differences in reference points can be attributed to
296 the assumption about density-dependence and its interaction with the spatial transience created
297 by movement between and differential exploitation among areas. **Code to reproduce the**
298 **analyses from this manuscript can be found at** www.github.com/mkapur/sptIRP.

299 *Alternative Scenarios (Sensitivity Runs)*

300 Sensitivity is explored to no movement (the areas are completely independent, Fig. 2B), to
301 varying degrees of exchange among areas (Figs. 2C-2E), to symmetric movement (Fig. 2F) and
302 to several source-sink configurations (Figs. 2G-2J). Most of the scenarios are based on
303 $M=0.15\text{yr}^{-1}$ but sensitivity is explored to $M=0.13\text{yr}^{-1}$ and $M=0.17\text{yr}^{-1}$ (“low M” and “high M”,
304 respectively). Weight-at-age is the same in both areas for the base-case scenario (Fig. 2K), with
305 sensitivity explored to higher weight-at-age in area 1 (Fig. 3A, “No movement, Higher WAA in
306 area 2”). Selectivity is the same in the two areas for the base-case scenario (ages-at-50% and -
307 95% selectivity of 9 and 13 years; Fig. 2L), with sensitivity explored to two alternative
308 selectivity patterns (Figs 3B and 3C; “lower/higher age-at-50% selectivity in A1”). Stock-
309 recruitment steepness is assumed to be 0.7 for both areas (0.7 for entire population for global
310 density-dependence), with sensitivity explored to different (area-independent) values for
311 steepness (0.6 and 0.8, “low/high h ”) as well to area-specific combinations thereof. **While not**
312 **exhaustive, we selected these sensitivities to illustrate how commonly modeled processes**
313 **with predictable impacts on single-area reference points influence equilibrium quantities**
314 **when recruitment is assumed to be local.**

315 *Performance metrics*

316 Analyses are conducted for a base-case scenario and a range of sensitivity scenarios. Each
317 scenario involved computing the two-dimensional yield curve surface with x- and y-axes defined
318 by the fishing mortality by area and identifying the combination of area-specific fishing

⁵ A sufficiently large number of years that the numbers at age 101+ are negligible even in an unfished state.

319 mortalities at which total yield is maximized (i.e., F_{MSY}). The results are articulated as system-
320 wide totals, which is in keeping with many management systems, in which a single reference
321 point will be calculated from a model comprised of more than one linked area.

322 4. Results

323 Each scenario (row) in Tables 2 and 3 took under one minute to optimize on a standard
324 laptop computer, with the maximum iterations set to 1,000 and the vector of step sizes for
325 the finite-difference approximation set to $1e-4$ (the default is $1e-3$). A finer step size is
326 recommended as coarser (i.e., greater than $1e-2$) search grids may cause the optimizer to
327 overlook intermediate combinations of F_{MSY} . We specified the starting values for the two
328 parameters at 0.47 after visualizing the yield surface (e.g., Fig. 4). The initial parameter
329 estimate returned by `optim()` was then fed back into the same optimizer until the estimates
330 did not change, for a maximum of five iterations. Scenarios with the base case movement
331 parameterization required less than 100 function calls to find the local minimum, and
332 fewer than 50 for the global case.

333

334 3.1 Base-case scenario

335 Fig. 4 shows the numbers-per-recruit in each region for the base-case scenario that includes area
336 1 as a sink. The numbers-per-recruit-at-age when summed over source area are identical between
337 recruitment assumptions. The numbers-per-recruit in the area in which the animals did not settle
338 is initially zero (as settlement is to a single area by construction) and increases given movement
339 but declines to zero under mortality. The third row of Fig. 5 shows total yield as a function of
340 fishing mortality by area for the case of global and local recruitment for the base-case scenario.
341 The local recruitment assumption leads to a total MSY that is 15% higher than the global
342 assumption, with a much higher F_{MSY} in the sink area, from which there is no movement of
343 individuals back into the source area (Table 2).

344 3.2 Sensitivity analyses

345 The values for the reference points and area-specific depletion at F_{MSY} (B_{MSY}/B_0) are
346 independent of movement rate if the two areas are identical (e.g., selectivity, weight-at-age and
347 steepness h are the same) and movement is symmetric (Figs 4A-D, Table 3). This is true
348 regardless of the proportion of recruitment that goes to each area (Table 3) because the local
349 assumption estimates χ to be the same as the input proportion. Reference points scale up or down
350 yet remain identical between assumptions if steepness or natural mortality increase or decrease
351 by the same amount in each area (cases “No movement, low h ”, “No movement, high h ”, “No
352 movement, low M ”, “No movement, high M ”). However, the values of the reference points differ
353 spatially when the areas differ in selectivity- or weight-at-age, or steepness. Higher weight-at-age
354 in one area results in a higher F_{MSY} for that area if there is no movement between areas (case
355 “No movement; Higher WAA in area 2”). Reducing the ages at 50%- and 95%-selectivity in one
356 area also induces differences in F_{MSY} spatially, with a lower F_{MSY} in the area where fish are
357 exploited at a younger age (case “No movement, low area 1 age-at-selectivity). The values for
358 the reference points for combinations of steepness values among unlinked areas are identical to
359 the values obtained for any scenario using that area-specific steepness value, e.g., a scenario with
360 steepness of 0.6 in area 1 and 0.8 in area 2 produces the same reference point for area 1 as a
361 scenario with a steepness of 0.6 in both areas in the absence of movement (cases “No movement,
362 Combo h I” and “No movement, Combo h II”).

363 3.3 Comparison of MSY-based reference points *and depletion* between local and global
364 assumptions

365 Any degree of exchange (movement) among areas results in differences in reference points both
366 among assumptions and between areas, with the local assumption consistently leading to a higher
367 total MSY, with a lower corresponding total B_{MSY} , than the global assumption. In our simulation,
368 out-migration from one area at levels of 30% or greater result in the global and local assumptions
369 (cases “Area 2 as Sink I” and “Area 2 as Sink II”) to estimate F_{MSY} at zero for the source area.
370 The local assumption is less sensitive to increased movement, such that F_{MSY} remained zero in
371 the source area when out-migration was 30% or 40% for ages 9 and older (cases “Exchange
372 among Areas I” and “Exchange among Areas II”), whereas the global assumption estimated
373 F_{MSY} in the source area to be 0.13yr^{-1} at 40% unidirectional movement (case “Exchange among
374 Areas II”). Under a true source-sink dynamic (“Base Case” and cases “Area 2 as Sink I-IV”), the
375 local assumption again leads to higher values of F_{MSY} for the sink area than the global
376 assumption.

377 Reference points are the same between density-dependence assumptions when movement
378 rates are the same between areas 1 and 2 and 2 and 1 (cases “No movement” and case
379 “Symmetrical Movement”). The local assumption generally estimates F_{MSY} to be higher in the
380 sink area than the source area and higher than the F_{MSY} defined for the sink area under the global
381 assumption (cases “Area 2 as Sink I-IV”). The base-case scenario, which is characterized by a
382 true source-sink dynamic (with area 1 as the sink), exhibits this same response (Table 3; Fig 3E-
383 F). Reducing the age at which fish in area 1 are selected by the fishery in the base-case
384 assumptions results in a decrease in F_{MSY} for area 1 and an increase in F_{MSY} for area 2 under
385 both density-dependence assumptions, though this effect is much more pronounced for the global
386 assumption (case “Base Case + low area 1 age-at-selectivity”). This is an expected outcome
387 given the different assumptions’ notions of equilibrium recruitment across the system.

388 MSY-based reference points for the local assumption are sensitive to area-specific
389 exploitation and are generally less exploitative than the global approach of an area that is more
390 vulnerable due to movement or demographics. In general, scenarios that include true source-sink
391 dynamics and/or variation in steepness lead to the largest differences in reference points between
392 the two density-dependence assumptions. **In such scenarios, depletion corresponding to MSY
393 was uniformly higher (less depleted) in the sink area, which was the same result found in
394 Goethel and Berger (2017). The local assumption also resulted in lower depletion levels
395 corresponding to MSY than the global assumption for both areas.** The largest difference
396 was found for a source-sink scenario with 40% of area 1 adults migrating to area 2, for which the
397 global assumption produced a B_{MSY} that was 88% higher and MSY that was 20% lower than the
398 local assumption (case “Area 2 as Sink I”). In a source-sink scenario with low movement from
399 area 1 to area 2 (10%) these quantities were 18% greater and 8% lower, respectively (case “A2
400 as Sink IV”). B_{MSY} for scenarios with movement rates of 0.6 or higher did not vary more than 9%
401 between density-dependence assumptions, while the corresponding MSY was only at most 2%
402 higher for the local assumption (case “Exchange among Areas I-III”). When steepness varies
403 among areas, the local assumption estimates area-specific F_{MSY} values that scale inversely with
404 area-specific steepness, whereas F_{MSY} from the global assumption (which uses mean steepness)
405 is equivalent.

406 Under a “pessimistic” version of the base-case scenario, where survivorship is low (high
407 natural mortality) and steepness is reduced (case “Base Case + low h high M ”), both density-
408 dependence assumptions suggest an F_{MSY} of zero for the source area (area 2), while the F_{MSY} for

409 the sink area is nearly double for the local assumption (0.6yr^{-1} vs 0.28yr^{-1}). Conversely, under an
 410 “optimistic” version of the base-case scenario (low M and increased steepness; case “Base Case
 411 + high h low M ”) both density-dependence assumptions result in higher F_{MSY} for each area,
 412 though the total MSY of the global assumption is 90% of the local assumption.

413 The results in Table 4, which are subject to some numerical variation, seem to suggest that
 414 total F_{MSY} under the local assumption is conserved across scenarios with movement among
 415 areas. This can be illustrated more clearly by allowing movement to mimic selectivity (so
 416 movement within a source area appears like an additional fishery):
 417

$$\begin{aligned}
 N_{a+1}^1 &= N_a^1 e^{-M} e^{-S_a^1 F_1} e^{-S_a^1 Q} \\
 N_{a+1}^2 &= N_a^2 e^{-M} e^{-S_a^2 F_2} + N_a^1 e^{-M} e^{-S_a^1 F_1} (1 - e^{-S_a^1 Q})
 \end{aligned}
 \tag{11}$$

419 where Q is related to the proportion of individuals leaving area 1 for area 2 (area 2 is assumed to
 420 be a sink area). In this formulation, fishing occurs before movement. Table 4 shows that in a
 421 source-sink situation, with movement specified as in Equation 11, the total value of F_{MSY}
 422 estimated using the local recruitment assumption is conserved across values of Q ranging from
 423 0.1 to 0.9 (to the numerical accuracy of a discrete model). As in the main simulation results, the
 424 greater proportion of fishing mortality is directed towards the sink area, and there is a movement
 425 threshold (here about 40% transfer from area 1 to area 2) after which F_{MSY} in the source area is
 426 reduced to zero. This result validates the rule of thumb (A.E. Punt, pers. comm.) that movement
 427 can substitute for increased fishing mortality such that the F_{MSY} for a sink area is roughly twice
 428 that expected for the entire population when two populations are of the same size in the absence
 429 of fishing and the age-specific rates of movement have the same pattern as that of fishery
 430 selectivity.
 431

432 4. Discussion

433 4.1 Spatial stock assessment and fisheries management

434 Although the focus of this paper is on spatial stock assessments and hence the provision of
 435 spatially-appropriate management advice, there are ways to produce the scientific advice that
 436 may be needed to meet management mandates even when it is not possible to correctly represent
 437 spatial structure (Fig. 1). These methods include allocating catch limits among fished areas based
 438 on the relative abundance within sub-areas, or limiting effort outright by implementing Marine
 439 Protected Areas, marine reserves, or closed areas. For example, catch limits determined from
 440 assessments that do not explicitly include spatial dynamics or estimate spatial reference points
 441 may be allocated among sub-stocks, based on a regional indicator of biomass, as is done for
 442 Alaskan sablefish (*Anoplopoma fimbria*) (e.g., Hanselman et al., 2019). Bosley et al. (2019)
 443 demonstrated that allocating catch limits in this manner can best approximate MSY in the absence
 444 of a spatial model. Similarly, jack mackerel (*Trachurus murphyi*) is an ecologically and
 445 commercially important pelagic fish in the south Pacific Ocean found in three regions (Arcos et
 446 al., 2001; SPRFMO, 2019). The stock assessment process considers two hypotheses regarding
 447 stock structure (single or two separate stocks). Under the two-stock hypothesis, the assessment
 448 model is spatially-implicit because the fisheries operate in different areas and no mixing of the
 449 stocks is assumed to occur. Management advice is based on comparing the MSY values from the
 450 single-stock model with the sum of MSY from each area in the two-stock model. The most
 451 precautionary advice (i.e., the lowest of the two MSY) is adopted for use (SPRFMO, 2019).
 452 Likewise, data from a spatial assessment might be aggregated to estimate a reference point for

453 the whole stock (for example, reference points for rockfish on the US West Coast are calculated
454 by area, then aggregated to determine TACs; R. Methot, *pers. comm.*). Finally, spatial
455 management occurs in the case of marine protected areas and spatial closures, even when
456 reference points are not estimated considering spatial structure (Anderson et al., 2019).

457 Assessments that do not have a spatial dimension can be tested for robustness to spatial
458 population structure using a management strategy evaluation (MSE) with a spatial operating
459 model (e.g., Morse et al., 2020). Studies using MSE to test the performance of non-spatial
460 management for spatially structured populations have shown that more precautionary harvest
461 rules can reduce the risk of overfishing in cases where spatial information is unknown or
462 incorrectly specified. For example, in the case of Pacific herring (*Clupea pallasii*) in British
463 Columbia, which have spatially distinct spawning grounds, management strategies that minimize
464 exploitation risk can reduce the risk of overfishing when TACs are allocated based on a
465 spatially-aggregated model (Benson et al., 2015).

466 Nevertheless, it is often better to explicitly include spatial structure in assessments. This is
467 evident for small pelagic species, which exhibit both spatial structure and regime shift-like
468 behavior through time. For example, biomass estimates for spatially-structured forage fish
469 populations such as Pacific herring are biased when the assessment assumes a coarser spatial
470 scale than that of the metapopulation dynamics (Benson et al., 2015). Punt et al. (2018) found
471 that accounting for spatial structure improves hindcast performance and short-term forecasting
472 when there is post-recruitment dispersal among sub-stocks, but the positive impact of including
473 spatial structure was weaker when there was time-varying natural mortality (M). The
474 development of reference points for ecosystem-based fisheries management (EBFM) of the
475 Atlantic menhaden (*Brevoortia tyrannus*), another forage fish, has encountered similar
476 challenges (Buchheister et al., 2017). Like Pacific herring, the potential for spatial variation in
477 predation rates and temporal shifts in survival and productivity become confounded when spatial
478 dynamics and temporal variation are both important. These examples highlight the importance of
479 accounting for spatiotemporal interactions in assessments.

480 4.2 Including multiple sources of recruitment density-dependence in assessments

481 Our findings illustrate scenarios that lead to distinct MSY-based reference points between
482 recruitment density-dependence assumptions. These scenarios are characterized by movement
483 dynamics that accumulate biomass in one area (source-sink dynamics, namely those with strong
484 unidirectional movement), or those in which either one or both areas are vulnerable to local
485 depletion due to lower steepness, higher natural mortality, or a combination thereof. Generally,
486 the local recruitment assumption suggests a rightward shift of the yield curve, leading to higher
487 MSYs at lower system wide B_{MSY} (Fig. 6). This finding is consistent with the observation that
488 spatial variation in fishing intensity (for example, in MPAs) can produce a “yield premium”
489 above what would be gleaned by fishing the entire system at a single rate (Ralston et al., 2008).

490 **In the presence of movement, yield curves are generally shallower (particularly under the**
491 **local assumption) than in the absence of movement (see extent of yellow areas in Fig. 4). A**
492 **similar finding was suggested by Bosley et al. (2019), who suggested that a greater number**
493 **of area-specific F combinations could return similar yield goals when movement occurred**
494 **among populations. It is possible that various configurations of area-specific F could return**
495 **yields close to MSY, which has implications for spatial apportionment of fishing effort in**
496 **an applied management context.**

497 Greater survivorship (lower M) or the ability to capture younger fish from one area can
498 reduce the difference in reference points between assumptions in certain movement scenarios. In

499 the first case, lower M means greater overall population productivity in both areas, which
500 reduces the relative differences between assumptions caused by asymmetrical movement
501 dynamics. In the second, the fishery capitalizes on the biomass subsidy from the area with higher
502 age-at-50% capture. These examples represent cases where calculating reference points based on
503 local recruitment may not greatly change management advice. However, given the difficulty to
504 estimate M with high precision, and the possibility of time-varying fishery selectivity **or**
505 **apportionment**, it would be prudent to model the density dependence as faithfully as possible.
506 Moreover, it would be fruitful to explore true spawning migration, larval dispersal and/or natal
507 homing patterns when conducting assessments as these are factors suspected to render
508 populations vulnerable to local depletion (Kerr et al., 2017). Time-varying movement, or the
509 misalignment of management boundaries with biological regimes, presents a large hurdle for the
510 calculation of spatial reference points (Berger et al., 2020). Our present approaches assume that
511 equilibrium quantities are derived for a given movement and demographic regime; further
512 simulation work could illustrate the degree to which temporal variation could accentuate or
513 diminish discrepancies between areas. **It is possible that equilibrium frameworks such as**
514 **these will not adequately address such situations.**

515 Incorporating spatial reference points into fisheries management may fulfill some
516 management requirements, such as those of the Magnuson-Stevens Act (MSA) in the United
517 States and the objectives of RFMOs. For example, the MSA mandates taking account of
518 ecosystem considerations in fisheries management, which could include the consideration of
519 spatial processes (Miller et al., 2018). **It is possible that equilibrium methods as the basis for**
520 **reference point calculation may become untenable as models become increasingly complex**
521 **representations of space and time. For example, Reuchlin-Hugenhotz et al. (2015) suggest**
522 **that simple metrics of spatial distribution are strongly correlated with spawning stock**
523 **biomass, and could be used to predict rapid population declines in population of fish**
524 **species in the Northwest Atlantic. Incorporation of such spatio-temporal indices, which do**
525 **not require the assumption of equilibrium may meet the requirement to determine** stock
526 status relative to reference points that account for stock structure (MSA National Standard 3).
527 Similarly, management bodies that operate based on a precautionary approach to management
528 must consider spatial structure to limit the risk of local depletion and maintain stocks at levels
529 that sustain optimum yield.

530 *4.3 Conclusion*

531 Management goals may not be met if stock structure is mis-specified in some part of the
532 assessment process, which is particularly likely if the stock-recruitment relationship is local but
533 is assumed to be global. This study demonstrates how accounting for local density dependence
534 within spatial assessment models can be included in next generation stock assessment packages
535 by illustrating how assessments that include spatial components can be extended to provide
536 MSY-based reference points for local as well as global recruitment density-dependence
537 assumptions. Unfortunately, Stock Synthesis (as well as several other assessment software used
538 for tactical management, Table 1) does not accommodate area-specific stock-recruitment curves,
539 although spatial structure is considered in SS via the calculation of area-specific spawning
540 biomass. Consequently, differences in expected productivity between areas, and the subsequent
541 impact on yields, are not represented. Local recruitment is being considered for implementation
542 in future versions of Stock Synthesis (R. Methot, NOAA Fisheries, *pers. comm.*) and the
543 approaches of this paper provide the technical basis for the necessary further development.

544 **5. Acknowledgements**

545 MCS was supported by a fellowship from the James S. McDonnell Foundation (Grant #
546 220020561). All other authors besides RM were funded by the Cooperative Institute for Climate,
547 Ocean, and Ecosystem Studies (CICOES) under NOAA Cooperative agreement No.
548 NA15OAR4320063. This manuscript was greatly improved by the feedback of three anonymous
549 reviewers, as well as discussions with Dr. Clay Porch (the author of VPA-PRO2BOX).

550 **6. References**

- 551 Anderson, C.M., Krigbaum, M.J., Arostegui, M.C., Feddern, M.L., Koehn, J.Z., Kuriyama, P.T., Morrisett, C., Allen
552 Akselrud, C.I., Davis, M.J., Fiamengo, C., Fuller, A., Lee, Q., McElroy, K.N., Pons, M., Sanders, J., 2019. How
553 commercial fishing effort is managed. *Fish Fish.* 20, 268–285. <https://doi.org/10.1111/faf.12339>
- 554 Arcos, J.M., Oro, D., Sol, D., 2001. Competition between the yellow-legged gull *Larus cachinnans* and Audouin's
555 gull *Larus audouinii* associated with commercial fishing vessels: The influence of season and fishing fleet. *Mar.*
556 *Biol.* 139, 807–816. <https://doi.org/10.1007/s002270100651>
- 557 Begley, J., Howell, D., 2004. An overview of Gadget, the globally applicable area-disaggregated general ecosystem
558 toolbox. *ICES C* 1–15.
- 559 Benson, A.J., Cox, S.P., Cleary, J.S., 2015. Evaluating the conservation risks of aggregate harvest management in a
560 spatially-structured herring fishery. *Fish. Res.* 167, 101–113. <https://doi.org/10/gg4skd>
- 561 Berger, A.M., Goethel, D.R., Lynch, P.D., Quinn, T., Mormede, S., McKenzie, J., Dunn, A., 2017. Space oddity:
562 The mission for spatial integration. *Can. J. Fish. Aquat. Sci.* 74, 1698–1716. <https://doi.org/10/gg4q5g>
- 563 Berger, A.M., Deroba, J.J., Bosley, K.M., Goethel, D.R., Langseth, B.J., Schueller, A.M., Hanselman, D.H., 2020.
564 Incoherent dimensionality in fisheries management: consequences of misaligned stock assessment and
565 population boundaries. *ICES J. Mar. Sci.* 78, 155–171. <https://doi.org/10.1093/icesjms/fsaa203>
- 566 Beverton, R.J.H., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations, Fisheries Investigations Series 2:
567 Sea Fisheries. <https://doi.org/10.1007/BF00044132>
- 568 Booth, A.J., 2000. Incorporating the spatial component of fisheries data into stock assessment models 858–865.
569 <https://doi.org/10.1006/jmsc.2000.0816>
- 570 Bosley, K.M., Goethel, D.R., Berger, A.M., Deroba, J.J., Fenske, K.H., Hanselman, D.H., Langseth, B.J., Schueller,
571 A.M., 2019. Overcoming challenges of harvest quota allocation in spatially structured populations. *Fish. Res.*
572 220, 105344. <https://doi.org/10.1016/j.fishres.2019.105344>
- 573 Buchheister, A., Miller, T.J., Houde, E.D., 2017. Evaluating ecosystem-based reference points for Atlantic
574 menhaden. *Mar. Coast. Fish.* 9, 457–478. <https://doi.org/10/gg4sj9>
- 575 Bull, B., Francis, R.I.C.C., Dunn, A., McKenzie, A., Gilbert, D.J., Smith, M.H., Bian, R., Fu, D., 2012. CASAL
576 (C++ algorithmic stock assessment laboratory): CASAL User Manual v2.30-2012/03/21. Wellington, New
577 Zealand.
- 578 Caddy, J.F., Mahon, R., 1995. Reference points for fisheries management. FAO Fish. Tech. Pap. No 347. FAO,
579 Rome. 83pp.
- 580 Cadrin, S.X., Goethel, D.R., Morse, M.R., Fay, G., Kerr, L.A., 2019. “So, where do you come from?” The impact of
581 assumed spatial population structure on estimates of recruitment. *Fish. Res.* 217, 156–168.
582 <https://doi.org/10.1016/j.fishres.2018.11.030>
- 583 Cadrin, S.X., Maunder, M.N., Punt, A.E., 2020. Spatial Structure: Theory, estimation and application in stock
584 assessment models. *Fish. Res.* 229, 105608. <https://doi.org/10/ggv8sb>
- 585 Doonan, I., Large, K., Dunn, A., Rasmussen, S., Marsh, C., Mormede, S., 2016. Casal2: New Zealand's integrated
586 population modelling tool. *Fish. Res.* 183, 498–505. <https://doi.org/10.1016/j.fishres.2016.04.024>
- 587 Fay, G., Punt, A.E., Smith, A.D.M., 2011. Impacts of spatial uncertainty on performance of age structure-based
588 harvest strategies for blue eye trevalla (*Hyperoglyphe antarctica*). *Fish. Res.* 110, 391–407.
589 <https://doi.org/10.1016/j.fishres.2011.04.015>
- 590 Field, J.C., Punt, A.E., Methot, R.D., Thomson, C.J., 2006. Does MPA mean “Major Problem for Assessments”?
591 Considering the consequences of place-based management systems. *Fish Fish.* 7, 284–302.
592 <https://doi.org/10.1111/j.1467-2979.2006.00226.x>
- 593 Fournier, D.A., Hampton, J., Sibert, J.R., 1998. MULTIFAN-CL: A length-based, age-structured model for fisheries
594 stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Can. J. Fish. Aquat. Sci.* 55,
595 2105–2116. <https://doi.org/10.1139/f98-100>
- 596 Francis, R.I.C.C., McKenzie, J.R., 2015. Assessment of the SNA 1 stocks in 2013. New Zealand Fisheries

597 Assessment Report 2015/76. 82 pp.

598 Goethel, D.R., Berger, A.M., 2017. Accounting for spatial complexities in the calculation of biological reference
599 points: Effects of misdiagnosing population structure for stock status indicators. *Can. J. Fish. Aquat. Sci.* 74,
600 1878–1894. <https://doi.org/10.1139/cjfas-2016-0290>

601 Hanselman, D.H., Rodgveller, C.J., Fenske, K.H., Shotwell, S.K., Echave, K.B., Malecha, P.W., Lunsford, C.R.,
602 2019. Assessment of the sablefish stock in Alaska, Stock Assessment and Fishery Evaluation Report for the
603 Groundfish Resources of the Gulf of Alaska. 605 W 4th Avenue, Suite 306, Anchorage, AK 99510.
604 <https://apps-afsc.fisheries.noaa.gov/refm/docs/2019/sablefish.pdf>

605 Kapur, M.R., Franklin, E.C., 2017. Simulating future climate impacts on tropical fisheries: Are contemporary spatial
606 fishery management strategies sufficient? *Can. J. Fish. Aquat. Sci.* 74, 1974–1989. <https://doi.org/10.1139/cjfas-2016-0200>

608 Kerr, L.A., Hintzen, N.T., Cadrin, S.X., Clausen, L.W., Dickey-Collas, M., Goethel, D.R., Hatfield, E.M.C., Kritzer,
609 J.P., Nash, R.D.M., 2017. Lessons learned from practical approaches to reconcile mismatches between
610 biological population structure and stock units of marine fish. *ICES J. Mar. Sci.* 74, 1708–1722.
611 <https://doi.org/10.1093/icesjms/fsw188>

612 Mangel, M., MacCall, A.D., Brodziak, J., Dick, E.J., Forrest, R.E., Pourzand, R., Ralston, S., 2013. A perspective on
613 steepness, reference points, and stock assessment. *Can. J. Fish. Aquat. Sci.* <https://doi.org/10.1139/cjfas-2012-0372>

615 McGarvey, R., Linnane, A., Matthews, J.M., Jones, A., 2017. Decision rules for quota setting to support spatial
616 management in a lobster (*Jasus edwardsii*) fishery. *ICES J. Mar. Sci.* 74, 588–597. <https://doi.org/10/gg5wxn>

617 McGilliard, C.R., Punt, A.E., Methot, R.D., Hilborn, R., 2015. Accounting for marine reserves using spatial stock
618 assessments. *Can. J. Fish. Aquat. Sci.* 72, 262–280. <https://doi.org/10/gg5wxm>

619 Methot, R.D., Wetzel, C.R., 2013. Stock synthesis: A biological and statistical framework for fish stock assessment
620 and fishery management. *Fish. Res.* 142, 86–99. <https://doi.org/10.1016/j.fishres.2012.10.012>

621 Miller, Thomas J., et al. "Scientific Considerations Informing Magnuson–Stevens Fishery Conservation and
622 Management Act Reauthorization: AFS Special Committee." *Fisheries* 43.11 (2018): 533-541.

623 Morse, M.R., Kerr, L.A., Galuardi, B., Cadrin, S.X., 2020. Performance of stock assessments for mixed-population
624 fisheries: the illustrative case of Atlantic bluefin tuna. *ICES J. Mar. Sci.* <https://doi.org/10/gg44r8>

625 National Research Council (NRC), 1994. An Assessment of Atlantic Bluefin Tuna., The National Academies Press.
626 Washington, DC. <https://doi.org/https://doi.org/10.17226/4801>

627 Okamoto, D.K., Hessing-Lewis, M., Samhoury, J.F., Shelton, A.O., Stier, A., Levin, P.S., Salomon, A.K., 2020.
628 Spatial variation in exploited metapopulations obscures risk of collapse. *Ecol. Appl.* 30, 1–16.
629 <https://doi.org/10.1002/eap.2051>

630 Porch, C., 2018. PRO-2BOX 3.0 User Guide (No. NMFS-SEFSC-708).
631 <https://doi.org/10.13140/RG.2.2.12258.17604>

632 Privitera-Johnson, K.M., Punt, A.E., 2020. A review of approaches to quantifying uncertainty in fisheries stock
633 assessments. *Fish. Res.* 226, 105503. <https://doi.org/10.1016/j.fishres.2020.105503>

634 Punt, A.E., Haddon, M., Little, L.R., Tuck, G.N., 2017. The effect of marine closures on a feedback control
635 management strategy used in a spatially aggregated stock assessment: a case study based on pink ling in
636 Australia. *Can. J. Fish. Aquat. Sci.* 74, 1960–1973. <https://doi.org/10.1139/cjfas-2016-0017>

637 Punt, A.E., Okamoto, D.K., MacCall, A.D., Shelton, A.O., Armitage, D.R., Cleary, J.S., Davies, I.P., Dressel, S.C.,
638 Francis, T.B., Levin, P.S., Jones, R.R., Kitka, H., Lee, L.C., McIsaac, J.A., Poe, M.R., Reifensstuhl, S., Silver,
639 J.J., Schmidt, J.O., Thornton, T.F., Voss, R., Woodruff, J., 2018. When are estimates of spawning stock biomass
640 for small pelagic fishes improved by taking spatial structure into account? *Fish. Res.* 206, 65-78.
641 <https://doi.org/10.1016/j.fishres.2018.04.017>

642 Punt, A.E., 2019a. Spatial stock assessment methods : A viewpoint on current issues and assumptions. *Fish. Res.*
643 213, 132–143. <https://doi.org/10.1016/j.fishres.2019.01.014>

644 Punt, A.E., 2019b. Modelling recruitment in a spatial context: A review of current approaches, simulation evaluation
645 of options, and suggestions for best practices. *Fish. Res.* 217, 140–155.
646 <https://doi.org/10.1016/j.fishres.2017.08.021>

647 Punt, A.E., Dunn, A., Elvarsson, B. Þór, Hampton, J., Hoyle, S.D., Maunder, M.N., Methot, R.D., Nielsen, A., 2020.
648 Essential features of the next-generation integrated fisheries stock assessment package: A perspective. *Fish.*
649 *Res.* 229, 105617. <https://doi.org/10.1016/j.fishres.2020.105617>

650 R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical
651 Computing, Vienna, Austria. URL <https://www.R-project.org/>

652 Ralston, S., O'Farrell, M. R., 2008. Spatial variation in fishing intensity and its effect on yield. *Can. J. Fish. Aquat.*
653 *Sci.* 65, 588-599. <https://doi.org/10.1139/f07-174>
654 Reuchlin-Hugenholtz, E., Shackell, N.L., Hutchings, J.A., 2015. The potential for spatial distribution indices to
655 signal thresholds in marine fish biomass. *PLoS One* 10, 1–22. <https://doi.org/10.1371/journal.pone.0120500>
656 Sampson, D.B., Scott, R.D., 2011. A spatial model for fishery age-selection at the population level. *Can. J. Fish.*
657 *Aquat. Sci.* 68, 1077–1086. <https://doi.org/10.1139/F2011-044>
658 SPRFMO, 2019. 7th Scientific Committee meeting report. Wellington, New Zealand. 98 pp.
659 Schaefer, M.B., 1968. Methods of Estimating Effects of Fishing on Fish Populations. *Trans. Am. Fish. Soc.* 97,
660 231–241. [https://doi.org/10.1577/1548-8659\(1968\)97\[231:moeeof\]2.0.co;2](https://doi.org/10.1577/1548-8659(1968)97[231:moeeof]2.0.co;2)
661 Ying, Y., Chen, Y., Lin, L., Gao, T., 2011. Risks of ignoring fish population spatial structure in fisheries
662 management. *Can. J. Fish. Aquat. Sci.* <https://doi.org/10.1139/F2011-116>

7. Tables

Table 1. Commonly used generic stock assessment frameworks that include spatial structure and the F -based reference points they estimate.

| Model | Primary citation(s) | Spatial structure | Movement Dynamics | Other features (multispecies, ecosystem, etc.) | Reference points | Spatial reference points |
|--|---|-----------------------------------|---|--|---|---|
| Globally applicable Area-Disaggregated General Ecosystem Toolbox (GADGET) | Begley and Howell (2004) | Multiple areas linked by movement | Movement between stocks based on age and maturity status | Multi-species and multi-stock | F_{MAX} | None available |
| Multiple Length Frequency Analysis with Catch-at-Length (MULTIFAN-CL) | (Fournier et al., 1998) | Multiple areas linked by movement | Limited movement, diffusive | Multi-stock | F_{MSY} | Area level, groups of areas or the whole model domain |
| Stock Synthesis (SS) | (Methot and Wetzel, 2013) | Multiple areas linked by movement | Age-specific | Single-stock | $F_{MAX}, F_{MSY}, F_{X\%}$ | Assume global recruitment |
| C++ Algorithmic Stock Assessment Laboratory (CASAL/Casal2) | Bull et al. (2012) & Doonan et al. (2016) | Multiple areas linked by movement | Movement dynamics allow natal homing | Multi-stock | <i>CASAL</i> : $F_{MSY}, F_{X\%}$ <i>Casal2</i> : B_0 (no MSY-based reference points) | Sum of B_0 across areas, or allocate to areas using pre-defined fraction |
| Dual Zone VPA Model (VPA-2BOX) | Porch (2018) | Two stocks | Users choose between two types of box-transfer models to simulate intermixing between the two stocks: diffusion and overlap | Two stocks | $F_{MSY}, F_{X\%}$ | Stock specific; in overlap case recruits are tracked based upon spawning area |

Table 2. Specifications for the scenarios. A dash indicates that the specification matches that of the base-case scenario.

| Scenario | Proportion of recruitment to area 1 | Natural mortality (yr ⁻¹) | Weight-at-Age | Movement | Selectivity | Steepness |
|--|-------------------------------------|---------------------------------------|---------------|----------|-------------|-----------|
| Base case (Area 1 as sink) | 0.5 | 0.15 | Fig. 2K | Fig. 2A | Fig. 2L | 0.7, 0.7 |
| No movement $\chi^1 = 0.5$ | - | - | - | Fig. 2B | - | - |
| No movement $\chi^1 = 0.6$ | 0.6 | - | - | Fig. 2B | - | - |
| No movement $\chi^1 = 0.7$ | 0.7 | - | - | Fig. 2B | - | - |
| No movement $\chi^1 = 0.8$ | 0.8 | - | - | Fig. 2B | - | - |
| No movement $\chi^1 = 0.9$ | 0.9 | - | - | Fig. 2B | - | - |
| No movement, Higher WAA in area 2 | - | - | Fig. 3A | Fig. 2B | - | - |
| No movement, low area 1 age-at-selectivity | - | - | - | Fig. 2B | Fig. 3B | - |
| No movement, low h | - | - | - | Fig. 2B | - | 0.6, 0.6 |
| No movement, high h | - | - | - | Fig. 2B | - | 0.8, 0.8 |
| No movement, combo h I | - | - | - | Fig. 2B | - | 0.6, 0.8 |
| No movement, combo h II | - | - | - | Fig. 2B | - | 0.8, 0.6 |
| No movement, low M | - | 0.13 | - | Fig. 2B | - | - |
| No movement, high M | - | 0.17 | - | Fig. 2B | - | - |
| Exchange among Areas I | - | 0.17 | - | Fig. 2C | - | - |
| Exchange among Areas II | - | 0.17 | - | Fig. 2D | - | - |
| Exchange among Areas III | - | 0.17 | - | Fig. 2E | - | - |
| Symmetrical Movement | - | - | - | Fig. 2F | - | - |
| Area 2 as Sink I | - | - | - | Fig. 2G | - | - |
| Area 2 as Sink II | - | - | - | Fig. 2H | - | - |
| Area 2 as Sink III | - | - | - | Fig. 2I | - | - |
| Area 2 as Sink IV | - | - | - | Fig. 2J | - | - |
| Base Case + low area 1 age-at-selectivity | - | - | - | - | Fig. 3B | - |
| Base Case + high area 1 age-at-selectivity | - | - | - | - | Fig. 3C | - |
| Base Case + combo h | - | - | - | - | Fig. 2L | 0.8, 0.6 |
| Base Case + low h high M | - | 0.17 | - | - | Fig. 2L | 0.6, 0.6 |
| Base Case + high h low M | - | 0.13 | - | - | Fig. 2L | 0.8, 0.8 |

Table 3. Results for the scenarios and values for reference points for each assumption. The values for F_{MSY} are the fully-selected fishing mortality rates by area, the MSY ratio is MSY for global recruitment relative to that for local recruitment, and B_{MSY}/B_0 is total spawning biomass at MSY relative to unfished spawning biomass. A dash indicates that the specification matches that of the base-case scenario.

| Scenario | F_{MSY} (area 1, area 2) yr ⁻¹ | | MSY | B_{MSY}/B_0 (area 1, area 2) | |
|--|---|------------|----------------------|--------------------------------|------------|
| | Global | Local | Ratio (global/local) | Global | Local |
| Base case (Area 1 as sink) | 0.33, 0.03 | 0.57, 0.02 | 0.85 | 0.26, 0.26 | 0.26, 0.26 |
| No movement $\chi^1 = 0.5$ | 0.27, 0.27 | 0.27, 0.27 | 1 | 0.26, 0.26 | 0.26, 0.26 |
| No movement $\chi^1 = 0.6$ | 0.27, 0.27 | 0.27, 0.27 | 1 | 0.26, 0.26 | 0.27, 0.27 |
| No movement $\chi^1 = 0.7$ | 0.27, 0.27 | 0.27, 0.27 | 1 | 0.26, 0.26 | 0.27, 0.26 |
| No movement $\chi^1 = 0.8$ | 0.27, 0.27 | 0.27, 0.27 | 1 | 0.26, 0.26 | 0.26, 0.27 |
| No movement $\chi^1 = 0.9$ | 0.27, 0.27 | 0.27, 0.27 | 1 | 0.33, 0.20 | 0.26, 0.27 |
| No movement, Higher WAA in area 2 | 0.19, 0.36 | 0.25, 0.27 | 1 | 0.42, 0.13 | 0.30, 0.24 |
| No movement, low area 1 age-at-selectivity | 0.16, 0.48 | 0.23, 0.28 | 1.01 | 0.30, 0.30 | 0.30, 0.30 |
| No movement, low h | 0.20, 0.20 | 0.20, 0.20 | 1 | 0.22, 0.22 | 0.22, 0.22 |
| No movement, high h | 0.39, 0.39 | 0.39, 0.39 | 1 | 0.21, 0.3 | 0.32, 0.21 |
| No movement, combo h I | 0.27, 0.27 | 0.2, 0.39 | 1 | 0.3, 0.21 | 0.21, 0.32 |
| No movement, combo h II | 0.27, 0.27 | 0.39, 0.20 | 1 | 0.27, 0.27 | 0.27, 0.27 |
| No movement, low M | 0.23, 0.23 | 0.23, 0.23 | 1 | 0.26, 0.26 | 0.26, 0.26 |
| No movement, high M | 0.33, 0.33 | 0.33, 0.33 | 1 | 0.39, 0.14 | 0.37, 0.12 |
| Exchange among Areas I | 0.45, 0 | 0.50, 0 | 0.97 | 0.36, 0.17 | 0.32, 0.17 |
| Exchange among Areas II | 0.42, 0.13 | 0.59, 0 | 0.97 | 0.32, 0.21 | 0.28, 0.22 |
| Exchange among Areas III | 0.39, 0.24 | 0.55, 0.11 | 0.98 | 0.26, 0.26 | 0.26, 0.26 |
| Symmetrical Movement | 0.27, 0.27 | 0.27, 0.27 | 1 | 0.02, 0.53 | 0.02, 0.33 |
| Area 2 as Sink I | 0, 0.29 | 0, 0.59 | 0.8 | 0.05, 0.5 | 0.04, 0.33 |
| Area 2 as Sink II | 0, 0.30 | 0, 0.59 | 0.81 | 0.11, 0.44 | 0.10, 0.32 |
| Area 2 as Sink III | 0.03, 0.33 | 0.02, 0.57 | 0.85 | 0.18, 0.36 | 0.15, 0.32 |
| Area 2 as Sink IV | 0.17, 0.32 | 0.17, 0.43 | 0.92 | 0.44, 0.11 | 0.32, 0.10 |
| Base Case + low area 1 age-at-selectivity | 0.23, 0.28 | 0.42, 0.04 | 0.86 | 0.51, 0.06 | 0.38, 0.08 |
| Base Case + high area 1 age-at-selectivity | 0.42, 0 | 0.78, 0.01 | 0.84 | 0.39, 0.15 | 0.27, 0.12 |
| Base Case + combo h | 0.33, 0.03 | 0.73, 0 | 0.78 | 0.50, 0.11 | 0.28, 0.10 |
| Base Case + low h high M | 0.28, 0 | 0.60, 0 | 0.78 | 0.52, 0.13 | 0.33, 0.10 |
| Base Case + high h low M | 0.38, 0.07 | 0.55, 0.08 | 0.90 | 0.37, 0.09 | 0.30, 0.08 |

Table 4. Results for vignette scenarios, in which the age-specific pattern of movement matches selectivity (Equation 11). The proportion of recruitment to area 1, natural mortality, selectivity and stock-recruitment steepness are as for the base-case scenario (Table 2). Q^1 is the proportion of individuals of all ages which move out of area 1 for area 2, where they remain.

| Scenario | Proportion movement out of area 1 and area 2 | F_{MSY} (area 1, area 2) yr ⁻¹ | | | MSY ratio (global/local) | B_{MSY}/B_0 | |
|-------------------------------|--|---|------------|--|--------------------------|---------------|-------|
| | | Global | Local | Total local F_{MSY} yr ⁻¹ | | Global | Local |
| Vignette $Q^1 = 0.10$ | 0.1, 0 | 0.22, 0.32 | 0.3, 0.29 | 0.59 | 0.97 | 0.26 | 0.25 |
| Vignette $Q^1 = 0.20$ | 0.2, 0 | 0.15, 0.37 | 0.28, 0.33 | 0.61 | 0.94 | 0.27 | 0.24 |
| Vignette $Q^1 = 0.25$ | 0.25, 0 | 0.11, 0.39 | 0.28, 0.35 | 0.63 | 0.93 | 0.27 | 0.24 |
| Vignette $Q^1 = 0.30$ | 0.3, 0 | 0.08, 0.42 | 0.26, 0.37 | 0.63 | 0.92 | 0.27 | 0.23 |
| Vignette $Q^1 = 0.35$ | 0.25, 0 | 0.04, 0.45 | 0.24, 0.39 | 0.63 | 0.91 | 0.27 | 0.23 |
| Vignette $Q^1 = 0.40$ | 0.4, 0 | 0, 0.47 | 0.22, 0.41 | 0.63 | 0.90 | 0.27 | 0.22 |
| Vignette $Q^1 = 0.50$ | 0.5, 0 | 0, 0.43 | 0, 0.59 | 0.59 | 0.90 | 0.27 | 0.24 |
| Vignette $Q^1 = 0.60$ | 0.6, 0 | 0, 0.4 | 0, 0.59 | 0.59 | 0.88 | 0.27 | 0.22 |
| Vignette $Q^1 = 0.70$ | 0.7, 0 | 0, 0.38 | 0, 0.6 | 0.60 | 0.87 | 0.27 | 0.21 |
| Vignette $Q^1 = 0.80$ | 0.8, 0 | 0, 0.37 | 0, 0.59 | 0.59 | 0.86 | 0.27 | 0.20 |
| Vignette $Q^1 = 0.90$ | 0.9, 0 | 0, 0.36 | 0, 0.6 | 0.60 | 0.86 | 0.27 | 0.20 |
| Vignette no movement | 0, 0 | 0.27, 0.27 | 0.27, 0.27 | 0.54 | 1.00 | 0.26 | 0.27 |
| Vignette symmetrical movement | 0.3, 0.3 | 0.27, 0.27 | 0.27, 0.27 | 0.54 | 1.00 | 0.26 | 0.27 |

8. Figures

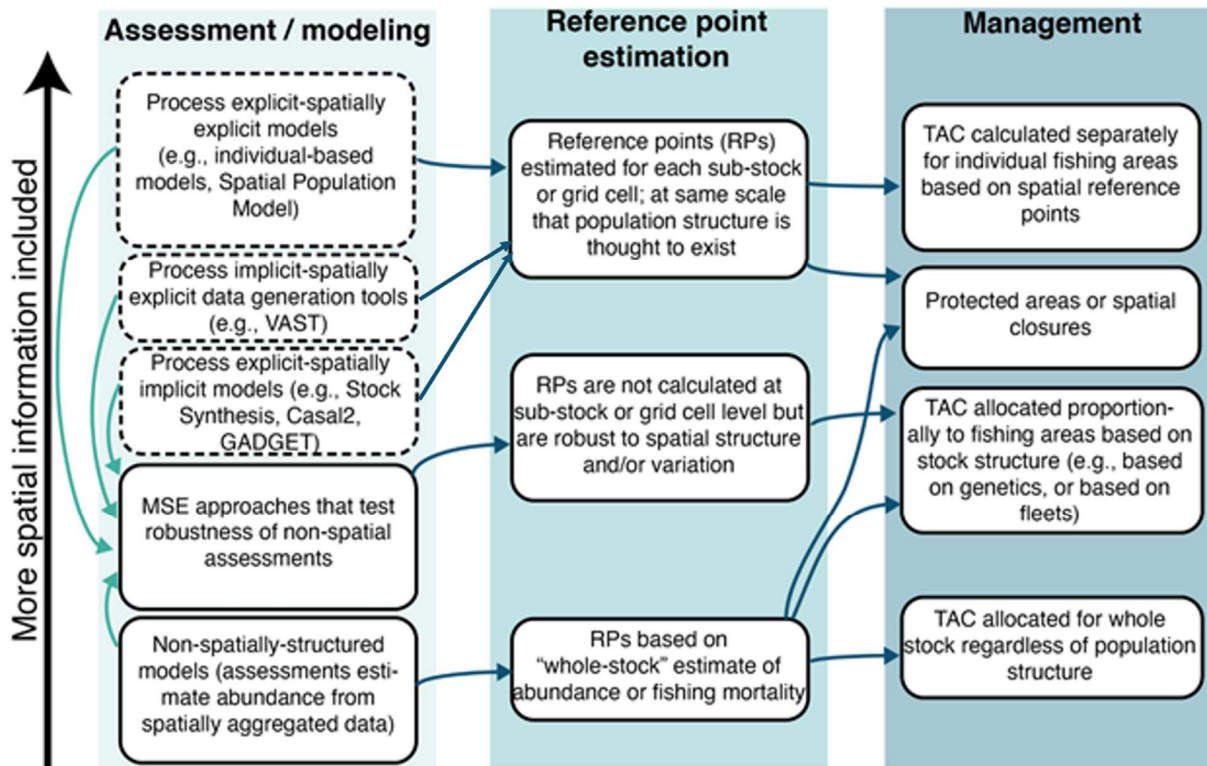


Figure 1. A schematic of how spatial information is used to estimate reference points for management and when implementing spatial management. Arrows indicate pathways through which information is used in science and management. Lighter arrows indicate where spatial models and data generation tools are used to improve management science, and dark arrows indicate ways that spatial information is or is not turned into spatial management practices. Spatially structured models and data-generation tools (dashed lines) consider differences in population dynamics among areas. See the Online Supplementary Material for a discussion of the distinction between process- and spatially-explicit vs. implicit models.

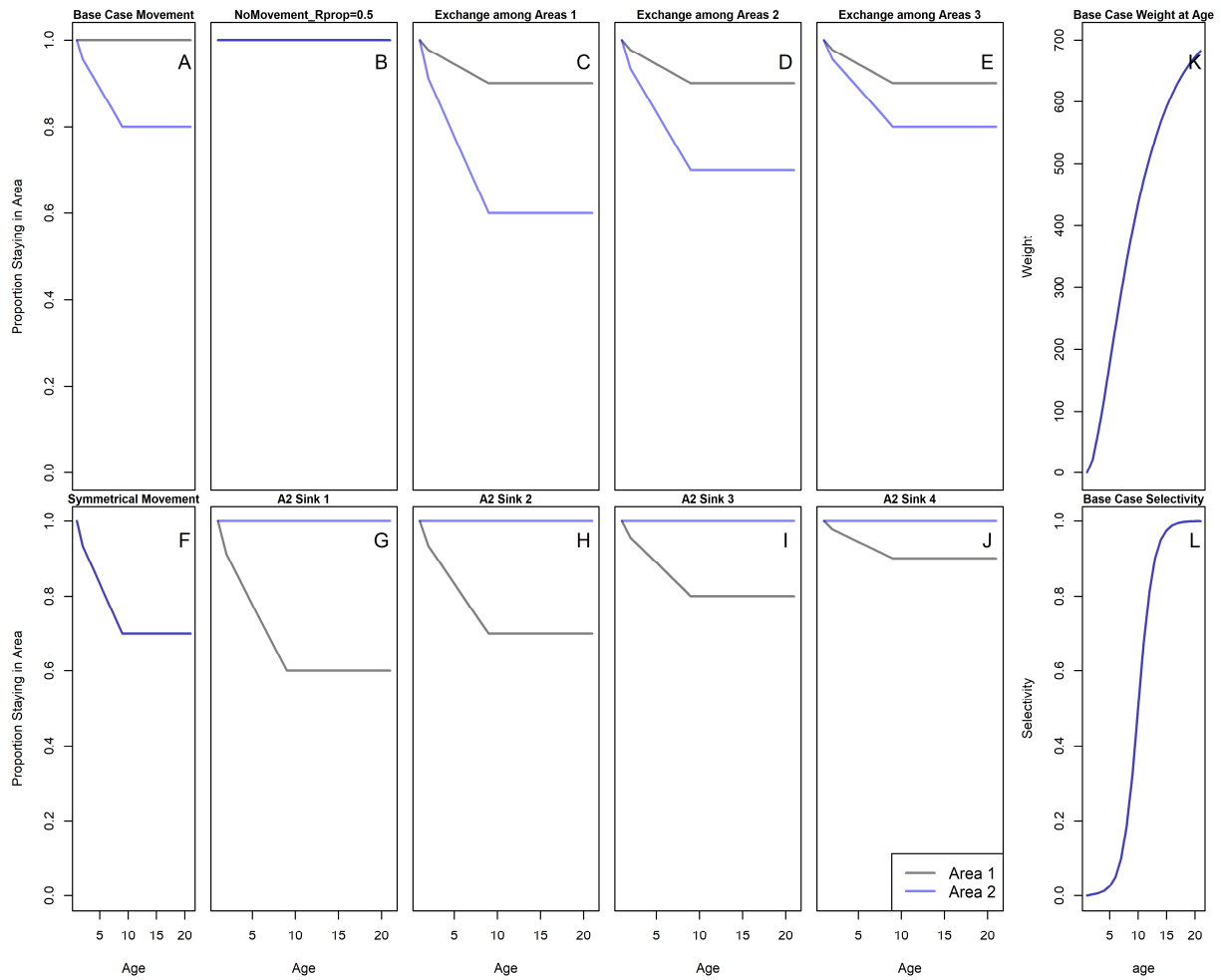


Figure 2. Age-specific specifications for the scenarios. A-J) Movement at age. Values indicate the proportion of individuals that remain in each area (colors) at each age. K) Weight-at-age for the base-case scenario, which is identical between areas. E-G) Fishery selectivity-at age for the base-case scenario, which is identical between areas. All values are identical for ages 20+.

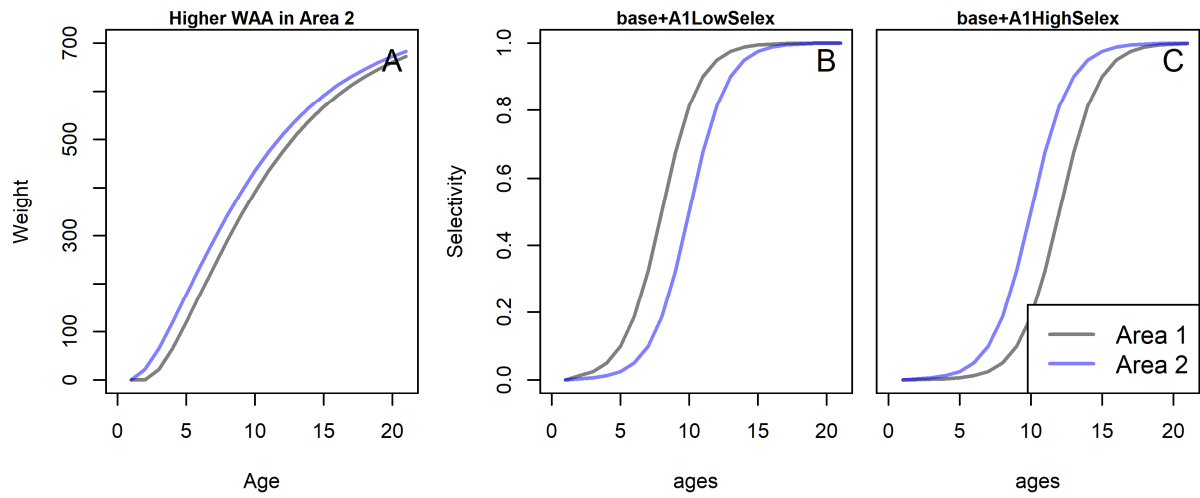


Figure 3. A) Weight-at-age for the “Higher Weight at Age in area 2” scenario. B) Fishery selectivity-at-age by area for scenarios that include lower selectivity at age in area 1. C) Fishery selectivity-at-age by area for scenarios that include higher selectivity at age in area 1. All values are identical for ages 20+.

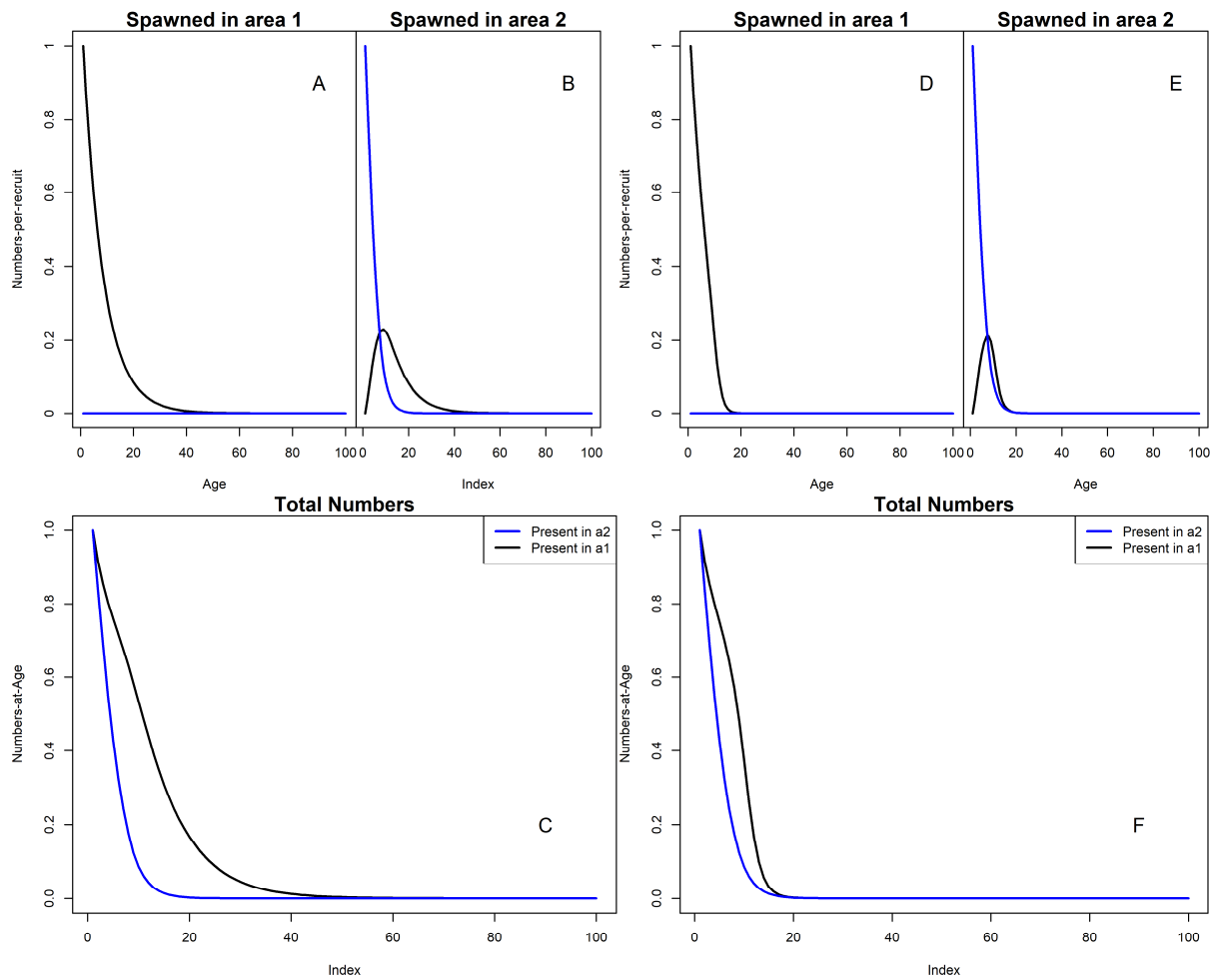


Figure 4. Equilibrium numbers-per-recruit (top row) and -at-age (bottom row) based on spawning origin for the base-case scenario (area 1 as sink) under $F=0$ (A-C) and $F=F_{MSY}$ (D-F). Figures A and D indicate the fate in numbers-at-age of a single recruit spawned in area 1; Figures B and E indicates the same for a recruit spawned in area 2; Figures C and F indicate the total numbers-per-recruit in each area under two different values for F . In each plot, blue lines represent individuals found in area 2 and black lines indicate those found in area 1.

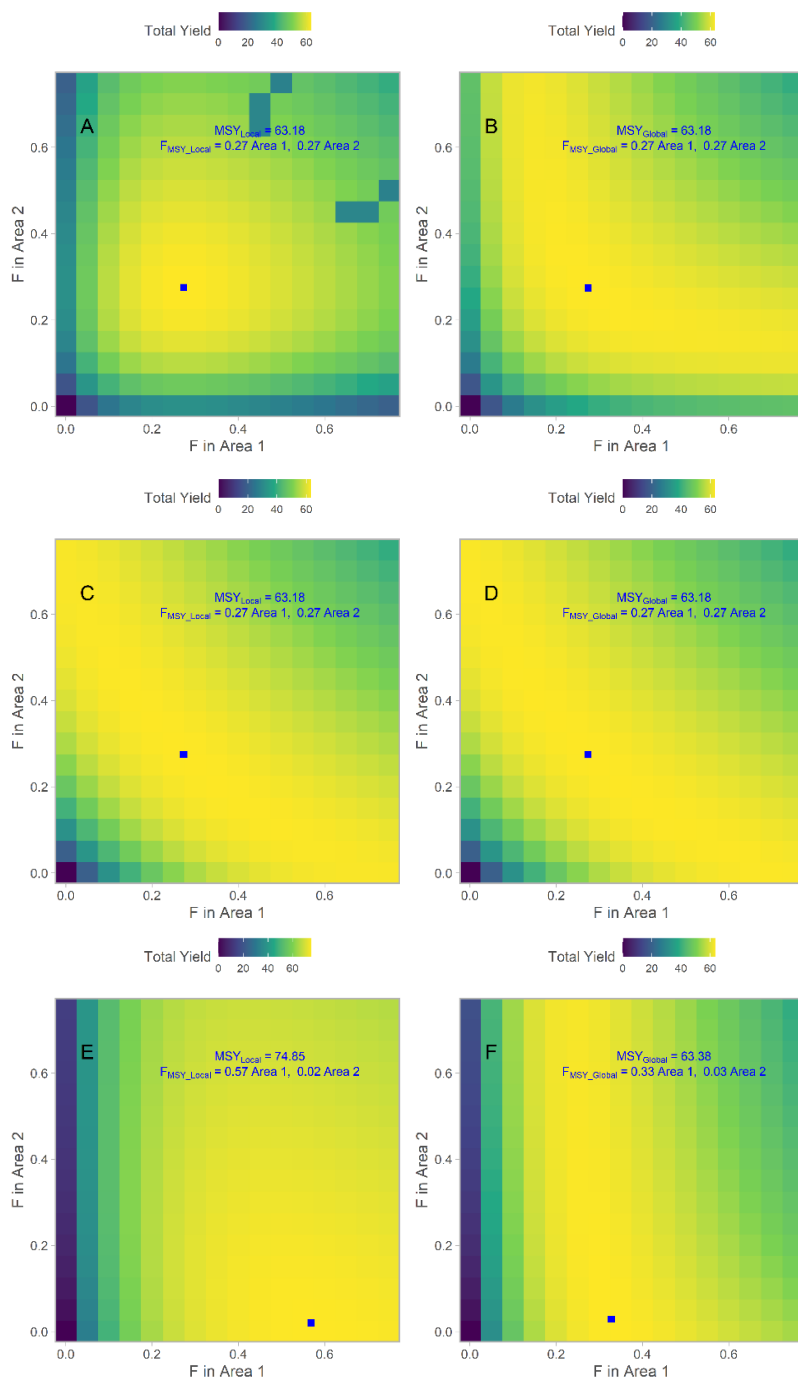


Figure 5. Total yield as a function of fishing mortality (yr^{-1}) by area for the local and global assumptions (left and right columns) for three scenarios: A-B) the first no-movement case, with χ^1 set to 0.5; C-D) a movement with symmetric exchange among areas, and E-F) the base-case scenario. The colors denote total yield and the solid square indicates F_{MSY} .

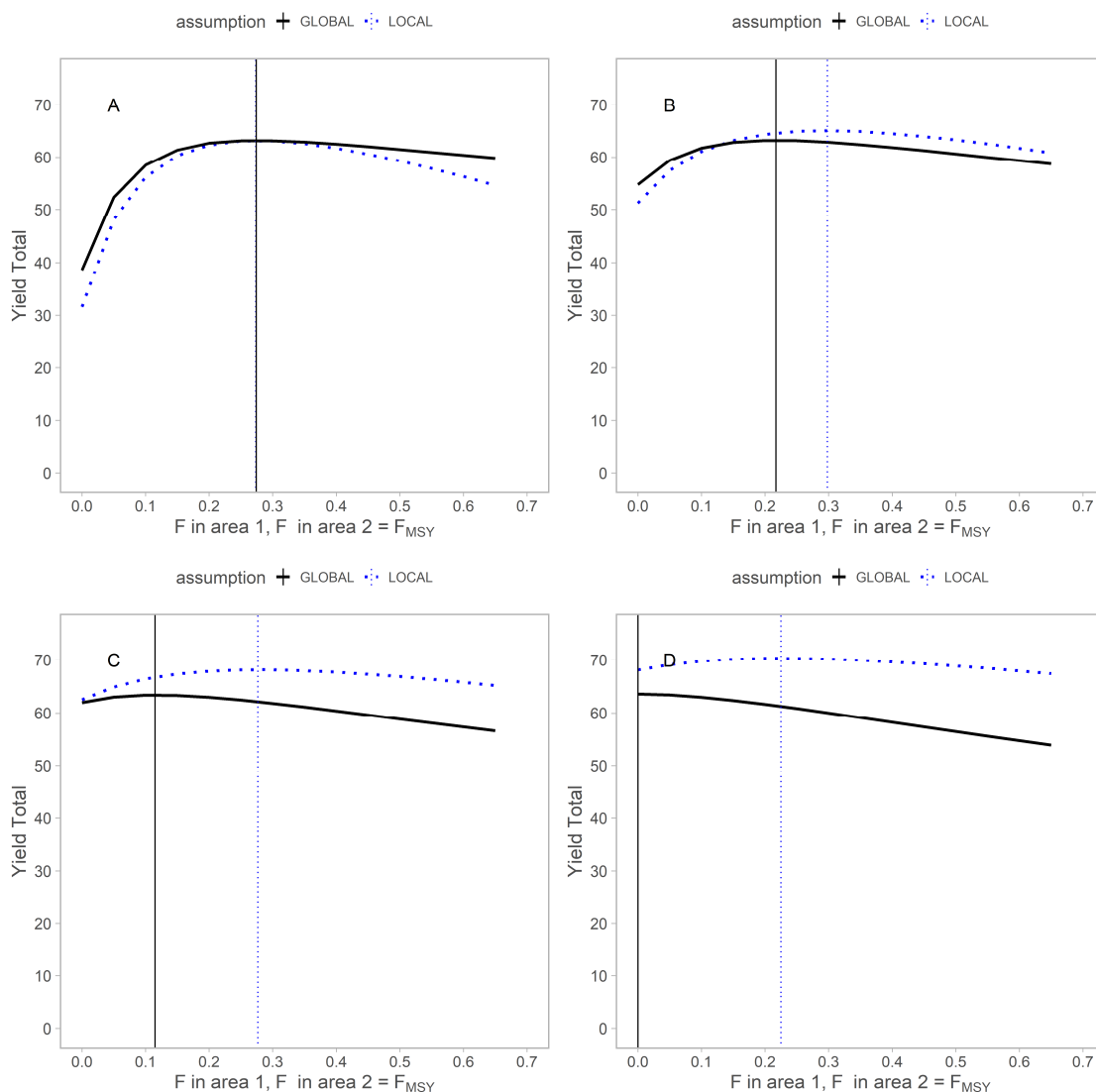


Figure 6. Illustration of the rightward shift of the yield curve due local density dependence for four scenarios (Table 2): A) No movement, input $\chi = 0.5$, B) C) D). In all figures, the x-axis represents various values of F (yr^{-1}) for area 1. Yield curves are generated by fixing F in area 2 to F_{MSY} for area 2 for the scenario in question. The vertical lines indicate the location of F_{MSY} in area 1. Blue dotted lines = local recruitment assumption, black solid lines = global recruitment assumption.