Title: Spatial variation in exploited metapopulations obscures risk of collapse

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Running Head: Cryptic collapses in metapopulations

Author contributions:

DKO designed, built and conducted analyses. AS conducted the home-range literature review. DKO and AKS wrote the initial manuscript draft. DKO, MHL, JFS, AOS, AS, PSL, and AKS initiated the research focus, refined analyses and contributed to revisions.

1

1   **Abstract**

2   Unanticipated declines among exploited species have commonly occurred despite harvests that

3   appeared sustainable prior to collapse. This is particularly true in the oceans where spatial scales

4   of management are often mismatched with spatially complex metapopulations. We explore

5   causes, consequences and potential solutions for spatial mismatches in harvested

6   metapopulations in three ways. First, we generate novel theory illustrating when and how

7   harvesting metapopulations increases spatial variability and in turn masks local scale volatility.

8   Second, we illustrate why spatial variability in harvested metapopulations leads to negative

9   consequences using an empirical example of a Pacific herring metapopulation. Finally, we

10 construct a numerical management strategy evaluation model to identify and highlight potential

11 solutions for mismatches in spatial scale and spatial variability. Our results highlight that spatial

12 complexity can promote stability at large scales, however ignoring spatial complexity produces

13 cryptic and negative consequences for people and animals that interact with resources at small

14 scales. Harvesting metapopulations magnifies spatial variability, which creates discrepancies

15 between regional and local trends while increasing risk of local population collapses. Such

16 effects asymmetrically impact locally constrained fishers and predators, which are more exposed

17 to risks of localized collapses. Importantly, we show that dynamically optimizing harvest can

18 minimize local risk without sacrificing yield. Thus, multiple nested scales of management may

19 be necessary to avoid cryptic collapses in metapopulations and the ensuing ecological, social and

20 economic consequences.

21

22 **Keywords:** Sustainable fisheries, Metapopulation, Population Dynamics, Conservation, Natural

23 Resource Management

24 **Introduction**

25 Mismatches in spatial scale create pervasive problems in ecology and natural resource

26 management (Cumming et al. 2006, Cope and Punt 2011). This problem occurs in part because

27 the spatial extent of management or conservation units is often defined by history, jurisdictional,

28 or institutional criteria rather than the scale of social and ecological processes at play (Levin

29 1992, Chesson 1998, Cumming et al. 2006). Such choices concerning the scale of management

30 can result in spatial mismatches, where feedbacks controlling interactions among groups occur at

31 different scales. In managed ecosystems like forestry and fisheries, mismatches may occur when

32 harvest recommendations are based on trends in large-scale abundance without accounting for

33 localized collapses (Johnson et al. 2012) or spatial variation in population structure and harvest

34 rates (Cope and Punt 2011). Yet these spatially isolated collapses can have far-reaching

35 consequences when the species play an indispensable role in local social-ecological systems,

36 including human communities with limited capacity to forage over wide geographic scales.

37 Empirical identification of appropriate spatial scales of management remains difficult for

38 spatially structured populations, but can be a pre-requisite for diagnosing and reconciling

39 challenges that spatial mismatches impose on the sustainable and equitable use of natural

40 resources.

41

42 In metapopulations – plant or animal populations connected through dispersal – it is well

43 established that the dynamics of individual populations can differ substantially from the

44 aggregate metapopulation (Chesson 1998, Mangel and Levin 2005, Melbourne and Chesson

45 2006). A combination of movement, shared climate drivers, and compensatory processes

46 determine whether dynamics of individual populations reflect the dynamics of the aggregate

47   metapopulation (Kendall et al. 2000). Consideration of metapopulation structure has improved

48   the management of the spotted owl (*Strix occidentalis*) (Lande 1988), salmon (*Onchorhyncus*

49   spp.) (Stephenson 1999, Rieman and Dunham 2000, Schtickzelle and Quinn 2007, Peterson et al.

50   2014), amphibians (Marsh and Trenham 2001), and mosquitoes (Adams and Kapan 2009). To

51   date, efforts to integrate metapopulation dynamics into natural resource management have

52   largely focused on either minimizing the risk of localized extinction (Chadès et al. 2011),

53   characterizing productivity of the metapopulation as a whole (sensu Takashina and Mougi 2015),

54   or valuing benefits of portfolio effects (i.e. stabilizing effects of spatial asynchrony sensu

55   Schindler et al. 2010). Less understood, both in theory and in practice, is if and when harvesting

56   metapopulations can increase spatial variability that yield mismatches in spatial scales of

57   management and population dynamics.

58

59   In this study, we assess how harvest dynamics interact with animal movement and recruitment to

60   shape spatial population variability and risk of collapse at different spatial scales. Our results

61   illustrate the challenge in managing spatially complex populations using three complementary

62   approaches. First, we develop new theory using a stochastic analytical model to examine when

63   and how harvesting in a metapopulation amplifies spatial variability that can create mismatches

64   in spatial scale. Second, we contextualize the problem of spatial variability and mismatches in

65   spatial scale by presenting historical analyses from spatial Pacific herring (*Clupea pallasii*)

66   fisheries in British Columbia, Canada and home-ranges of associated predators and fishers that

67   may be impacted by localized collapses. Finally, we evaluate how and when different harvest

68   management approaches can ameliorate such mismatches using a numerical risk analysis in

69   Pacific herring fisheries.

70

71   *Pacific herring case study in British Columbia's Central Coast*

72   Pacific herring exemplify the challenges inherent to managing metapopulations that exhibit

73   spatial variation in population trends. In British Columbia (BC), Canada, herring return annually

74   to nearshore coastlines in the late winter/early spring to reproduce. During this annual migration,

75   they are harvested and preyed upon by a range of consumers. Mobile commercial fishing fleets

76   harvest adult herring, largely for their roe, in the days prior to spawning. In contrast, Indigenous

77   fishers are constrained to a local area and largely harvest eggs after spawning events (though

78   some adults as well) as an important food, trade, and cultural resource (Lepofsky and Caldwell

79   2013, McKechnie et al. 2014, Department of Fisheries and Oceans 2015, von der Porten et al.

80   2016, Okamoto et al. 2019). These activities create trade-offs among commercial roe fisheries

81   that remove spawning adults, which truncates adult age structure and reduces abundance, versus

82   those that remove only eggs from shorelines (Shelton et al. 2014). Unfortunately, a core

83   uncertainty for herring management, as for many species, is the extent of movement between

84   areas (Flostrand et al. 2009, Benson et al. 2015, Jones et al. 2016, Levin et al. 2016)**.** Similar

85   uncertainty surrounds spatial variation in spawning biomass (Siple and Francis 2016), which

86   may result in part from the degree of demographic synchrony between areas (e.g. synchrony in

87   recruitment). Pacific herring in British Columbia are currently managed as stocks at regional

88   scales (100s of kilometers) by Canada's federal fisheries agency. Within these stocks, multiple

89   spawning aggregations (substocks) seasonally occupy individual stretches of coastline, many of

90   which are of important traditional and cultural value to Indigenous groups. Thus, Pacific herring

91   fisheries present a valuable system in which to explore how spatial population dynamics, scales

92   of management, and spatial constraints of fishers and predators interact to influence differential

93   risk exposure to population collapses.

94

95   **Methods**

96   *Methodological Overview*

97

98   We used three distinct modeling approaches in this study to explore how harvest can affect

99   spatial dynamics in metapopulations. In **Model 1,** we developed a novel analytical approach to

100   modeling stochastic age-structured metapopulations to illustrate how and when harvest can

101   interact with migration and both the magnitude and spatial synchrony of environmental

102   stochasticity. We illustrated these important interactions using this model because of its

103   simplicity and interpretability relative to more complicated nonlinear numerical models.   In

104   **Model 2,** we analyzed Pacific herring data from British Columbia using a Bayesian hierarchical

105   model to estimate spatiotemporal variation in spawning biomass and harvest rates. In **Model 3,**

106   to evaluate potential solutions for spatial mismatches and conditions for their success, we

107   developed and applied a spatially explicit stochastic numerical model of metapopulations and

108   their interaction with the fishery. Together, these approaches (Models 1-3) generate theoretical,

109   empirical, and numerical results for understanding the complex, spatially-structured interactions

110   among populations, harvest, and environmental variability. The collective results are then

111   applied to evaluate the consequences for the availability of important natural resources for both

112   human and non-human user groups.

113

114   *Theoretical effects of harvest on spatial variability in metapopulations (Model 1)*

115   We used a simple metapopulation model to evaluate how harvest alters spatial variability,

116   conditional on the underlying properties of the metapopulation. For our purposes, spatial

117   variability is the degree to which volatility of the populations are masked by the observed

118   volatility of the metapopulation.

119

120   We considered a simple metapopulation consisting of two populations, linked through the annual

121   fraction migrating between populations (δ). We assumed both populations have the same

122   dynamics (identical density independent adult total mortality rate (Z), maturity at age 2,

123   Gompertz stock-recruit relationship, and symmetric adult annual migration) and trends in

124   recruitment variability are controlled by a spatially correlated lognormal environmental

125   stochasticity.

126

127   Let represent the abundance of age class a at location i at time t as $Y_{a,i,t}$. Adult dynamics are

128   shaped by mortality (Z - the sum of mortality from natural causes and harvest) and migration

129     $(0 \le \delta \le 0.5)$:

130   **Eq. 1:** $Y_{a,i,t+1} = \begin{cases} e^{-Z}\left[(1-\delta)Y_{a-1,i,t} + \delta Y_{a-1,j,t}\right] & 2 \le a \le n-1 \\ e^{-Z}\left[(1-\delta)(Y_{a-1,i,t} + Y_{a,i,t}) + \delta(Y_{a-1,j,t} + Y_{a,j,t})\right] & a = n \text{ (plus group)} \end{cases}$

131   Total reproduction is the sum of adults across all adult age classes multiplied by 0.5 to account

132   for an equal sex ratio:

133   **Eq. 2:** $Y_{a=0,i,t+1} = 0.5 e^{-z} \sum_{a=1}^{n}\left((1-\delta)Y_{a,i,t} + \delta Y_{a,j,t}\right)$

7

134   Both Eq. 1 and 2 are identical for both subpopulations (i.e. the system is symmetrical). We used

135   a stochastic Gompertz model as the compensatory function that determines how zygotes translate

136   into one-year-olds:

137   **Eq. 3:** $Y_{a=1,i,t+1} = \alpha(Y_{a=0,i,t})^{1-\beta} e^{\zeta_{i,t}}$

138   α, β and $\zeta_{i,t}$ represent, respectively, the density independent productivity parameter, the within-

139   location compensatory parameter, and environmental stochasticity that operates on post-

140   dispersing larvae. The vector $\boldsymbol{\xi}_t = [\zeta_{1,t}, \zeta_{2,t}]'$ follows a multivariate normal distribution with

141   mean zero and covariance controlled by the common within-site variance (σ_R^2) and spatial

142   correlation (ρ_R) yielding $\text{cov}[\zeta_{1,t}, \zeta_{2,t}] = \begin{bmatrix} \sigma_R^2 & \sigma_R^2 \rho_R \\ \sigma_R^2 \rho_R & \sigma_R^2 \end{bmatrix}$.

143

144   To analyze the stochastic metapopulation model, we converted the model to a first order vector

145   autoregressive model where statistical properties of stochastic forcing in multivariate systems are

146   well described (Lütkepohl 2005). We first vectorized the model by aligning variables from both

147   populations in a single vector:

148    $\mathbf{Y}_t = [Y_{a=0,L=1,t} \quad \cdots \quad Y_{n,L=1,t} \quad Y_{a=0,L=2,t} \quad \cdots \quad Y_{n,L=2,t}]'$

149   We then cast the model in terms of log-scale deviations from the equilibrium (i.e. $x_{a,i,t} =$

150    $\ln Y_{a,i,t} - \ln Y_{a,i}^*$ where $Y_{a,i}^*$ is the equilibrium) and linearized about the equilibrium (Nisbet and

151   Gurney 1982, Bjørnstad et al. 2004) to create a first order vector autoregressive model. This

152   approach approximates the deterministic dynamics of the nonlinear model with a Jacobian matrix

153   (**J**) of first order dependencies and an environmental covariance matrix.

154

8

155   The matrix of Jacobian coefficients (with plus groups summed at age *n*) are partial derivatives

156   for each age class within each subpopulation with respect to each other age class in each

157   subpopulation. **J** can be represented by the block matrix comprised of matrices describing

158   among and within population age transitions:

159   **Eq. 4: $\mathbf{J} = \begin{bmatrix} J_1 & J_2 \\ J_2 & J_1 \end{bmatrix}$**

160   Where J_1 is within population dynamics and J_2 is among population dynamics defined by:

161   **Eq. 5: $J_i =$**

162
$$
\begin{bmatrix}
0 & \frac{D}{1+\sum_{a=1}^{n-1}(e^{-Z})^a} & \frac{D(e^{-Z})}{1+\sum_{a=1}^{n-1}(e^{-Z})^a} & \frac{D(e^{-Z})^2}{1+\sum_{a=1}^{n-1}(e^{-Z})^a} & \cdots & \frac{D(e^{-Z})^{n-2}}{1+\sum_{a=1}^{n-1}(e^{-Z})^a} & \frac{D(e^{-Z})^{n-1}}{1+\sum_{a=1}^{n-1}(e^{-Z})^a} \\
1-\beta & 0 & 0 & 0 & \cdots & 0 & 0 \\
0 & D & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & D & 0 & \cdots & 0 & 0 \\
\vdots & \vdots & \vdots & \vdots & \ddots & 0 & 0 \\
0 & 0 & 0 & 0 & \cdots & \frac{D}{(e^{-Z})+1} & \frac{D(e^{-Z})}{(e^{-Z})+1}
\end{bmatrix}
$$

163   If $J_i = J_1$, $D = (1-\delta)$ and if $J_i = J_2$, $D = \delta$. Z is the annual total mortality rate and *n* is the

164   number of age classes. See Appendix S1 for full derivation of the Jacobian and VAR(1)

165   properties. The resulting VAR(1) model is:

166   **Eq. 6: $\mathbf{x}_t = \mathbf{J}\mathbf{x}_{t-1} + \mathbf{Z}\boldsymbol{\xi}_t$**

167   **Eq. 7: $\mathbf{x}_t = [x_{a=0,L=1,t} \quad \cdots \quad x_{n,1,t} \quad x_{a=0,L=2,t} \quad \cdots \quad x_{n,2,t}]'$**

168   **Z** is a 2n x 2 binary matrix (2 age classes for each location, two locations) that controls which of

169   the entries in $\mathbf{x}_t$ are subject to stochasticity from $\boldsymbol{\xi}_t$ (i.e. translating the 2x1 vector of location

170   specific stochasticity to a 2n x 1 sparse vector). In this case, only age class 1 (corresponding to

171   the second column of J_1) for each subpopulation is subject to stochasticity.

172

9

173   We used the known statistical properties of a VAR(1) model (Lütkepohl 2005) in tandem with

174   the moments of a multivariate lognormal to derive the coefficient of variation for the

175   subpopulations and metapopulation that yields the spatial variation in the metapopulation.

176   Finally, to evaluate how local environmental sensitivity of population growth changes with

177   mortality rate, we used a first-order impulse response analysis (Lütkepohl 2005) to estimate the

178   annual intrinsic growth rate response to a recruitment pulse. The impulse response in our case

179   describes how a recruitment perturbation affects the intrinsic growth rate of each subpopulation.

180   Specifically, it is given by the entry of the 2nd column of the 1st row of the Jacobian matrix in Eq.

181   5. See Appendix S1 for full derivations and details.

182

183   *Pacific herring case-study: spatial variability in biomass and catch (Model 2)*

184   To estimate patterns of spatial and temporal variability in herring biomass and harvest rates, we

185   used spawn deposition and harvest data for six major Pacific Herring spawning units that

186   comprise the Central Coast stock in British Columbia, Canada. Briefly, SCUBA surveys are

187   used to estimate herring egg abundance which is converted to total spawning biomass with the

188   assumed conversion of ~100 eggs/g and an equal sex ratio (DFO 2015). For consistency we use

189   the same index as in the DFO stock assessment but in the spatially disaggregated form. Catch

190   (which occurs in the days prior to spawning) is reported by geographic section that are delineated

191   and aggregated geographically. For full description of the time series see DFO (2015) and

192   references therein.

193

194   To estimate spatial biomass trends from the survey and harvest time series observations, we used

195   a nonlinear model in a Bayesian hierarchical state-space framework. We assumed survival,

196   reproduction, and competition were location specific. We modeled expected change in biomass

197   in year t+1 using a combined growth and survival model (individual growth and survival from

198   year t) and Gompertz recruitment model (from year t-1, because fish mature at or after age 2 -

199   Table 1, Eq. 8).

200

201   We estimated both process error and observation error in the model.   We estimated spatially

202   correlated process error that represents deviations from the expected log-scale pre-harvest

203   biomass within each location. Process error may arise from a diverse combination of factors

204   including immigration or emigration and temporal variation in growth, recruitment, or mortality

205   (Table 1, Eq. 9). We also estimated location-specific observation error (Objective function -

206   Table 1, Eq. 10), and a common survey bias (a "catchability" coefficient quantifying the mean

207   proportion of eggs that are observed in fishery-independent surveys - Table 1, Eq. 10). Thus, we

208   estimated trends conditional on estimated survival, biomass growth, process error covariance,

209   observation error, and survey bias.

210

211   Because we estimated log-scale pre-harvest biomass but observations are of post-harvest

212   biomass and harvested biomass, the model requires a change of variables and thus the posterior

213   requires a Jacobian adjustment of the inverse transform (Gelman et al. 2013, Carpenter et al.

214   2016, Table 1, Eqs 10, 11). See Table 1 for all model equations, parameter definitions, and prior

215   distributions. For details of estimation, posteriors, and model validation, see Appendix S2. We

216   estimated the models using Stan (Stan Development Team 2016b, a) with 3 independent Markov

217   Chains with 1000 iteration chains after 1000 iteration burn-in. We confirmed chain mixing and

218   convergence using Gelman-Rubin statistic (R<1.01, Gelman and Rubin 1992) and for mdel

219   adequacy and model fit using posterior predictive checks (see below). Posteriors compared with

220   priors for core parameters are shown in Appendix S2: Fig. S1.

221

222   We used the full model posterior of post-harvest biomass to calculate the following metrics: 1)

223   temporal and spatial variation in biomass (see Appendix S2: Fig. S1), and 2) the exploitation

224   rate. We compared the estimated local harvest rates from the model posterior to the theoretical

225   proportional allocation where fishing mortality is constant in space and an optimized allocation

226   of harvest given the quota (see Appendix S2: Fig. S3 for results, Appendix S3 for methods) and

227   the posterior mean. Here, we defined "optimized allocation" of catch as one that distributes

228   catches in space according to the ideal free distribution (see Appendix S3 for methods). This

229   distribution removes proportionally more biomass from subpopulations with higher biomass and

230   is the spatial allocation of catch that minimizes effort to achieve the overall quota (assuming

231   catch per unit effort is linearly related to biomass).

232

233   ***Solutions for spatial scale mismatches in fished herring metapopulations (Model 3)***

234   We used a stochastic model to simulate how spatial metapopulation dynamics and alternative

235   management scenarios interact to influence risk of collapse at the subpopulation and

236   metapopulation scales under a diverse suite of scenarios. The scenarios we examined include a

237   factorial gradient of 1) annual movement (see Annual adult migration among spawning areas

238   below), 2) environmental recruitment synchrony (the degree of correlation in recruitment in

239   space – see Spatiotemporal Recruitment Dynamics below), 3) a range of harvest rates (see Stock

240   Harvest Quota below), and 4) allocation of harvest in space (see Spatial Harvest Prosecution

241   below). For this analysis, we defined a "collapse" as years with spawning biomass below 20%

242   of unfished biomass. We used this definition for herring because, 1) it is generally seen as a

243   conservative estimate of biomass below which traditional Indigenous harvest becomes difficult

244   and, 2) it lies below the current closure threshold of 25% unfished biomass. Alternative

245   thresholds defining collapse were also assessed but yielded qualitatively similar results (data not

246   shown).

247

248   For all analyses, we simulated 10 populations placed around a hypothetical circular island of

249   arbitrary size, where distances among adjacent populations were equal. Fish spawning at any

250   site in a given year were able to move to any other site in the next year. The probability of

251   migration from one site to another declines as alongshore distance between the locations

252   increases and is controlled by a periodic kernel. Likewise, synchrony in stochastic recruitment

253   among sites decays with distance between locations controlled by a periodic covariance kernel.

254   Stochasticity in dynamics was included in recruitment (spatial and temporal variation), survival

255   (temporal variation only) and movement probabilities (spatial and temporal variance). The order

256   of operations mathematically was 1) recruitment, 2) survival, 3) movement, 4) roe fishery

257   harvest, and 5) spawning.   Details of the simulation are outlined below with core equations

258   listed in Table 2 and definitions in Table 3.

259

260   *Spatiotemporal Recruitment Dynamics*

261   Following the assumptions of the current British Columbia herring assessments (DFO 2015),

262   recruitment of age 2 individuals at location i is a function of eggs produced 2-years prior and

263   local density dependence via a Beverton-Holt model. We allowed recruitment to exhibit both

264   spatial and temporal variability and autocorrelation with a first-order vector autoregressive

13

265   model. Spatial correlations in recruitment followed a Gaussian spatial decay with distance (d),

266   and location specific recruitment variability was tuned such that net recruitment variability was

267   approximately constant across scenarios (CV of metapopulation recruitment = 0.8; DFO 2015).

268

269   *Annual Adult Survival and Migration Among Spawning Areas*

270   All adult survival occurred prior to movement into spawning locations, was constant in space

271   and was randomly drawn from a beta-binomial with mean $\lambda = 0.6$ with coefficient of variation of

272   0.2 (DFO 2015). Survivors migrated to new spawning locations with a probability that decays

273   with distance from the previous site, controlled by a periodic kernel, tuned to achieve the desired

274   retention rate.

275

276   *Stock Harvest Quota*

277   We followed the existing harvest control rules of Pacific herring in British Columbia (DFO

278   2015). The annual biomass harvest quota for the stock ($\hat{Q}_{t+1}$) was designed to achieve a target

279   harvest rate (H_{Target}) and a minimum spawning escapement (25% of B_0 – the average steady

280   state biomass without fishing). For simplicity and to avoid evaluating stock assessment model

281   performance (which is out of the scope of this study) we assume forecasts are unbiased with no

282   observation noise.

283

284   *Spatial Harvest Prosecution*

285   We used and compared two spatial fleet allocation scenarios to generate the distribution of

286   spatial commercial roe harvest given the stock quota: 1) the fleet prosecuted the fishery equally

287   in space whereby the absolute harvest was directly proportional to spawning biomass within a

288   given year (***proportional allocation***) or 2) the fleet was allocated according to the ideal free

289   distribution (IFD) that in theory would optimize catch efficiency if fleets are not spatially

290   constrained (***optimized allocation -*** See Appendix S3 for details in generating the IFD). Here,

291   realized catch was nonlinearly related to spawning biomass, harvesting more from areas with

292   higher biomass and leaving alone areas with lower biomass. See Appendix S3 for methods and

293   results from a third allocation strategy, a random spatial allocation that is more similar to the

294   fleet allocation in the empirical case study. In all cases, fishery selectivity was identical to

295   maturity-at-age reflecting that harvest occurs on mature fish at the spawning grounds.

296

297   *Simulation details*

298   For each simulation, we 1) evaluated deterministic equilibria without fishing, 2) initiated

299   stochastic forcing of recruitment from the equilibrium for 12 years (allowing the full suite of age

300   classes to be influenced by environmental stochasticity), 3) initiated the fishery in year 13, and 4)

301   recorded performance metrics for years 23-52. We ran 100 replicate simulations for each

302   combination of migration probability and recruitment synchrony. Primary performance metrics

303   summarized for each simulation included a) mean number of years below 20% B_0 at both stock

304   and substock scales to assess risk of collapse, b) mean stock and substock level catch, c) mean

305   stock and substock biomass, d) stock and substock temporal variability (coefficient of variation)

306   in biomass, and e) mean spatial variation in biomass (difference between squared coefficient of

307   variation at the substock versus stock scale).

15

308

309   **Results**

310   *Theoretical effects of harvest on spatial variability in metapopulations (Model 1)*

311   Our model illustrates that spatial variation among subpopulations increases with higher harvest

312   rates (Fig. 1a) and decreases with synchronizing forces of migration and environmental

313   correlation (difference in surfaces in Fig. 1b). As a result, the metapopulation trend and

314   coefficient of variation are less reflective of trends and variation in its subpopulations as harvest

315   increases (Fig. 1b). Biologically, this higher mortality rate decreases longevity and increases

316   local-scale sensitivity to spatially explicit recruitment pulses.   The amplification of fluctuations

317   occurs at a higher rate at local scales than on aggregate. This response decreases spatial coupling

318   and predictability. Reduced longevity of adults (via higher mortality) reduces the abundance of

319   adults in each subpopulation that buffers against local stochasticity through survival and

320   migration.

321

322   Mathematically, this result emerges for several related reasons. Increases in mortality (constant

323   across space in this case) reduce local subpopulation inertia (predictability, measured as 1st order

324   temporal autocorrelation, thick black line in Fig. 1c). This reduction in inertia increases

325   subpopulation sensitivity to temporal variation in local subpopulation recruitment (red line in

326   Fig. 1c). This sensitivity is illustrated by the primary impulse response at a single lag which in

327   this case always increases with total mortality (Z) derived from Eq. 5:

328   Eq. 22: $(1 - \delta)/(1 + \sum_{a=1}^{n-1}(e^{-Z})^a)$

329

16

330   Such increases in local environmental sensitivity reduce spatial coupling (measured as the spatial

331   autocorrelation, dotted black line in Fig. 1c) and thereby increase spatial variability in

332   abundance.

333

334   Importantly these patterns of spatial variability can persist even in the presence of modest

335   migration rates (Fig. 1b). While spatial variability decreases with synchronizing forces of

336   migration (δ) and environmental correlations (ρ_R) (Fig. 1b, see Appendix S1 for solutions),

337   spatial variability only diminishes as migration and environmental correlations are substantially

338   high (i.e. as migration probabilities approach 0.5 to produce 100% mixing).   This phenomenon

339   is illustrated by the discrepancies between temporal variability of the metapopulation and

340   component subpopulations that produce spatial variation (Fig. 1b).

341

342   Next we illustrate challenges imposed by spatial variation in exploited metapopulations using an

343   empirical case study of Pacific herring and present solutions using a numerical management

344   strategy evaluation.

345

346   ***Pacific herring case-study: spatial variability in biomass and catch (Model 2)***

347   Pacific herring subpopulations on the Central Coast of BC exhibit substantial spatial variability

348   in subpopulation trends (Fig. 2a, b, c). The estimated biomass of individual ("local")

349   subpopulations has varied by more than an order of magnitude over the past three decades, and

350   similar differences in biomass are evident among subpopulations in the same year. As a

351   consequence, aggregate ("regional") stock biomass at any one point in time is bolstered by a few

352   subpopulations, while others linger at low levels (Fig. 2b, Appendix S2: Fig. S2). Synchrony in

17

353   biomass among subpopulations is low (0.29), with much higher variability at the subpopulations

354   scale (average CV = 0.88) than in aggregate (CV = 0.54). This discrepancy results from high

355   spatial variability in subpopulations trends (Fig. 1c - also known as β variability; (Wang and

356   Loreau 2014). In fact as much as an estimated 91% of an individual subpopulation's biomass is

357   harvested annually, though the aggregate exploitation rate fluctuates around the target of 20%

358   (Fig. 2d, e, Appendix S2: Fig. S3). Counterproductively, this can result in occurrences where

359   subpopulations experiencing periods of lower-than-average biomass are heavily exploited

360   preceding collapse (e.g. Fig. 2d, in 2006). Harvest rates generally differ in magnitude among

361   subpopulations in any given year (Appendix S2: Fig. S3) and higher harvest rarely focus on the

362   subpopulations with highest biomass (Appendix S2: Fig. S3). This is illustrated directly by

363   spatial harvest distributions that deviate substantially from baselines of spatial harvest evenness

364   used here and in the simulation model (proportional vs optimized allocation - Appendix S2: Fig.

365   S3). Next we explore the potential consequences of different spatial harvest distributions via a

366   closed-loop simulation model.

367

368

369   ***Solutions for spatial scale mismatches in fished herring metapopulations (Model 3)***

370   We used numerical simulation of a metapopulation to determine whether and under what

371   conditions exploitation rates that appear sustainable in aggregate can risk collapse of local

372   subpopulations, and by extension, adversely affect predators and the fishers who target them at

373   this scale. The divergence in risk among scales, an effect of the mismatch in spatial scale, is

374   controlled by the magnitude of harvest rates, allocation of harvest in space, annual migration,

375   and spatial recruitment synchrony. Our simulations show that risk of collapse can be 10 times

376   greater at local subpopulation scales than at aggregate metapopulation scales (Fig. 3) for the 20%

377   harvest rule. While it may seem intuitive that relatively modest adult migration would minimize

378   differences in risk to subpopulations and the metapopulation, our results do not support this

379   supposition. Even relatively high migration rates can impose substantial discrepancies in the risk

380   of collapse between subpopulation and metapopulation scales (Fig. 3). This principle holds so

381   long as spatial synchrony in recruitment is not exceedingly high (Fig. 3 upper portions of

382   heatmaps). For most scenarios, high spatial variability (i.e. from low annual migration among

383   subpopulations or low spatial recruitment synchrony) leads to low apparent risk at the aggregate

384   metapopulation scale, despite high risk of collapse for local subpopulations (Fig. 3; risk increases

385   towards the lower left quadrants).

386

387   We find that risk to local subpopulations greatly exceeds risk to the aggregate metapopulation

388   with both a simulated 10% and 20% target harvest rate. Under the 20% target harvest, risk of

389   collapse at the local scale exceeds 10%, even with annual migration among subpopulations

390   approaching 50% (Fig. 3 h). When harvest is optimized in space or target harvest rates are

391   reduced to 10%, risks of collapse at local scales are substantially reduced (Fig. 3 d,f,j versus Fig.

392   3 h) and limited to scenarios where migration is ~10-15% and spatial synchrony in recruitment is

393   low. Local scale risks of collapse are even worse under a random (or opportunistic) spatial

394   allocation, but also ameliorated by reductions in harvest (Appendix S3: Fig. S2). Importantly, a

395   10% target harvest with optimized spatial allocation never exceeded 10% risk of collapse in our

396   simulations.

397

398   The discrepancy in risk of collapse at local subpopulation versus aggregate metapopulation

399   scales is shaped by both overall harvest rates and spatial variance in subpopulation trend (Fig.

400   S5). Risk at the subpopulation scale matches that of metapopulation scales when subpopulations

401   exhibit little spatial variance (i.e. when there is high recruitment synchrony or high migration,

402   top vs bottom panels in Fig. 3 c-j, SI Fig. S6). In contrast, risk diverges with increases in spatial

403   variance (Fig. S5).   Spatial variance is shaped not only by spatial recruitment synchrony and

404   migration, but also harvest rates and allocation in space. Fig. 4b-c illustrates how different

405   harvest allocations impact spatial variation in trends (Fig. 4 d, e). Higher harvest rates increase

406   risk at subpopulation scales in part because of higher depletion at the metapopulation scale (Fig.

407   3 d,f,h,i) and also because harvest can increase spatial variance (Fig. 4d, also explored more

408   generally in Fig. 1) when efforts are allocated proportionally. This result demonstrates how low

409   demographic synchrony creates a portfolio effect at the metapopulation scale but simultaneously

410   masks risks of collapse at the subpopulation scale which can be exacerbated with higher harvest

411   rates.

412

413   However, dynamically optimizing harvest rates in space to match local scale variability lowers

414   the risk of subpopulation and aggregate metapopulation collapse (Fig. 3 d vs f and Fig. 3 h vs i)

415   with no cost to aggregate catch (Appendix S3: Fig. S3). These results emerge from simulating a

416   form of spatially optimized fishing effort that leaves underperforming locations unexploited and

417   heavily targets overperforming local subpopulations, in accordance with predictions of ideal free

418   distribution theory. Optimal spatial allocation of harvest rates reduces the effects of harvest

419   intensity on spatial variability (Fig. 4d) which is strongly related to the bias in estimating risk

420   among scales (Appendix S3: Fig. S1) and also reduces length of individual collapses (Appendix

421   S3: Fig. S3). Thus, approaches that optimize spatial harvest to account for subpopulation

422   dynamics can minimize the spatially destabilizing effect of harvest as well as disparity in

423   exposure to risk of collapse among spatial scales. The benefits of spatially optimized harvest in

424   terms of risk to subpopulations diminishes as migration and spatial synchrony in recruitment

425   productivity decline to low levels (i.e. approach the lower left quadrant of panels in Fig. 3 d,f,h,j,

426   where subpopulations are nearly autonomous with low connectivity).

427

428   **Discussion**

429   Harvest strategies that appear appropriately prescribed at large spatial scales can, at local scales,

430   lead to declines or even effective extirpation of local subpopulations. We call these small-scale

431   declines "cryptic collapses". Specifically, regional harvest strategies can create a "gilded trap"

432   (Steneck et al. 2011) where, in this case, management focuses on the aspects of metapopulations

433   that can benefit conservation and economics at the aggregate scale, but neglect social-ecological

434   inequity in the exposure to risk at local scales. Our results show that spatial mismatch among

435   scales is not merely an esoteric concern. Indeed, they occur in current management situations,

436   and are supported by ecological theory we develop here. Our multiscale risk analysis highlights

437   the impacts of scale mismatch on consumers and the potential value of optimized spatial

438   management for sustainability and equity. Previous studies have also investigated spatial

439   mismatches in fisheries contexts to understand consequences stemming from spatial mismatches

440   among biological processes and available data, as well as the spatial implementation of fisheries

441   for yield and measure of population status assessments (Cope and Punt 2011, McGilliard et al.

442   2011, Spies et al. 2015, McGilliard et al. 2017). Our work expands on previous investigations by

443   considering how spatial dynamics of fish and fisheries affect resource sustainability at multiple

444   spatial scales that are relevant to different species and fishing communities. Our models address

445   this gap by building on existing research with increased biological realism to allow for 1) adult

446   migration rates among subpopulations rather than only dispersal associated with recruitment (e.g.

447   Cope and Punt 2011, McGilliard et al. 2011, Spies et al. 2015, McGilliard et al. 2017) ; 2) a

448   range of complex spatio-temporal correlations in the stochastic populations dynamics (but see

449   McGilliard et al. 2011 for an implementation of spatio-temporal variation in adult mortality); and

450   3) a novel suite of fisheries spatial harvest strategies.

451

452   *Insights into the benefits of population portfolios to manage risk for different groups*

453

454   Our work adds critical resolution and understanding to the literature on portfolio effects that is

455   focused on the benefits of spatial variability. Recent work viewing multiple populations as a

456   "portfolio" of assets has shown benefits of maintaining a diversity of subpopulations with high

457   asynchrony. These benefits include reducing local extinctions through so called 'rescue effects'

458   (Hill et al. 2002, Secor et al. 2009, Fox et al. 2017), providing increased stability in the form of

459   food security for people or animals (Nesbitt and Moore 2016) and minimizing economic risks

460   over large scales by minimizing variance in harvestable abundance (Schindler et al. 2010). Yet

461   these portfolio analyses typically focus on the attributes of the aggregate metapopulation,

462   whereas the risk of localized subpopulation collapse (e.g. depletion below a threshold of

463   ecological functionality or socioeconomic value) affects the interests of locally constrained

464   fishers and spatially constrained organisms with small home ranges. Using theory and data we

465   show that the same spatial variation that leads to resilience at the metapopulation scale, when left

466   unaccounted for in management strategies, can also produce unforeseen negative consequences

467   in the form of magnified spatial variation and local risk of collapse (see also Spies et al. 2015).

468

469   In the case of Pacific herring in the Central Coast of British Columbia, local reductions in some

470   subpopulations occurred well before the entire stock showed substantial declines in the mid-

471   2000s. These collapses had greater impact on spatially constrained groups; namely Indigenous

472   communities for whom herring is a source of cultural and economic vitality (Brown and Brown

473   2009, Gavreau et al. 2017). In contrast, mobile fishing fleets and transient predators should be

474   less vulnerable to local depletion events in the short term. Such context dependent effects of

475   ignoring spatial variation are exemplified through considering the dramatic differences in the

476   spatial scale at which predators and fishers operate. Indigenous fishers are spatially constrained

477   by boat size, fuel costs, and political/cultural boundaries (Fig 2a, Table 4, Harris 2000, von der

478   Porten et al. 2016). In contrast, the commercial fleet of seine and gillnet fishers are highly mobile

479   and can pursue fish throughout the region. Similarly, non-human predators of herring and

480   herring roe have a diversity of home-ranges and therefore interact with herring at multiple scales

481   (Table 4). Many predators rely on herring when they move inshore around spawning season.

482   Many crustaceans (Hines 1982, Stone and O'Clair 2001), echinoderms (Mattison et al. 1976,

483   Cieciel et al. 2009), rockfishes and lingcod (Jorgensen et al. 2006, Mitamura et al. 2009,

484   Tolimieri et al. 2009, Beaudreau and Essington 2011, Green and Starr 2011, Freiwald 2012),

485   harbor seals (Peterson et al. 2012, Ward et al. 2012), some seabirds (Peery et al. 2009, Barbaree

486   et al. 2015, Lorenz et al. 2017), and some flatfishes (Moser et al. 2013), exhibit restricted

487   patterns of movement and are likely to exploit one to several major subpopulations, but generally

488   not the entire spatial distribution of the metapopulation (stock). In contrast, humpback whales

23

489 (Dalla Rosa et al. 2008, Kennedy et al. 2014), orcas (Hauser et al. 2007, Fearnbach et al. 2014),

490 some seabirds (Pearce et al. 2005), sea lions (Merrick and Loughlin 1997, Fearnbach et al. 2014,

491 Kuhn and Costa 2014), fur seals (Kuhn et al. 2014), halibut (Loher 2008, Seitz et al. 2011,

492 Nielsen et al. 2014), and gadiforms (Wespestad et al. 1983, Hanselman et al. 2014, Rand et al.

493 2014) can, given ranges reported, access the geographic area covered by the stock (Table 4, see

494 DataS1:Appendix S4). Thus, herring provide food resources to groups with varying movement

495 constraints. As a result, herring collapses that range from small-scale subpopulations to

496 metapopulation-wide phenomena may have differential impacts on the diverse predators that

497 depend on this resource. These spatial scale dependencies affect which fishing communities or

498 species bear the brunt of management risks and who reaps the benefits from the portfolio payoff

499 of regional metapopulation stability. These outcomes highlight that ignoring space can exclude

500 critical social, ecological, and economic responses central to the triple bottom line (Elkington

501 1994, Okamoto et al. 2019).

502

503 Pacific herring fisheries on Canada's west coast provide an empirical case where the scale of

504 regional stock assessments masked episodic local overexploitation and subpopulation collapses.

505 Here, high local harvest rates appear to be commonplace even when local subpopulations are

506 depleted presumably because of at least two key factors. First, schooling fish are easy to catch

507 even at low abundances (Mackinson et al. 1997) and thus the quota is likely to be achieved even

508 if the abundance of spawning fish in a particular location is small. Second, managers are

509 challenged with fulfilling quotas with imperfect spatial information about spawning abundances.

510 While high local harvest rates may have contributed to subsequent local collapses observed in

511 this case study, quantifying other confounding demographics (i.e. spatial variation in stochastic

24

512   adult mortality) are necessary to explicitly test this hypothesis. While recent local collapses may

513   have occurred in the absence of fishing, fishing is very likely imposing higher subpopulation

514   sensitivity to any environmental or biotic influence on recruitment or survival by reducing adult

515   longevity thereby eroding an important buffer against recruitment volatility (Essington et al.

516   2015) that we show can contribute to spatial variation. Importantly, spatial variation may not

517   only affect the localized groups. In the long term, assumptions of spatial homogeneity can

518   generate biased estimates of total productivity (Takashina and Mougi 2015) that may lead to

519   overly optimistic harvest strategies. Thus, high local harvest rates may produce sequential

520   depletion over time that eventually erodes the principal of the stock with potential to generate

521   collapse of the portfolio as a whole (Spies et al. 2015).

522

523   *Linking harvest dynamics to spatial variation in population dynamics*

524

525   Importantly, spatial variation in population dynamics is not independent of harvest dynamics.

526   Rather, we demonstrate numerically and analytically that spatial variation is likely to increase

527   with harvest. This can occur in part because harvesting reduces spatial coupling. Higher

528   mortality is known to reduce the abundance of older age classes (Barnett et al. 2017) and

529   increase sensitivity to fluctuations in recruitment (Beddington and May 1977, Bjørnstad et al.

530   2004, Hsieh et al. 2006, Shelton and Mangel 2011, Okamoto et al. 2016). In spatially structured

531   systems, such reduced longevity diminishes the synchronizing effect of migration and elevates

532   sensitivity of subpopulations to localized environmental effects.   However, if the distribution of

533   harvest in space can be optimized to more adequately accommodate the spatial distribution of

534   fish, we show how the overall portfolio can benefit at multiple scales. Here, demographic

535   asynchrony (in this case asynchrony in recruitment productivity) can be maintained while

536   minimizing subpopulation risk. Translated into practice, our simulation and analytical results

537   highlight two non-mutually exclusive solutions that provide more equitable spreading of risk

538   among scales. First, reductions in overall harvest rates can ameliorate biases in risk among

539   scales. This occurs by reducing baseline levels of risk and reducing effects of harvest on spatial

540   variability. Second, spatially optimizeing harvest allocations can minimize spatial variance and

541   ease pressure on at-risk subpopulations, thereby reducing risk of local scale depletion without

542   sacrificing catch. The first solution creates a trade-off between commercial yield and local risk;

543   the second solution between the costs of management and fleet transportation, and local risk of

544   subpopulation collapse. Specifically, achieving something similar to the latter (second solution)

545   in a realistic setting is likely to require either some combination of greater investment in spatial

546   monitoring, spatial stock assessments (Punt et al. 2018), and in season-management. Thus,

547   moving in the direction of spatial optimization is likely to require substantial investment in costs

548   and personnel for research, stock assessment, and management.

549

550   Addressing spatial inequity in risk exposure requires confronting these economic and logistical

551   trade-offs. For species such as Pacific herring that have volatile spatiotemporal dynamics and

552   complex migratory phenology (Benson et al. 2015), polycentric governance structures where

553   governing authorities are nested at different spatial scales may help balance these trade-offs by

554   addressing the problems of fit between ecosystems, social systems, and management agencies

555   (Young 2002, Berkes 2006, Borgström et al. 2006, Folke et al. 2007, Biggs et al. 2012, von der

556   Porten et al. 2016). Such systems can capitalize on scale-specific ecological knowledge

557   (including local, traditional, and scientific knowledge), scientific capacity and socioeconomic

558   experience to 1) guide decision analyses, 2) co-coordinate data collection and harvest allocation

559   in space, and 3) test policies (e.g. in the Maine Lobster fishery (Acheson 2003)). Polycentric

560   management schemes, however, are not a silver bullet. For systems like Pacific herring where

561   placed-based Indigenous fishing communities often object to purely centralized scales of

562   management for social, ecological, and economic reasons (Brown and Brown 2009, Thornton

563   and Kitka 2015, von der Porten et al. 2016, Gavreau et al. 2017, von der Porten et al. 2019),

564   opportunities to integrate knowledge and objectives into management strategies (and their

565   evaluation) at smaller spatial scales is well placed in managing these fisheries, and may be

566   critical to their perpetuity (Okamoto et al. 2019, Salomon et al. 2019).

567

568   The models used to generate inference in this study are simple in comparison to the nature of

569   complex stochastic systems in space. The analytical model (Model 1) makes numerous

570   simplifications (linearization, biological simplicity) in order to generate analytical and

571   generalizeable solutions but may ignore more nuanced nonlinearities. The numerical model

572   (Model 3) on the other hand is more detailed but outcomes are context dependent. Moreover,

573   both models ignore many biological and management scenarios that are likely to further

574   complicate spatial patterns (e.g. behaviorally or geographically complex migration (MacCall et

575   al. 2018, Rogers et al. 2018), spatial and age specific mortality (McGilliard et al. 2011), spatially

576   complex density dependence (McGilliard et al. 2017), Allee effects, cost, and data limitations for

577   spatial management). We also ignore many alternative spatial allocation strategies that may be

578   explicitly designed to maximize long-term yields or minimize spatiotemporal variability in part

579   because these approaches would require a spatial assessment model, which is out of the scope of

580   this study. However, the principles from our simulation and analytical models should generalize

581 regardless of the degree of complexity in the system: a precautionary approach cognizant of

582 resource users across multiple spatial scales may necessitate the incorporation of some degree of

583 locally based management to minimize spatial discrepancies in risk exposure. Our results

584 highlight the need to consider diverse scenarios and incorporate fundamental biological attributes

585 that may impact resource dynamics and people at different scales. Overall, our models suggest a

586 mixture of management scales may be key to selecting and coordinating harvest levels in space

587 to navigate towards sustainable and equitable outcomes (Cope and Punt 2011, Biggs et al. 2012).

588

589 *Conclusion*

590

591 Our analyses illustrate the importance of considering spatial dynamics for determining how to

592 most effectively balance equity in management and conservation strategies aimed at achieving

593 social, economic, and ecological outcomes (Halpern et al. 2013, Law et al. 2017). These issues

594 are often ignored by centralized management and conservation initiatives focused on larger

595 spatial scales. For over half a century, fisheries scientists have debated how best to exploit and

596 conserve "mixed stocks" that have separate dynamics but are inseparable in space, with the aim

597 of balancing conservation of weak stocks and maximizing total yields (Ricker 1958). Our work

598 inverts this focus to metapopulations where subpopulations have inseparable dynamics but are

599 separated in space. We show how, in these settings, exploitation can magnify local scale

600 fluctuations and spatial variability. As a result, aggregate metrics poorly represent local scale

601 dynamics and the risk of collapse at the local scale increases at a greater rate than the aggregate

602 large scale. This phenomenon creates cryptic collapses with ensuing discrepancies in risk

603 exposure. Fortunately, the magnitude of these discrepancies can potentially be controlled by

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604 lowering harvest rates or seeking harvest dynamics that are spatially optimized. Overall, these

605 conclusions are relevant not only to Pacific herring fisheries, but also to the great number of

606 exploited natural resources that exhibit spatial structure and are valuable to species and people

607 that operate on multiple scales.

608

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904

905   Table 1: Equations used in Model 2 (Pacific herring case-study: spatial variability in biomass and

906   catch)

Eq	Description	Equation
Eq. 8	Expected pre-spawn biomass	$\hat{b}^+_{t+1,l} = \exp\left(\alpha_l + (1-\beta_l)\ln(b_{t-1,l})\right) + \lambda_l b_{t,l}$
Eq. 9	Estimated log-biomass	$\ln \boldsymbol{b}^+_t = \ln(e^{\ln \boldsymbol{b}_t} + \boldsymbol{h}_t) \sim \text{MVN}(\ln \hat{\boldsymbol{b}}^+_t, \text{diag}(\boldsymbol{\sigma})\Omega)$
Eq. 10	Objective function	$\ell = \sum_{t=1}^{T}\sum_{l=1}^{L} \dfrac{\left(\ln(\text{obs}[b_{t,l}]) - \left(\ln b_{t,l} + \ln q\right)\right)^2}{(2\sigma^2_{obs})} - \ln(|\mathrm{d}|)$
Eq. 11	Jacobian adjustment for change of variables in Eq. 10	$\mathrm{d} = \dfrac{\partial}{\partial \ln b_{t,l}} \ln(e^{\ln b_{t,l}} + h_{t,l}) = \dfrac{b_{t,l}}{b_{t,l}+h_{t,l}}$
Symbol	Description	Prior or Data Source
α_l	Site-specific Gompertz productivity	
β_l	Site-specific Gompertz compensation	$[\alpha_l \quad \text{logit}(\beta_l) \quad \text{logit}(\lambda_l)]' \sim \text{MVN}(\boldsymbol{\Theta}, \boldsymbol{\sigma_\Theta}\Omega_\Theta);$
λ_l	Site-specific aggregate mortality & somatic growth	
Θ	Mean vector for $\alpha, \text{logit}(\beta), \text{and logit}(\lambda)$	$\boldsymbol{\Theta} \sim \text{MVN}(0, \text{diag}(1.5)\Omega_{\bar{\Theta}});$
$\sigma_{\Theta l}$	Among site variances in $\alpha, \text{logit}(\beta), \text{and logit}(\lambda)$	$\sigma_{\Theta l} \sim \text{half-cauchy}(0, 2.5)$
Ω	Process error spatial corr. matrix	
Ω_Θ	parameter corr. matrix	LKJ prior (Lewandowski et al. 2009): scale = 2
$\Omega_{\bar{\Theta}}$	mean parameter corr. matrix	
$\boldsymbol{\sigma}$	Vector of site-specific lognormal process variances	$\sigma_l \sim \text{normal}(\sigma_\mu, 0.15); \ \sigma_\mu \sim \text{normal}(0, 0.15)$
σ_{obs}	Lognormal obs. error	$\sigma_{obs} \sim \text{half-cauchy}(0, 2.5)$
$\ln q$	Survey bias (egg "catchability")	$\ln q \sim \text{normal}(0, 0.05)$ (Martell et al. 2012)
$\text{obs}[b_{t,l}]$	Input Data	observed spawning biomass at time t at location l
$h_{t,l}$	Input Data	harvest at time t at location l

907   Table 2: Equations used in Model 3 (Solutions for spatial scale mismatches in fished herring

908   metapopulations). See Table 3 for parameter values and definitions.

909

Eq	Description	Equation
Eq. 12	Recruits (age 2) prior to movement	$n^{++}_{a=2,l,t+2} = \text{eggs}_{l,t} \exp\left[\epsilon_{l,t} - \frac{\sigma_r{}^2}{2}\right] / (\alpha + \beta\,\text{eggs}_{l,t})$
Eq. 13	Total eggs lain	$\text{eggs}_{l,t} = \sum_{a=2}^{10} m_a f_a [0.5 n_{a,l,t}]$
Eq. 14	Environmental recruitment stochasticity	$\boldsymbol{\epsilon_t} = \phi \boldsymbol{\epsilon_t} + \text{MVN}(0, \sigma_r{}^2[1-\phi^2]\boldsymbol{\Omega_r})$
Eq. 15	Spatial correlation in recruitment stochasticity	$\rho_{i,j} = \exp\left(-\frac{2\sin^2\pi\left\lvert dist_{i \to j}\right\rvert}{\eta^2}\right)$
Eq. 16	Pre-harvest abundance	$n^{++}_{a,l,t+1} = \begin{cases} \lambda_t\, n_{a-1,l,t} & 2 < a < 10 \\ \lambda_t\, n_{a-1,l,t} + \lambda_t\, n_{a,l,t} & a = 10 \text{ (plus group)} \end{cases}$
Eq. 17	Post-migration abundance	$\boldsymbol{N_t^+} = \boldsymbol{N_t^{++} S}; \ \ S_{i,j} = P(i \to j)$
Eq. 18	Recruit or Adult migration by distance function	$P(i \to j) = \exp\left(-\frac{2\sin^2\pi\left\lvert dist_{i \to j}\right\rvert}{\gamma^2}\right) \sum_{j=1}^{N} \exp\left(-\frac{2\sin^2\pi\left\lvert dist_{i \to j}\right\rvert}{\gamma^2}\right)^{-1}$
Eq. 19	Quota	$\hat{Q}_{t+1} = \begin{cases} min\left(H_{Target} * \hat{B}_{forecast,t}, \ \hat{B}_{forecast,t} - L_{crit} * \hat{B}_{0,t}\right) & \text{if } \hat{B}_{forecast,t} \geq L_{crit} * \hat{B}_{0,t} \\ 0 & \text{otherwise} \end{cases}$
Eq. 20	Post-harvest abundance at age in year t	$n_{a,l,t} = (1 - m_a) n^+_{a,l,t} - m_a n^+_{a,l,t} e^{-F_{t,l}}; \ \ F_{t,l} = \ln h_{t,l} / \sum_{a=2}^{10} w_a m_a\, n^+_{a,l,t}$
Eq. 21	Biomass at location l in year t	$B_{l,t} = \sum_{a=2}^{10} w_a m_a\, n^+_{a,l,t}$

910

44

911 Table 3: List of key parameters and state-variables in Model 3 with definitions, values and

912 citations. Note that equilibrium considerations are generated by simulating with no harvest and

913 no stochasticity ($\sigma_r = 0$, cv in $\lambda_t = 0$, and harvest = 0). Selectivity-at-age in all cases is equal to

914 maturity-at-age.

Parameter	Description	Value(s)	Source
α, β	Beverton-Holt stock-recruit parameters	583.43, 2.089 x 10^{-8}	1
ϕ	1st order partial autocorrelation	0.6	Chosen
m_a	Maturity-at-age (=Selectivity-at-age)	Age 1 = 0, Age 2= 0.2, Age 3=0.9, Age 4 + = 1	2
w_a	Weight-at-age	4.5x10^{-6} [27(1-Exp(-0.48*age))]$^{3.127}$	3
f_a	Fecundity-at-age	$\exp(4.69)(1000w_a)^{1.13}$	3
λ_t	Annual pre-harvest survival rate	Beta-binomial: mean = 0.6, cv= 0.2	Derived from 1
σ_r	Stock-scale standard deviation of rec-devs	0.8	1
η	Scale parameter regulating distance decay in rec-dev spatial covariance	Numerically tuned to achieve desired spatial correlations	Chosen
L_{crit}	Lower biomass threshold for fishing closure relative to $\hat{B}_0$	0.25	1
$\overline{P}(i \rightarrow j)$	Mean migration probability	0.01 to 0.8	Chosen
$\bar{\rho}_{i,j}$	Spatial synchrony in recruitment	0.15 to 0.85	Chosen
State Variable	**Description**		
$n^{++}_{a,l,t}$	Abundance at age a in time t at location l prior to movement and harvest (Eq. 16)		
$n^{+}_{a,l,t}$	Abundance after movement and prior to harvest (Eq. 17)		
$F_{t,l}$	Fishing mortality of susceptible fish at time t at location l after movement and natural mortality (Eq. 20)		

915 1: (Department of Fisheries and Oceans 2015)

916 2: (Martell et al. 2011)

917 3: (Tanasichuk et al. 1993)

918   Table 4: Home-range categories of different Pacific herring predator groups. Details of sources

919   and home-ranges are provided in the DataS1:Appendix S4.

920

Home-Range Category	Home-Range Description	Herring Predator Groups
Localized	single subpopulation *(< 10 km radius)*	Indigenous fishers**, Seabirds*, Flatfishes*, Crustaceans*, Urchins, Cucumbers, Reef Fishes, Rockfishes
Centralized	multiple subpopulations *(~10-40 km-radius)*	Indigenous fishers**, Seabirds*, Flatfishes*, Crustaceans*, Gadiforms*, Salmonids**, Halibut**, Harbor Seals
Transient	full stock or greater	Seine & Gillnet Fishers, Cetaceans, Sea Lions, Seabirds*, Gadiforms*, Salmonids**, Halibut**

921
922   *Varies by species, ** Varies by migration phase, location or individual
923

924   List of Figures:

925   Figure 1: Effect of elevating harvest mortality rate on asynchrony related spatial variability in the

926   metapopulation from Model 1. **(a)** Spatial variation increases as a function of total mortality for

927   different levels of spatial synchrony in recruitment productivity. Here migration is held at 0.25

928   and log-scale recruitment variability (σ_R) is 0.7 (i.e. CV = 0.8). Note spatial variation is a result

929   of the discrepancy in population versus metapopulation temporal variation in panel

930   (b); **(b)** Temporal variability (squared coefficient of variation) of the population and

931   metapopulation. The arrows illustrate spatial variability as the difference between

932   surfaces. **(c)** Measures of local population predictability (measured by first order within

933   population autocorrelation, thick black line), among population coupling (measured by among

934   population correlations, thin black line), and local environmental sensitivity (measured by the

935   response at the population level to a unit environmental impulse affecting recruitment

936   productivity, red line).

937

938   Figure 2: **(a)** Map of major Pacific Herring spawning substocks ("Sections" - denoted by

939   different symbols) as defined by Canada's Federal Fisheries Agency in the Central Coast of

940   British Columbia. Indigenous communities noted with *. **(b)** Trends for the six main

941   supopulations (substocks - thin colored lines & points) and the metapopulation (stock) mean

942   (thick blue line). Trends were estimated using multivariate hierarchical Bayesian state-space

943   model integrating spawn surveys and catch information (model 2). Individual plots for each

944   substock are shown, along with catch, spawn observations, and 95% posterior credible intervals

945   in Appendix S2. **(c)** Temporal coefficients of variation estimated from the Bayesian state-space

946   mode over 25 years for each substock, the mean of each substock CV (large black symbol), the

47

947   regional stock coefficient of variation (blue point), and the spatial variability (black point with

948   error bar) which is the standardized variance of the system after accounting for the variance of

949   the stock and the variance of the substock means. Error bars are 95% credibility intervals. (d)

950   Trends in annual harvest rate for 2 of the 6 local substocks (Higgins and Lower Spiller) with

951   points, 95% credibility intervals and the mean for the aggregate stock (thick blue line). For full

952   results see Appendix S2. The dotted line represents the target harvest rate of 20%.

953

954   Figure 3: Mean risk of collapse (%) at metapopulation and subpopulation scales for different

955   harvest rates and spatial harvest allocation strategies under varying spatial scenarios. Results are

956   derived from simulation-based risk analysis of hypothetical Pacific herring fisheries. Axes

957   present simulations with different levels of annual migration and spatial synchrony in

958   recruitment productivity, columns represent different harvest strategies and rows represent the

959   spatial scales of inference. Risk of collapse is the probability of falling below 20% of unfished

960   equilibrium (i.e. the dotted lines in Fig. 4 a-c); at the subpopulation scale, risk is measured as the

961   mean probability of collapse for each population. *Optimized allocation* harvests proportionally

962   more from subpopulations with higher biomass; *Proportional allocation* removes the same

963   proportion of biomass from each subpopulation. Annual migration is the mean percent of each

964   subpopulation that emigrates each year and spatial synchrony is the mean pairwise correlation in

965   recruitment productivity. For full results see Appendix S3: Fig. S2. Note that the allocation

966   strategies produce equivalent average yields (Figure 3c vs. 3e and 3g vs. 3i; see Appendix S3:

967   Fig. S3 for yield comparisons). For an illustration of how alternative strategies affect the mean

968   duration of collapses, see Appendix S3: Fig. S4.

969

970   Figure 4: **(a-c)** Example simulations (a single simulation run) showing spatial variation in

971   biomass measured at the subpopulation level (colored lines) or metapopulation mean (thick blue)

972   for **(a)** an unexploited metapopulation, **(b)** a 20% target harvest allocated proportional to

973   spawning biomass in space, or **(c)** a 20% target harvest allocated optimally in space according to

974   the ideal free distribution (see Appendix S3: Fig. S4 for summaries across runs). B_0 =

975   deterministic biomass in the absence of fishing, dotted line = lower conservation threshold of

976   20% of B_0. **(d)** change in spatial variation for different harvest rates and spatial harvest allocation

977   across different spatial parameter scenarios for migration rates and spatial synchrony. Each point

978   represents the spatial variance from 100 runs from a single 52-year simulation using a unique
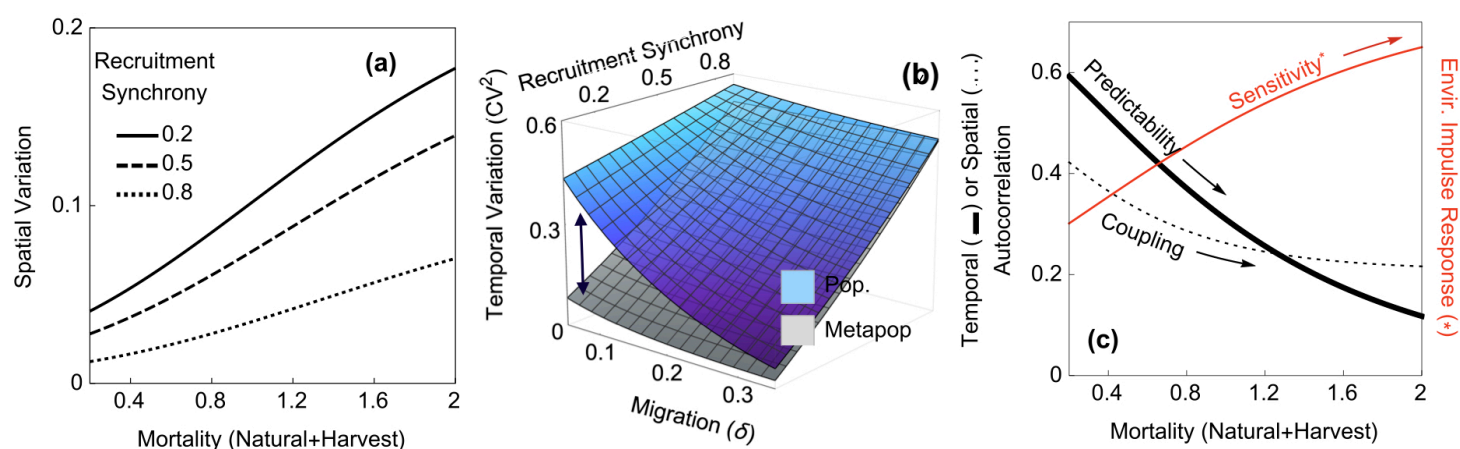
979   migration-synchrony parameter combination.
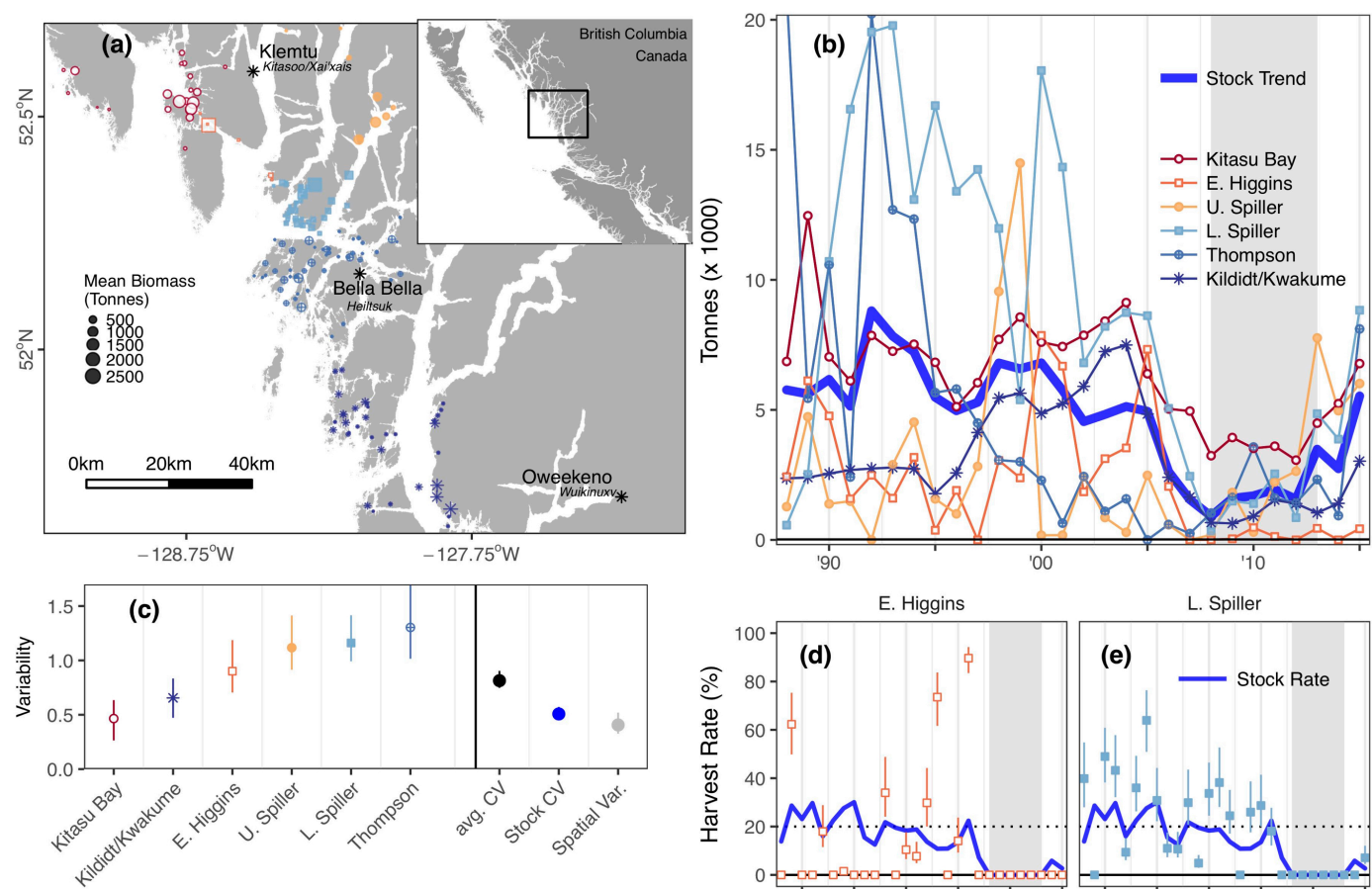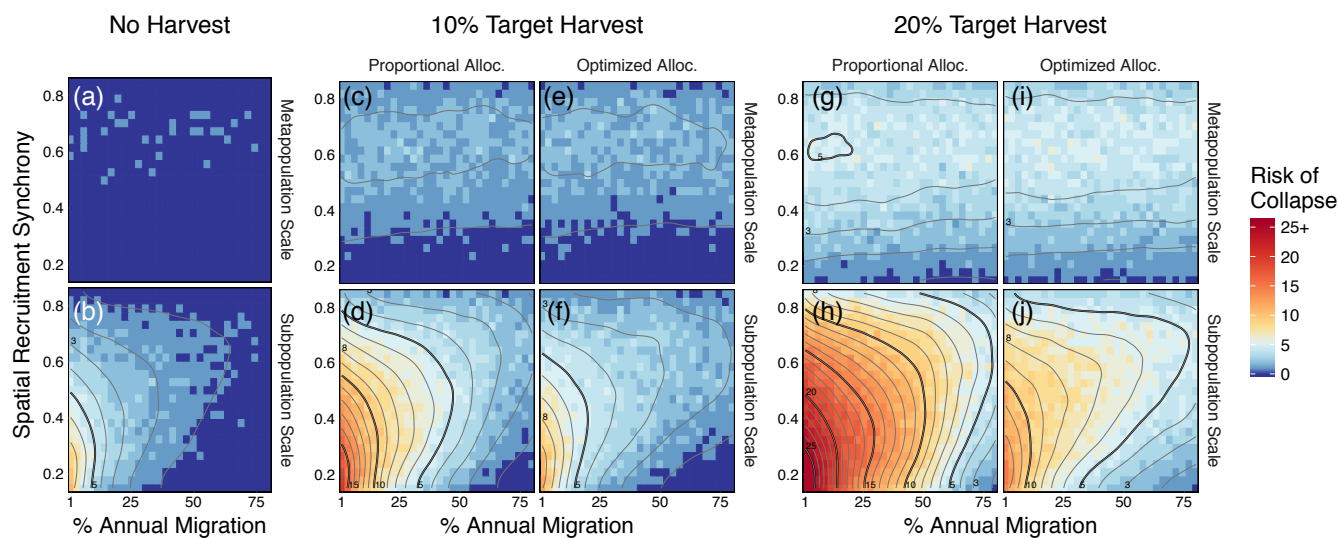
980

Figure 1

Figure 2

Figure 3

Figure 4