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Summary

Coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*O. tshawytscha*), and steelhead (*O. mykiss*) in Puget Sound and the Strait of Georgia have exhibited declines in marine survival over the last 40 years. While the cause of these declines is unknown, multiple factors, acting cumulatively or synergistically, have likely contributed. To evaluate the potential contribution of a broad suite of drivers on salmon survival, we used qualitative network modeling (QNM). QNM is a conceptually based tool that uses networks with specified relationships among the variables. In a simulation framework, linkages are weighted and then the models are subjected to user-specified perturbations. Our network had 33 variables, including: environmental and oceanographic drivers (e.g., temperature, precipitation), primary production variables, food web components from zooplankton to predators, and anthropogenic impacts (e.g., habitat loss, hatcheries). We included salmon traits (survival, abundance, residence time, fitness, and size) as response variables. We invoked perturbations to each node and to suites of drivers and evaluated the responses of these variables. The model showed that anthropogenic impacts resulted in the strongest negative responses in salmon survival and abundance. Additionally, feedbacks through the food web were strong, beginning with primary production, suggesting that several food web variables may be important in mediating effects on salmon survival within the system. With this model, we were able to compare the relative influence of multiple drivers on salmon survival.

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Introduction

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23   Problems of complex interactions are common in many fields, including medicine,

24   economics, and ecology (Levins 1974). In ecology, much attention has been given to describing

25   food webs and interactions among species (Paine 1966, May 1974, Pimm et al. 1991, Dunne et

26   al. 2002a). But often, these food webs are nested within larger ecological or social-ecological

27   contexts where exogenous forces influence components of the food web system. External

28   forcings may include physical drivers, anthropogenic impacts, or ecosystem components that

29   are not characterized within the focal network. In social-environmental systems, tools that

30   incorporate ecological properties, abiotic variables, and management actions within the same

31   analytical framework are needed to accurately understand the dynamics of complex systems

32   and evaluate potential management actions (Liu et al. 2007). However, rarely are compatible

33   datasets available for this type of analysis. Here we use a qualitative network model, a

34   conceptually based modeling approach, and a suite of simulations to address questions about

35   the relative impacts of human and natural influences on early marine survival of juvenile

36   salmon.

37   In recent years, attention has turned to marine life-history stages of Pacific salmon

38   (*Oncorhynchus* spp.) in an effort to understand population declines and the subsequent failure

39   to rebound, given myriad conservation and restoration efforts in freshwater streams. In

40   Chinook salmon, coho salmon, and steelhead (*O. tshawytscha*, *O. kisutch*, and *O. mykiss*,

41   respectively), declines in marine survival have been evidenced within the Salish Sea (Puget

42   Sound, WA, USA and the Strait of Georgia, BC, Canada) that have not been seen in coastal

43   populations (Beamish et al. 2010, Johannessen and McCarter 2010, Zimmerman et al. 2015,

44 Ruff et al. 2017, Kendall et al. 2017). These inland water bodies serve as habitats for juvenile

45 salmon as they pass from natal streams to ocean waters during their outmigration. Yet, because

46 of complex anthropogenic changes brought about by population increases and the associated

47 human activity in these waters, it is likely that a number of factors and their cumulative—

48 synergistic or additive—effects are contributing to early-marine mortality. Other salmon

49 species, such as chum, pink and sockeye salmon (*O. keta*, *O. gorbuscha*, and *O. nerka*,

50 respectively), have not experienced similar declines (Debertin et al. 2017), suggesting that life-

51 history characteristics may also contribute to increased mortality for some species in this

52 region. Teasing apart which factors have negatively impacted survival of juvenile salmon in

53 marine waters is of concern to local, regional, and federal governments and other stakeholders

54 (e.g., Salish Sea Marine Survival Project, http://marinesurvivalproject.com/) and management

55 actions are being sought to lessen impacts and increase survival during this period.

56 Correlative studies of salmon abundance and environmental factors have been ongoing

57 in the greater region for many years (Pearcy 1988, Beamish et al. 2000, Teo et al. 2009, Burke et

58 al. 2013). Food web models for the Strait of Georgia (Priekshot 2008) and Puget Sound (Harvey

59 et al. 2012) show primary production as an important driver in the biological system and also

60 the effects of top predators in creating trophic cascades and influencing food web dynamics in

61 the mid-trophic levels where time-series data are sparse (Harvey et al. 2012). Even with an

62 understanding of the main variables in a given system, measuring abundances of each variable

63 and the flux of energy among them often poses a logistical challenge (Christensen and Walters

64 2004). These models do not easily incorporate non-fisheries anthropogenic impacts, such as

65 habitat loss or contaminant exposure, yet we understand that in many systems diverse but

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66   cumulative impacts can play a role in species population change. For this reason, conceptually

67   based models, incorporating a broader array of variables, are an important tool in providing an

68   integrated picture of ecological and human drivers of ecosystem change.

69   One tool for evaluating the relative influence of ecosystem components is Qualitative

70   Network Modeling (QNM, also called Qualitative Network Analysis, QNA, or Loop Analysis,

71   Levins 1974, Puccia and Levins 1985, Raymond et al. 2011, Melbourne-Thomas et al. 2012,

72   Harvey et al. 2016), which is advantageous for understanding a system of complex interactions

73   which are not fully specified and when precise measurement is impossible, but when some

74   mechanistic understanding of interactions exists. It allows for the testing of competing

75   hypotheses, given different model structures or the invocation of perturbations to one or more

76   of the model variables. QNM does not explicitly include non-linear direct effects, which occur in

77   and influence social and ecological systems, however, it may help to determine the relative

78   impacts of competing hypothesized factors or indicate where empirical work could be focused

79   to improve system understanding (Levins 1974).

80   Researchers have used QNM for evaluating ecosystem response to ocean acidification in

81   shellfish management (Reum et al. 2015) and the impacts of eutrophication and species

82   management within a food web (Carey et al 2013), and for discerning the impact of

83   management actions for species recovery (Harvey et al. 2016) in the Pacific Northwest. QNM is

84   an important conceptual tool for discerning relative impacts of ecosystem components from

85   which more complex, data-driven modeling efforts can stem. Here we apply this technique to

86   evaluate a suite of potential drivers thought to be contributing to increased early marine

87   mortality in a group of Pacific salmon in the Salish Sea. Using a simulation framework, we

88   invoke perturbations to each model variable and suites of variables based on salmon early

89   marine survival hypotheses, and assess model response related to the salmon species of

90   concern. This work is a foundational step in understanding the impacts of multiple drivers of

91   marine survival declines in Salish Sea salmon.

Methods

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93   We used QNM to address our primary question regarding the relative impacts of various

94   factors on salmon early marine survival. Our analysis had three main steps: (1) construct an

95   enhanced conceptual model showing positive, negative, and neutral relationships; (2) generate

96   a pool of stable simulated models with random weights applied to each model linkage; and (3)

97   invoke one or more perturbations based upon mechanistic understanding of the system and

98   determine the model response.

Conceptual Model

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100   To construct our conceptual model of the Salish Sea system, we gathered existing

101   literature and experts on ecosystem components from within and outside of the project

102   technical team. The technical team includes scientists from resource agencies, universities, and

103   tribal entities, with expertise ranging from salmon genetics to disease ecology to numerical

104   ocean modeling. We began by developing a list of over 40 possible variables drawn from

105   hypotheses about the decline of Pacific salmon survival within the system (Salish Sea Marine

106   Survival Project hypotheses, http://marinesurvivalproject.com/the-project/key-hypotheses/).

107   The variables included: physical forcings, biological components from primary production to top

108   predators and competitors, and anthropogenic variables. We drew a draft model based upon

109   our knowledge of the system and existing literature and then we conducted small meetings

110   with experts on particular components, such as disease ecology or oceanography, and

111   iteratively developed a working conceptual model. We sought out additional feedback from

112   those working within the Salish Sea, but not on the technical team, on both the model

113   components and structure, and received further feedback during public presentations to refine

114   the conceptual model.

115   For the final model, we grouped model variables into several driver groups:

116   environmental factors, primary production, food web interactions, and anthropogenic impacts

117   (Table 1). While the conceptual model is not exhaustive, it does include many of the drivers

118   identified in our working hypotheses and reflects known interactions within the ecosystem. The

119   inclusion of model variables that are not biomass pools (e.g., temperature, habitat loss)

120   highlights the flexibility of the qualitative modeling approach. Focusing on physical, bottom-up,

121   top-down, and anthropogenic factors fit with the working hypotheses of the Marine Survival

122   Project and enabled exploration of combinations of diverse variables.

123   The emphasis of the modeling effort was on understanding sources of decreased

124   survival of the focal salmon species (Chinook, coho, and steelhead), which have shown an

125   overall declining population trend (Figure 1, left panel, Appendix 1 for details), in addition to a

126   decline in marine survival (Zimmerman et al. 2015, Ruff et al. 2017, Kendall et al. 2017). Central

127   to our approach was specifying multiple salmon characteristics as modeled network nodes,

128   namely: size, fitness, residence time, abundance, and survival. We used these traits as primary

129   response variables throughout our analysis. While marine survival (herein 'survival') was our

130   principal variable of interest, we included additional traits to evaluate the relative impact to

131   metrics of salmon performance. We included 'other salmon' as a model variable, representing

132   pink, chum, and sockeye salmon, because the migration timing of all Pacific salmon species

133   means competitive interactions occur. However, the species represented by the 'other salmon'

134   variable have not experienced the same negative population trends (Irvine and Ruggerone

135   2016, Figure 1 and Appendix 1 for details) and are seen as important to the analysis but

136   different from the focal species. While the emphasis was on representing the most direct

137   impacts on the focal salmon traits, we recognize that many of the model variables (e.g.,

138   temperature) could potentially have direct connections to other model nodes; we have

139   included these where interactions were important for understanding implications for the focal

140   salmon variables or where existing literature has shown strong connections.

141   We defined relationships among variables as positive, negative, or null, based upon

142   mechanistic understanding of the Salish Sea system and input from regional experts. To

143   implement the simulation modeling, we developed a conceptual digraph using the directed

144   graphing software, Dia (v.0.97.2) to represent the model system and the interactions among

145   variables. This diagram served as the foundation for our qualitative modeling.

146   Simulated Networks

147   We used the *QPress* package for Qualitative Network Analysis (Melbourne-Thomas et al.

148   2012) with custom modifications in R (R Core Team 2016) to interpret the conceptual digraph,

149   construct simulated networks, and perform our analyses. The digraph is interpreted as an

150   interaction matrix, **A**, where each directed pairwise interaction is represented as coefficients a_{ij}.

151   **A** is treated similarly to a community interaction matrix, wherein the rate of change of any

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152   given node is a continuous function of all other interacting nodes (Levins 1974; Puccia and

153   Levins 1985). The interacting components (i.e., model nodes) are set up as a series of

154   differential equations:

$$\frac{dx_i}{dt} = f_i(x_1, x_2, \ldots, x_n;\ c_1, c_2, \ldots, c_m)$$

155   where x_i is the density of model component (population) i, the cs are growth parameters, and f_i

156   is a function describing per capita growth-rate of that population (Raymond et al. 2011).

157   Therefore, the interaction coefficients a_{ij} describe the effect of a change in the level of

158   component j on the level of component i, as defined by the partial derivative of f_i with respect

159   to N_j: $a_{ij} = \partial f_i / \partial x_j$ evaluated at the equilibrium (Levins 1974, Raymond et al. 2011, Melbourne-

160   Thomas et al. 2012).

161   Given a network model and corresponding interaction matrix, **A**, the negative of the

162   inverse community matrix ($-\mathbf{A}^{-1}$) yields estimated changes in the equilibrium abundances of

163   each component x as a function of a sustained (press) perturbation of one or more system

164   components (Puccia and Levins 1985). The *QPress* analysis package provides routines for

165   evaluating the impact of a press perturbation to the system through simulation. For each

166   simulation, a weight (drawn from a random uniform distribution, 0-1) was assigned to each

167   linkage (edge). These weights were positive or negative depending upon the relationship

168   between the two endpoints. If the resulting model with all assigned weights was stable (i.e.,

169   converged), the model was accepted. We simulated the network c. 122,000 times to result in

170   10,000 stable simulated networks. We then assessed the proportion of model runs with

171   positive, negative, and neutral responses given changes to particular nodes (see below).

172   We assessed the sensitivity and robustness of the model. We experimented with

173 changing both the distribution and the variance of the weighting scheme, but did not find large

174 differences in results, so maintained the default weighting for our analyses. We explored the

175 weights of linkages in the balanced models to look for anomalies (methods and results in

176 Appendix 2). Additionally, we calculated distance to the Survival node via pathways from each

177 model variable to check for effects of model structure, described network properties such as

178 connectance and linkage density, and evaluated model behavior with the sequential addition of

179 perturbed nodes and a set of 'cumulative effects' of both influential and neutral nodes.

180 Invoking Perturbations

181   To test hypotheses regarding marine survival, we developed *a priori* perturbations to

182 each model node (Table 2). The direction of the perturbation (increase or decrease) was based

183 upon our understanding of the system, changes that have occurred concomitant with declines

184 in salmon marine survival (since the 1970s), and expected impacts as a result of anthropogenic

185 change (Appendix 3). We employed several cumulative effects scenarios and modified existing

186 software functions to meet our analytical objectives.

187   First, we perturbed each node individually and observed outcomes to all other model

188 variables. This allowed for a simple comparison of impacts on the focal salmon metrics from

189 each variable and the ability to compare the extent of the impact to that from any other

190 variable. Second, we evaluated the relative effects of different groups of drivers (Table 3). For

191 example, we were interested in food web effects, so we simultaneously decreased forage fish,

192 increased marine mammals, decreased piscivorous fish, and increased gelatinous

193   zooplankton—trends that have been observed in Puget Sound—and observed the impacts to

194   the other model components. For each driver group, we selected four nodes to perturb,

195   thereby standardizing the level of change invoked. By comparing impacts to salmon traits from

196   primary production, food web, environmental, and anthropogenic drivers, we were able to

197   query the relative impacts of each of these groups.

198   Finally, we developed scenarios based upon observed changes within three regions of

199   Puget Sound to see how well the model reproduced cumulative impacts in terms of response to

200   the focal salmon metrics, especially survival. The three regions were: (a) South Sound, with a

201   known decline in salmon abundance and cumulative impacts including increased gelatinous

202   zooplankton, nutrients, contaminants and hatchery production, and decreased forage fish

203   abundance; (b) Hood Canal, which has had relatively stable salmon abundances, but impacts in

204   oceanography, including increased stratification and temperature and low dissolved oxygen;

205   and (c) Central Basin which has shown a decline in salmon abundance, relatively less than South

206   Sound, but with a different suite of cumulative impacts including habitat loss, contaminant

207   input, and decreased primary production. In reality, causes of declining survival are likely multi-

208   faceted, complex, and non-linear, and this modeling exercise allowed us to examine the relative

209   influence of many factors within one modeling framework.

210   Results

211   Model

212   Our final conceptual model had 33 nodes including salmon traits and atmospheric,

213   oceanographic, primary production, food web, and anthropogenic drivers (Table 1, Fig. 2,

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214   Appendix 3). There were a total of 150 linkages out of 1089 potential linkages within the model.

215   This gives a network density or connectance (realized linkages/potential linkages) of 0.138 and

216   a linkage density (average # of linkages/node) of 4.55. Connectance has been linked with

217   network stability in ecological networks (Dunne et al. 2002b) and in social network theory

218   applied to behavioral ecology (Sih et al. 2009), and also to resilience in social-ecological systems

219   (Janssen et al. 2006). The most highly connected nodes were temperature, diatoms, and

220   (salmon) abundance with a total of 11 connections each; the other salmon and zooplankton

221   nodes were both highly connected (10 linkages) and highly influenced by other variables (10

222   and 9 influencing nodes, respectively, Table 1). All nodes were a minimum distance of four

223   nodes or fewer from survival, but the range of feedback linkages varied greatly, from 1 to 10.

224   Each model node included a self-regulating feedback to better represent ecological limits and

225   to aid in model convergence; the exception was survival, which was considered the primary

226   variable of interest and was not constrained.

227   To assess whether the proximity of each model node to survival influenced the

228   outcomes of our analysis (i.e., are nodes more directly connected to survival more likely to

229   result in stronger outcomes?), we evaluated the proportion of negative results for survival with

230   the minimum nodal distance to survival and found no relationship. Both closely connected

231   nodes (minimum nodal distance of 1) and those more distant (≥2 nodes away), resulted in a

232   range of negative responses (<20% to >95%) with respect to survival. Thus, we do not believe

233   the model structure strongly confounded our results.

234   Perturbations

235   The results of the press perturbations to each node showed that anthropogenic impacts

236   resulted in the most consistent negative responses in salmon traits, specifically survival and

237   abundance (Table 2, Appendix 4). Here we use consistency of response to refer to the relative

238   proportion of outcomes that were positive or negative given a perturbation—a strongly

239   consistent response was when proportionally more simulated models (here >80%) had positive

240   or negative responses for the node of interest, while a neutral response resulted when the

241   simulated outcomes were equally positive/negative in outcome.

242   Individual perturbations showed an increase in CO_2 resulted in a consistently positive

243   response in survival and abundance; CO_2 positively influences diatoms in the model, with

244   positive effects cascading through the food web. Conversely, a decrease in diatoms (primary

245   production) resulted in a consistently negative response in survival and abundance, as well as

246   negatives outcomes to zooplankton and turbidity. A direct perturbation to zooplankton

247   (decrease) resulted in strongly consistent negative responses in fitness and size, but less

248   consistently negative results in survival and abundance. On the other hand, a direct decrease to

249   turbidity resulted in a consistent positive response in the individual traits, fitness and size, but

250   slightly negative responses in survival and abundance, population-level traits. This is despite the

251   fact that turbidity directly and positively affects survival in the model; this relationship is a

252   result of the association of turbidity with primary production and the resulting predation

253   dynamics in the model. A decrease in the predators (piscivorous fish and birds) resulted in

254   positive responses in survival and abundance and more ambiguous impacts to size and fitness.

255   Marine mammals, also known predators of salmon, but with increasing populations (and thus a

256   positive perturbation), had a neutral response on all salmon response variables. Unexpectedly,

257   increased harvest had a positive effect on survival; harvest has a direct negative effect on

258   abundance within the model, but the feedback to survival is mediated by the food web,

259   specifically forage fish and zooplankton, which may moderate the harvest impacts to survival

260   through reduced competition. This same result indicates that strong feedback mechanisms, like

261   density dependence, were simulated by the model and highlights the importance of complex

262   food web interactions for salmon survival.

263   The results of the driver group analysis, which evaluated cumulative impacts from one

264   section of the network, showed anthropogenic impacts to have predominantly negative effects

265   on survival, abundance, and fitness, with over 85% of the simulations having negative

266   responses within these model groups (Fig. 3). For the environmental driver group, most

267   simulation results were positive for survival and abundance, but neutral for the other response

268   variables. The primary production group showed consistently negative results in survival and

269   abundance, indicating that changes to primary production can have strong impacts on salmon

270   via the food web. Interestingly, the food web manipulation yielded strong negative responses

271   on the salmon individual traits (size and fitness) but more neutral response on the population-

272   level traits (abundance and survival). The other salmon category had a consistently positive

273   response in both the food web and anthropogenic driver simulations, indicating that conditions

274   that are less favorable within the food web for the focal salmon species may not be detrimental

275   for other species, with diets that tend to be more planktivorous and generally shorter rearing

276   times within the Salish Sea.

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277   For the regional differences, where we modeled three different regions of Puget Sound

278   with respect to salmon survival, our model replicated the observed trends within these regions,

279   with strong negative responses in focal salmon survival, abundance, and fitness in both South

280   Sound and Central Basin. The results for Hood Canal were more weakly negative for salmon

281   survival and abundance than in the other regions, and were neutral for fitness and size,

282   suggesting that some of the oceanographic changes evidenced in Hood Canal may be less

283   detrimental for salmon. Responses of other salmon were consistently positive in all three

284   regions, reflecting observed population trends (Fig. 1). Therefore, although our model is a

285   generalization of the processes occurring in the southern portion of the Salish Sea, it does

286   replicate observed trends in the region.

287   We recognize that many of the perturbations invoked within the model are happening

288   concurrently. To evaluate whether the model would maintain robustness when multiple

289   interacting factors (e.g. cumulative effects) were invoked, we sequentially added disturbances

290   to the model and evaluated the outcomes. When influential individual drivers were included

291   (from Table 2), the results were strongly negative for survival and abundance. We compared 10

292   of the strongest responding nodes with 10 that showed neutral influence on survival and

293   compared the results (Fig. 4). We observed that the influential individual nodes resulted in

294   consistently negative impacts to survival, while the response was neutral for the weaker suite

295   of disturbances.

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Discussion

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297   Our model showed that a wide variety of drivers had negative effects on early marine

298   survival of coho salmon, Chinook salmon and steelhead. The impacts on the other salmon

299   variable (representing pink, chum, and sockeye) were neutral or positive. With only five drivers

300   (precipitation, river flow, microbial detritivores, zooplankton, and ichthyoplankton) negatively

301   influencing the other salmon node in our simulations, the model structure seemed to capture

302   the reduced impacts to these species within the Salish Sea (Fig. 1, Debertin et al. 2017). The

303   combination of drivers having negative effects on attributes of salmon fitness and survival

304   suggests that a single sector of the network is insufficient for explaining increased marine

305   mortality and that feedbacks and complex interactions may both exacerbate and mediate the

306   effects of individual drivers.

307   Anthropogenic factors induced negative responses in salmon traits, especially survival,

308   abundance, and fitness. The factors are both direct (e.g., contaminants and disease) and

309   mediated by the food web (e.g., hatcheries, with increased production leading to competitive

310   interactions; and habitat loss, which has a negative effect on salmon residency and fitness, but

311   also on forage fish, because nearshore habitat is critical to forage fish spawning). There are

312   likely indirect connections that were unaccounted for in our model that may make these

313   impacts even stronger in the real world. The food web components individually did not yield

314   strong responses in salmon survival and abundance, but did impact size and fitness.

315   Considering that many of these linkages are both directly and indirectly tied to salmon, the

316   negative outcomes, even where marginal, should be noted. Additionally, many of the feedbacks

317   present in the model were through the food web. In the driver group analysis, the negative

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318   responses from food web changes to the individual traits of size and fitness is notable. Our

319   model does not have a temporal component, but negative impacts to individual traits would

320   likely manifest in survival and population declines over time.

321   The conceptual model exhibited particularly strong sensitivity to changes in key linkages:

322   the effects of fitness upon size and vice-versa, and of survival upon abundance. These results

323   suggest that processes influencing these factors will strongly influence marine survival and

324   point to the importance of monitoring these pathways. Size and fitness are relatively easy-to-

325   monitor characteristics measured in standard salmon sampling programs. The measurement of

326   size, combined with techniques that can measure growth and fitness, including the use of

327   chemical-based indicators of fitness, such as fatty acid biomarkers (Hook et al. 2014) or

328   hormone markers (Beckman 2011), would provide some indication of how these attributes are

329   changing over time. However, understanding mechanisms for changes in size and fitness is

330   more complex. As our model and existing literature suggest, several factors contribute to

331   changes in size over time, with food web alteration being one of the likely mechanisms.

332   However, these changes are not yet fully understood in the Salish Sea. Our model allowed for

333   comparison of multiple factors and showed that a decrease in primary production had the

334   strongest negative impact on salmon survival. Additional research on the impacts of changing

335   primary production in this system and the links to salmon condition would aid in further teasing

336   apart this relationship.

337   Our response metrics focused on model runs that converged on an equilibrium (i.e., only

338   balanced models were used in the perturbation scenarios). The number of model runs needed

339   (c. 122,000) to get a subset of converged models (10,000) suggests that most models did not

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340   converge to a stable solution. The 'real' Salish Sea is likely represented by one of the many

341   possible combinations and may in fact be unstable, not in a 'converged' state, as our model

342   assumed. Such unstable states are predicted outcomes when ecosystems surpass tipping

343   points (Carpenter and Brock 2006, Samhouri et al. 2017). Alternately, the Salish Sea ecosystem

344   may have reached a new equilibrium: analysis of marine survival trends indicate a steep decline

345   in the 1970s and 80s, leveling off at a low level that has persisted to the present (Zimmerman et

346   al. 2015). Hence, the simulation framework with multiple sets of initial conditions may have

347   allowed us to detect endpoints that include a new equilibrium for marine survival of salmon.

348   The conceptual model underlying the analysis represents a complex set of feedbacks.

349   Additional interconnections that we did not represent would tend to stabilize the system even

350   more (Dunne et al. 2002a, Ives and Carpenter 2007). And while nonlinear properties are

351   fundamental to ecological systems, they are nearly always influenced by feedbacks, an essential

352   component built into our model structure (DeAngelis and Waterhouse 1987, Scheffer et al.

353   2001). The lack of explicit spatial or temporal components within the model limits our ability to

354   make predictions beyond a static snapshot. However, through our comparison of three sub-

355   regions within our system, we were able to compare different starting conditions and gauge

356   model response. While additional complexity in the temporal component would allow for

357   detecting evidence of change over time, the lack of comprehensive empirical data across all

358   ecosystem components currently limits the tractability of such a modeling approach.

359   The model results in and of themselves are informative for comparing among a suite of

360   potential causes of declining marine survival in salmon and in evaluating cumulative effects of

361   these drivers. Additionally, this conceptual model forms the foundation for additional research

362   efforts. Currently, development of multivariable time-series analysis and an end-to-end

363   ecosystem model (Atlantis) is ongoing, via the Salish Sea Marine Survival Project. The

364   development of the Atlantis ecosystem model has been aided by the conceptual underpinnings

365   presented herein. Efforts have been made to develop data streams where the conceptual

366   model has shown important linkages (e.g., a sub-project was initiated using satellite-derived

367   data to better understand variability in primary production in the system). In this way, the

368   qualitative network model is foundational for continuing quantitative modeling work, but is

369   also an important tool for conveying the complexity of the system and the problem to diverse

370   audiences.

371   Our results suggest that teasing out the causes of declines in marine survival will be

372   challenging, multi-faceted, and will involve both understood and unknown feedbacks. Multiple

373   singular factors led to declines in most of the simulations, and suites of ecosystem components

374   had strong effects on marine survival and other salmon attributes. Nevertheless, our ability to

375   distinguish causal factors will likely be improved by tracking multiple ecosystem indicators,

376   especially those influencing salmon size and fitness. As with any model, ours is a simplified

377   version of the ecosystem; however, our approach resulted in a complex representation of

378   declining populations in an ecosystem context that served as a useful tool for identifying

379   relative influences of numerous hypothesized drivers of marine mortality. Through this

380   examination, we have identified some sectors of the ecosystem, such as the food web and

381   anthropogenic impacts, which warrant further examination.

382 Supplementary material

383 For supplementary material accompanying this paper, visit:

384 http://www.journals.cambridge.org/ENC

385

386

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Conflict of Interest

401   None

Human and/or Animal Experimentation

403   None

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Table and Figure Captions

Tables

Table 1. Descriptions of model nodes (variables) in the Salish Sea qualitative network model by driver group. Also shown are: connectivity among nodes, the number of influencing nodes, and the distance to the survival node.

Table 2. Model variables in the Salish Sea qualitative network model with the direction of the press perturbation invoked in the simulations. The response of perturbations to each individual model node on the focal salmon traits (survival, abundance, fitness, size, residence) and the other salmon model group are indicated by the colored boxes. The key to direction and strength of responses of model simulations is in the lower left portion of the table.

Table 3. Perturbations and responses by driver group. Total nodal distance is the sum of the nodal distances of each node to the survival node.

Table 4. Salish Sea subbasin analysis with perturbations invoked and outcomes.

Figures

Figure 1. Salmon population trends within Puget Sound (left most subbasins), the Strait of Georgia (center subbasins) and the Pacific Coast (right) for species with generally decreasing trends (Chinook, coho, and steelhead, left) and increasing or stable populations trends (chum, pink, and cockeye, right). Two abnormally high Pink salmon runs were omitted from the right panel for ease of presentation—these runs had trends of 1.05 and 0.43 and were both from Puget Sound subbasins. Data are from Washington Department of Fish and Wildlife, Pacific States Marine Fisheries Commission, Ogden et al. 2015, and Zimmerman et al. 2015.

Figure 2. Conceptual model of the Salish Sea related to salmon survival. Model variables (shapes) represent food web components (ovals), physical drivers (rectangles), anthropogenic impacts (diamonds) and salmon traits of interest (triangles). Survival is shown as a hexagon and was the primary variable of interest.

Figure 3. Results for the primary response variables for each of the four groups of drivers. Perturbations were according to Table 3 and in all four figures, bars represent the number of runs resulting in negative (dark bars) or positive (light bars) response in the response variable.

Figure 4. Comparison of multiple (*n*=10) strongly influential (top) and neutral (bottom) variables on salmon survival. The influential variables (resulting from the analysis presented in Table 2) were: CO_2, contaminants, diatoms, disease, gelatinous zooplankton, habitat loss, hatcheries, other salmon, temperature, and zooplankton. The neutral variables were: global warming, forage fish, ichthyoplankton, marine mammals, microbial detritivores, nutrients, precipitation, stratification, sunlight, and upwelling. The variables in each set were perturbed simultaneously to simulate cumulative impacts and assess model response. Dark bars show negative impacts to the response variable and light bars show positive responses.

1   Supplementary Material—Salish Sea Salmon Qualitative Network

2   Model

3   Appendix 1. Methods and Data Supporting Figure 1.

4   Methods

5   To arrive at population trends, we compiled available adult run sizes for salmon in rivers
6   throughout the Salish Sea. Data were from Pacific Fishery Management Council Stock
7   Assessment and Fishery Evaluation (SAFE) Documents (http://www.pcouncil.org/salmon/stock-
8   assessment-and-fishery-evaluation-safe-documents/review-of-2015-ocean-salmon-fisheries/),
9   Pacific Salmon Commission Technical Committee Reports
10 (http://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/),
11 Washington Department of Fish and Wildlife, Ogden et al. 2015, and Zimmerman et al. 2015
12 (Table A1.1). We used the longest time series available (typically from 1970s to >2010) and
13 used the methods of Holmes (2001) to estimate a population trend and confidence interval for
14 each run. If total run size (TRS, a total of catch and escapement or number of spawners) was
15 not available, we used escapement/spawner (E) data.

16 Table A1.1 Salmon runs used in the calculation of population trends. TRS=Total Run Size,

17 E=Escapement.

Run	Species	Data	Years	Data Source	Subbasin	Population Trend	95% Confidence Interval
Lake Washington	Chinook	TRS	1975-2014	PSC Joint Tech. Comm. 2016	Central Puget Sound	0.004	0.009
Green	Chinook	TRS	1975-2014	PSC Joint Tech. Comm. 2016	Central Puget Sound	-0.027	0.006
Snohomish	Chinook	TRS	1975-2014	PSC Joint Tech. Comm. 2016	Whidbey	-0.035	0.004
Hood Canal	Chinook	TRS	1981-2014	PFMC 2016	Hood Canal	0.035	0.010
Juan de Fuca	Chinook	TRS	1981-2014	PFMC 2016	Juan de Fuca	-0.006	0.006
South Puget Sound	Chinook	TRS	1981-2014	PFMC 2016	South Sound	0.013	0.005
Nooksack	Chinook	TRS	1981-2014	PFMC 2016	San Juan and Gulf Islands	-0.046	0.007
Skagit Spring	Chinook	TRS	1975-2014	PSC Joint Tech. Comm. 2016	Whidbey	0.014	0.006
Skagit Summer/fall	Chinook	TRS	1975-2014	PSC Joint Tech. Comm. 2016	Whidbey	-0.026	0.005
Stillaguamish	Chinook	TRS	1975-2014	PSC Joint Tech. Comm. 2016	Whidbey	-0.030	0.011

Willapa	Chinook	TRS	1976-2014	PFMC 2016	Pacific Coast	0.021	0.007
Grays Harbor Spring/Summer	Chinook	TRS	1976-2014	PFMC 2016	Pacific Coast	0.018	0.005
Grays Harbor Fall	Chinook	TRS	1975-2014	PSC Joint Tech. Comm. 2016	Pacific Coast	0.013	0.005
Queets Spr/Summer	Chinook	TRS	1976-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	-0.025	0.007
Queets fall	Chinook	TRS	1976-2014	PSC Joint Tech. Comm. 2016	Pacific Coast	0.002	0.004
Hoh Spring/Summer	Chinook	TRS	1976-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	-0.019	0.006
Hoh fall	Chinook	TRS	1976-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	-0.002	0.004
Quillayute spring/summer	Chinook	TRS	1976-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	-0.029	0.005
Quillayute fall	Chinook	TRS	1976-2015	PFMC 2016	Pacific Coast	-0.005	0.005
Hoko fall term	Chinook	TRS	1986-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	0.021	0.009
Fraser Spring/summer	Chinook	TRS	1975-2015	PSC Joint Tech. Comm. 2016	Central Strait of Georgia	0.017	0.002
Harrison	Chinook	TRS	1984-2015	PSC Joint Tech. Comm. 2016	Central Strait of Georgia	0.050	0.004
Lake Shuswap	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Central Strait of Georgia	0.026	0.006
Nanaimo	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	South Strait of Georgia, San Juan and Gulf Islands	-0.018	0.007
Cowichan	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	South Strait of Georgia, San Juan and Gulf Islands	-0.006	0.007
Nimpkish	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Johnstone Strait	-0.052	0.015
Klinaklini	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Johnstone Strait	0.030	0.009
Kakweiken	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Johnstone Strait	-0.043	0.011
Kingcome	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Johnstone Strait	-0.064	0.018
Wakeman	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Johnstone Strait	-0.151	0.028
Marble	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	0.013	0.005
Burman	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	0.061	0.012
Tahsis	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	0.024	0.014
Artlish	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	0.029	0.016
Kaouk	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	0.041	0.026
Tahsish	Chinook	E	1975-2015	PSC Joint Tech. Comm. 2016	Pacific Coast	0.004	0.011
Cedar River Winter	Steelhead	TRS	1987-2013	N. Kendall, WDFW pers. comm	Central Puget Sound	-0.220	0.023
Green River Winter	Steelhead	TRS	1978-2013	N. Kendall, WDFW pers. comm	Central Puget Sound	-0.053	0.004
Puyallup/Carbon Winter	Steelhead	TRS	1983-2013	N. Kendall, WDFW pers. comm comm	Central Puget Sound	-0.077	0.006
White River (Puyallup) Winter	Steelhead	TRS	1986-2013	N. Kendall, WDFW pers. comm	Central Puget Sound	-0.042	0.008

Englishman River winter	Steelhead	E	1982-2015	K. Pellett, pers. comm	Central Strait of Georgia	-0.063	0.011
East Hood Canal Winter	Steelhead	TRS	1989-2013	N. Kendall, WDFW pers. comm	Hood Canal	0.088	0.016
Skokomish Winter	Steelhead	TRS	1985-2006	N. Kendall, WDFW pers. comm	Hood Canal	-0.020	0.013
South Hood Canal Winter	Steelhead	TRS	1988-2013	N. Kendall, WDFW pers. comm	Hood Canal	-0.004	0.009
West Hood Canal Winter	Steelhead	TRS	2003-2013	N. Kendall, WDFW pers. comm	Hood Canal	0.015	0.021
Tsitika River summer	Steelhead	E	1976-2015	K. Pellett, pers. comm	Johnstone Strait	0.008	0.007
Salmon River winter	Steelhead	TRS	1981-2015	N. Kendall, WDFW pers. comm	Johnstone Strait	0.021	0.036
Sequim and Discovery Bays Tributaries Winter	Steelhead	TRS	1987-2013	N. Kendall, WDFW pers. comm	Juan de Fuca	-0.101	0.100
Strait of Juan de Fuca Independent Tributaries Winter	Steelhead	TRS	1991-2009	N. Kendall, WDFW pers. comm	Juan de Fuca	-0.028	0.022
Glendale winter	Steelhead	E	1992-2014	K. Pellett, pers. comm	Pacific Coast	-0.178	0.085
Ahnuhati winter	Steelhead	E	1992-2014	K. Pellett, pers. comm	Pacific Coast	-0.186	0.065
Kakweiken winter	Steelhead	E	1992-2014	K. Pellett, pers. comm	Pacific Coast	-0.206	0.063
Atwaykellesse winter	Steelhead	E	1992-2014	K. Pellett, pers. comm	Pacific Coast	-0.116	0.062
Wahpeeto winter	Steelhead	E	1992-2014	K. Pellett, pers. comm	Pacific Coast	-0.201	0.066
Heber River summer	Steelhead	E	1975-2015	K. Pellett, pers. comm	Pacific Coast	-0.012	0.004
Gordon River summer	Steelhead	E	1998-2015	K. Pellett, pers. comm	Pacific Coast	0.030	0.042
Nisqually Winter	Steelhead	TRS	1980-2013	N. Kendall, WDFW pers. comm	South Sound	-0.107	0.016
Samish Winter	Steelhead	TRS	1979-2013	N. Kendall, WDFW pers. comm	South Strait of Georgia	0.039	0.011
Pilchuck Winter	Steelhead	E	1981-2014	N. Kendall, WDFW pers. comm	Whidbey	-0.020	0.009
Skagit River Summer and Winter	Steelhead	TRS	1978-2013	N. Kendall, WDFW pers. comm	Whidbey	-0.034	0.007
Snohomish System Winter	Steelhead	TRS	1987-2013	N. Kendall, WDFW pers. comm	Whidbey	-0.048	0.012
Snohomish/Skykomish Winter	Steelhead	TRS	1987-2013	N. Kendall, WDFW pers. comm	Whidbey	-0.061	0.010
Snoqualmie Winter	Steelhead	TRS	1987-2013	N. Kendall, WDFW pers. comm	Whidbey	-0.056	0.008
Stillaguamish Winter	Steelhead	TRS	1987-2013	N. Kendall, WDFW pers. comm	Whidbey	-0.075	0.022
Green	Coho	TRS	1973-2010	Zimmerman et al. 2015	Central Puget Sound	0.039	0.014
Puyallup	Coho	TRS	1974-2010	Zimmerman et al. 2015	Central Puget Sound	-0.038	0.008
Big Qualicum	Coho	TRS	1973-2010	Zimmerman et al. 2015	Central Strait of Georgia	-0.143	0.011
Inch	Coho	TRS	1984-2010	Zimmerman et al. 2015	Central Strait of Georgia	0.103	0.023
Big Beef Creek	Coho	TRS	1977-2010	Zimmerman et al. 2015	Hood Canal	-0.025	0.009
Quilcene	Coho	TRS	1979-2010	Zimmerman et al. 2015	Hood Canal	0.039	0.014
Skokomish	Coho	TRS	1973-2010	Zimmerman et al. 2015	Hood Canal	0.013	0.008
Straits	Coho	TRS	1985-2010	Zimmerman et al. 2015	Juan de Fuca	-0.034	0.012
Black	Coho	TRS	1978-2010	Zimmerman et al.	North Strait of	-0.052	0.021

				2015	Georgia		
Puntledge	Coho	TRS	1974-2010	Zimmerman et al. 2015	North Strait of Georgia	-0.151	0.020
Quinsam	Coho	TRS	1978-2004	Zimmerman et al. 2015	North Strait of Georgia	-0.104	0.010
Bingham Creek	Coho	TRS	1976-2010	Zimmerman et al. 2015	Pacific Coast	0.017	0.014
Cowlitz	Coho	TRS	1982-2010	Zimmerman et al. 2015	Pacific Coast	-0.126	0.030
Grays	Coho	TRS	1982-2010	Zimmerman et al. 2015	Pacific Coast	-0.036	0.009
Quinault	Coho	TRS	1977-2010	Zimmerman et al. 2015	Pacific Coast	0.079	0.015
Robertson	Coho	TRS	1975-2010	Zimmerman et al. 2015	Pacific Coast	-0.014	0.013
Satsop	Coho	TRS	1973-2010	Zimmerman et al. 2015	Pacific Coast	0.036	0.010
Washougal	Coho	TRS	1976-2010	Zimmerman et al. 2015	Pacific Coast	-0.102	0.023
Deschutes	Coho	TRS	1977-2008	Zimmerman et al. 2015	South Sound	-0.048	0.041
Chilliwack	Coho	TRS	1982-2004	Zimmerman et al. 2015	South Strait of Georgia	-0.066	0.060
Nooksack	Coho	TRS	1976-2009	Zimmerman et al. 2015	South Strait of Georgia	-0.071	0.028
Skagit	Coho	TRS	1991-2010	Zimmerman et al. 2015	Whidbey	-0.049	0.014
Stilliguamish	Coho	TRS	1981-2014	Zimmerman et al. 2015	Whidbey	-0.013	0.013
Snohomish	Coho	TRS	1981-2014	Zimmerman et al. 2015	Whidbey	-0.026	0.010
Baker	Coho	TRS	1983-2010	Zimmerman et al. 2015	Whidbey	-0.048	0.018
Skykomish	Coho	TRS	1978-2010	Zimmerman et al. 2015	Whidbey	0.012	0.010
Tulalip Bay	Coho	TRS	1974-2010	Zimmerman et al. 2015	Whidbey	0.011	0.017
Green River (Area 10A)	Pink	TRS	2001-2013	A. Dufault, WDFW, pers. comm.	Central Puget Sound	1.053	0.364
Puyallup River (Area 11A)	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Central Puget Sound	0.133	0.038
Chambers	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Central Puget Sound	0.096	0.206
Nisqually R. Drainage	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Central Puget Sound	0.167	0.088
Area 13A streams	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Central Puget Sound	-0.029	0.054
Area 13B streams	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Central Puget Sound	0.036	0.035
Port Gamble	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Hood Canal	0.425	0.593
Dosewallips	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Hood Canal	-0.095	0.028
Duckabush	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Hood Canal	-0.025	0.054
Hamma	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Hood Canal	0.091	0.052
Hoodsport Hatchery	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Hood Canal	0.063	0.024
Misc 12C	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Hood Canal	-0.002	0.041
Skokomish R. Drainage	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Hood Canal	0.093	0.055

Dungeness River	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Juan de Fuca	-0.009	0.053
Elwha River	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Juan de Fuca	-0.182	0.093
Nooksack River	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	South Strait of Georgia	-0.012	0.035
Samish River	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	South Strait of Georgia	0.221	0.068
Fraser	Pink	TRS	1959-2011	Ogden et al. 2015	South Strait of Georgia	0.070	0.030
Skagit River	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Whidbey	0.004	0.030
Snohomish River	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Whidbey	0.080	0.025
Stillaguamish River	Pink	TRS	1959-2013	A. Dufault, WDFW, pers. comm.	Whidbey	0.000	0.027
Lake Washington	Sockeye	E	1972-2015	A. Dufault, WDFW, pers. comm.	Central Puget Sound	-0.005	0.006
Fraser	Sockeye	TRS	1960-2012	Ogden et al. 2015	South Strait of Georgia	0.003	0.004
Baker Lake	Sockeye	E	1970-2015	A. Dufault, WDFW, pers. comm	Whidbey	0.044	0.012
Misc 10 -Seattle	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Central Puget Sound	0.084	0.009
Green-Duwamish River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Central Puget Sound	0.135	0.014
Misc 10e -Port Orchard	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Central Puget Sound	0.022	0.007
Misc 11 -Tacoma	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Central Puget Sound	0.020	0.006
Puyallup River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Central Puget Sound	0.062	0.012
Port Gamble Pens (9a)	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	-0.016	0.009
N. Hood Canal (12)	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	-0.015	0.008
Misc 12b -Hood Canal	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	0.013	0.007
Quilcene River (12a)	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	0.034	0.011
Misc 12c -Hood Canal	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	0.063	0.006
Hoodsport Hatchery	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	0.049	0.010
Skokomish River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	0.073	0.007
Misc 12d -Hood Canal	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Hood Canal	0.025	0.007
Dungeness River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Juan de Fuca	0.052	0.012
Elwha River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Juan de Fuca	-0.061	0.014
Misc Strait Streams	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Juan de Fuca	0.023	0.009
Grays Harbor Wild Runsize	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Pacific Coast	-0.006	0.006
Willapa Bay Wild And Hatchery Escapement And Total Runsize	Chum	TRS	1980-1999	A. Dufault, WDFW, pers. comm	Pacific Coast	-0.010	0.006
Inside South Coast (Non-Fraser)	Chum	TRS	1953-2012	Ogden et al. 2015	Pacific Coast	0.000	0.005
Hecate Lowlands	Chum	E	1954-2012	Ogden et al. 2015	Pacific Coast	-0.014	0.004

North Haida Gwaii	Chum	E	1954-2012	Ogden et al. 2015	Pacific Coast	-0.028	0.009
Portland Inlet	Chum	E	1954-2012	Ogden et al. 2015	Pacific Coast	-0.006	0.005
Rivers Inlet	Chum	E	1954-2012	Ogden et al. 2015	Pacific Coast	-0.009	0.014
Skidegate	Chum	E	1954-2012	Ogden et al. 2015	Pacific Coast	-0.013	0.006
Misc 13 -South Puget Sound	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Sound	-0.018	0.050
Chambers Creek	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Sound	0.004	0.032
Nisqually River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Sound	0.026	0.054
Misc 13a -Minter Creek	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Sound	0.062	0.008
Misc 13b -Olympia	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Sound	0.029	0.003
Nooksack River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Strait of Georgia	0.019	0.005
Samish River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Strait of Georgia	0.007	0.010
Misc 7b Streams	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	South Strait of Georgia	0.082	0.011
Skagit River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Whidbey	-0.026	0.006
Tulalip Tribe	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Whidbey	0.063	0.013
Snohomish River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Whidbey	-0.001	0.011
Stillaguamish River	Chum	TRS	1968-2009	A. Dufault, WDFW, pers. comm	Whidbey	-0.011	0.008

18

19   Appendix 2. Model Sensitivity Analysis

20   Methods

21   To assess the sensitivity of the model linkages in the simulations, we calculated means and

22   standard deviations of the weights for all linkages from the pool of accepted models. Our

23   hypothesis was that some linkages would be more influential in model stability and that those

24   with mean weights different than the expected mean (μ=0.5, given assignments that were

25   random ($U(0,1)$)) would provide some indication of linkage sensitivity.

26   Results

27   Our sensitivity analysis showed that most model edges (linkages between groups) were

28   stable with regard to the weights applied in the simulation routine, with means from the pool

29   of balanced models very close to the expected mean of 0.5 (>75% of 148 edges). However,

30   some model linkages in the pool of accepted models had mean weights above or below the

31   expected mean and we considered these model groups more sensitive (Fig. A2.1). Linkages

32   among salmon traits were most sensitive, with means in the balanced models considerably

33   higher or lower than the expected mean (e.g., Fitness to Size and Survival to Abundance, self-

34   limiting loops on salmon traits). However, some food web components such as Ichthyoplankton

35   and Forage Fish were also in the group of lower-than-expected model means, suggesting that

36   certain food web pathway weights were sensitive in the model simulations. The links with

37   bidirectional connectivity (positive feedbacks, e.g. Fitness to Size, arrows shown in royal blue in

38   Fig. 2) tended to be the most sensitive to the weighting scheme, with lower-than-average

39   weights resulting in balanced models. Model linkages with mean weights above the expected

40   mean included many high trophic level linkages (e.g., Piscivorous Fish to Marine Mammals), as

41   well as self-limiting loops (salmon traits especially), highly connected nodes (e.g. Zooplankton),

42   and top-level predators (Marine Mammals and Piscivorous Birds). The linkages with both

43   higher- and lower-than-expected means (that were not self-limiting loops) tended be highly

44   connected food web components rather than anthropogenic impacts or physical drivers.

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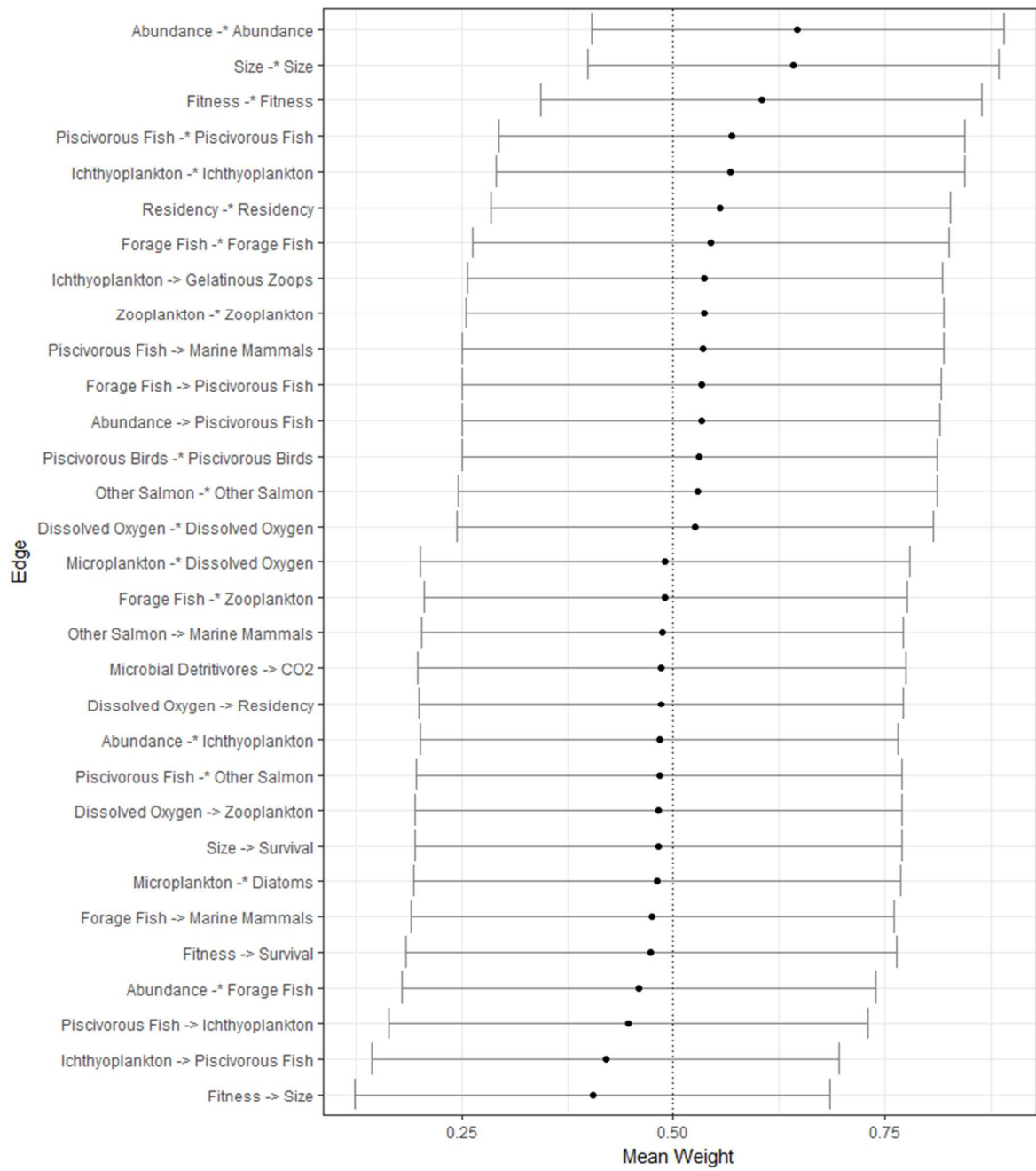
48   Figure A2.1. Calculated means and standard deviations from all model runs for edges (model
49   linkages) with mean values different from the expected mean (0.5). The expected mean is
50   denoted by the black dashed line. Positive linkages are indicated by an arrow and negative
51   linkages are indicated by a dash and asterisk.

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53   Appendix 3. Model Perturbations and References

Drivers	Variables	Reference	Invoked Perturbation
Environmental	Sunlight	Littell et al. 2009	↑
	Winter Storms	Littell et al. 2009	↑
	Precipitation	Mauger et al. 2015, Littell et al. 2009	↑
	Upwelling[1]	Mauger et al. 2015	↓
	Stratification[2]	Mauger et al. 2015	↑
	Temperature	Littell et al. 2009, Field et al. 2006, Hollowed et al. 2001	↑
	River Flow	Littell et al. 2009[3]	↑
	Turbidity	PSEMP 2016, WADOE 2017	↓
	Dissolved Oxygen	Roberts et al. 2014	↓
Production	Nutrients	Roberts et al. 2014	↑
	Microplankton	Moore et al. 2015	↑
	Microbial Detritivores	PSEMP 2016	↑
	Diatoms	Brandenberger 2008, WADOE 2017	↓
Food web	Zooplankton[4]	Li et al. 2013	↓
	Gelatinous Zooplankton	Greene et al. 2015	↑
	Forage Fish	Greene et al. 2015	↓
	Ichthyoplankton	Palsson et al. 1998	↓
	Other Salmon	PFMC 2016, Figure 1	↑
	Piscivorous Fish	Palsson et al. 1998	↓
	Piscivorous Birds	Gaydos and Pearson 2011, Anderson et al. 2009	↓
	Marine Mammals	Chasco et al. 2017	↑
Anthropogenic	Hatcheries	Christie et al. 2012, Waples 1999	↑
	Harvest[5]		↑
	Habitat Loss	Puget Sound Water Quality Action Team 2002	↑
	CO2	Feely et al. 2010	↑
	Global Warming	IPCC 2014	↑
	Contaminants	O'Neill et al. 2009, Meador et al. 2006, Crecelius et al. 1995	↑
	Disease	Roon et al. 2015	↑

54   Literature Cited

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[1] While impacts to upwelling are unknown, we invoked a decrease in upwelling because it would reduce the delivery of nutrients to Puget Sound and potentially disrupt primary production.

[2] Decreased mixing as a result of changes in freshwater flow could lead to increased stratification; while the exact response is unknown (see Mauger et al. 2015), we have invoked an increase in stratification because decreased mixing would likely lead to declines in primary productivity.

[3] River flow is projected to be higher during the winter/spring period of salmon outmigration, but lower in the summers due to decreased precipitation and higher temps. during this season (Littell et al. 2009).

[4] While it is unknown if total abundance of zooplankton has decreased, there is some indication that the community has shifted. We invoked a decrease in zooplankton to reflect this shift.

[5] Harvest has decreased over the time period we used to frame this analysis; however, we were interested in the impacts of increased harvest on salmon survival so invoked an increase in harvest as the perturbation

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163   Appendix 4. Model Output for Individual Perturbations

164   Model output showing 6 model nodes of interest: salmon survival, abundance, size, residency,
165   fitness and other salmon. Other salmon refers to the populations (chum, pink, and sockeye)
166   which have not seen a noticeable decline in survival in recent decades. In each plot box, the
167   model node that was perturbed is shown in the title, with the direction of the press (increase or
168   decrease) shown below. The bar graphs indicate the proportion of model simulations with
169   negative (red bars) and positive (blue bars) outcomes for that model node, given the invoked
170   press perturbation. Where the bars are dark gray, there was no impact to those nodes.
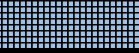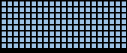
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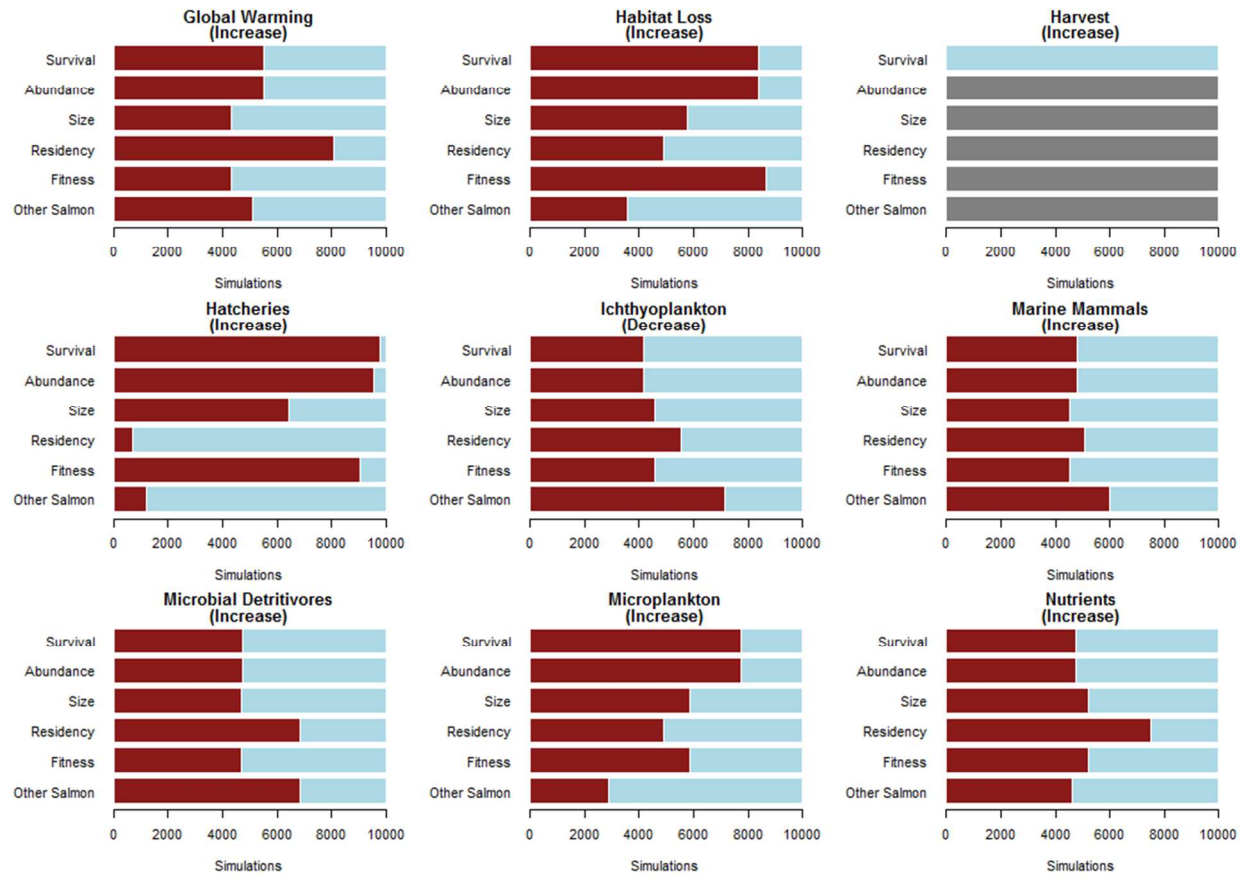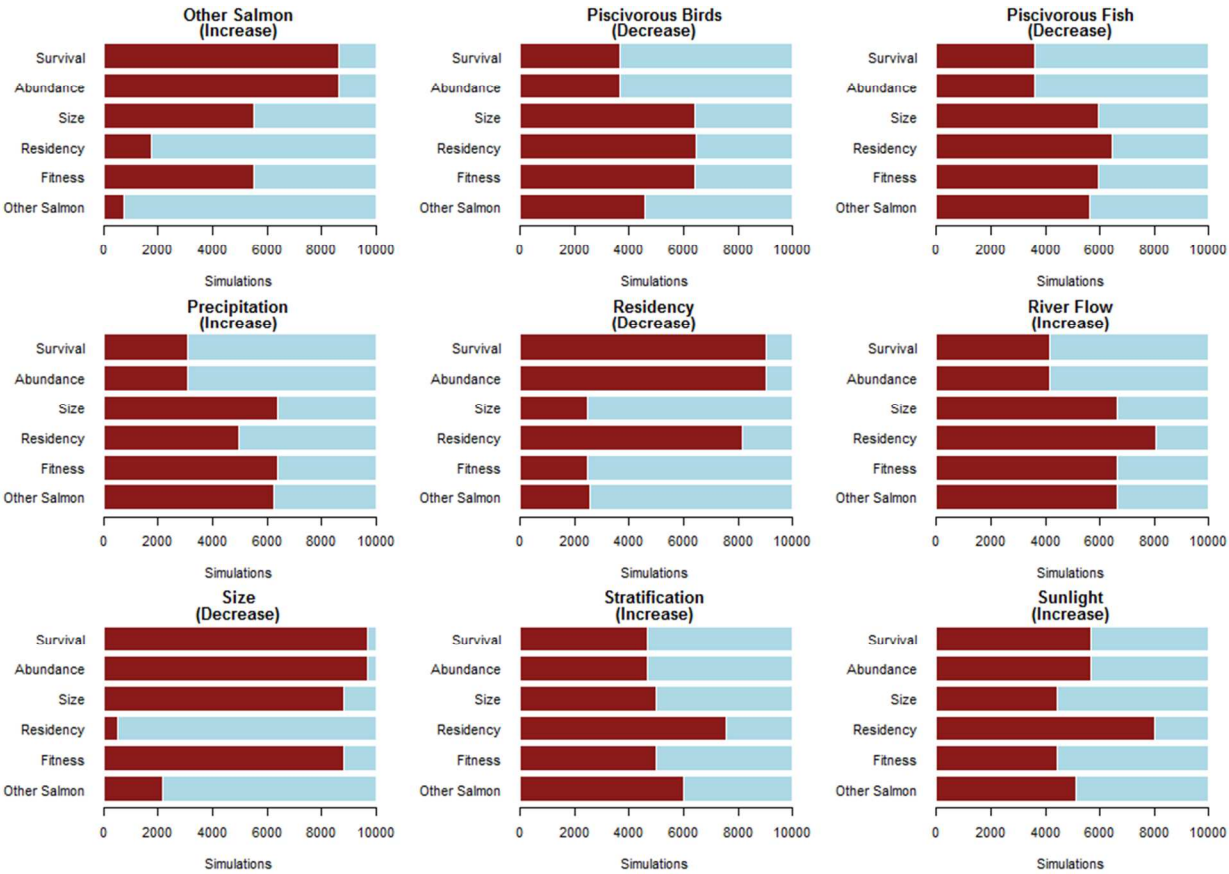
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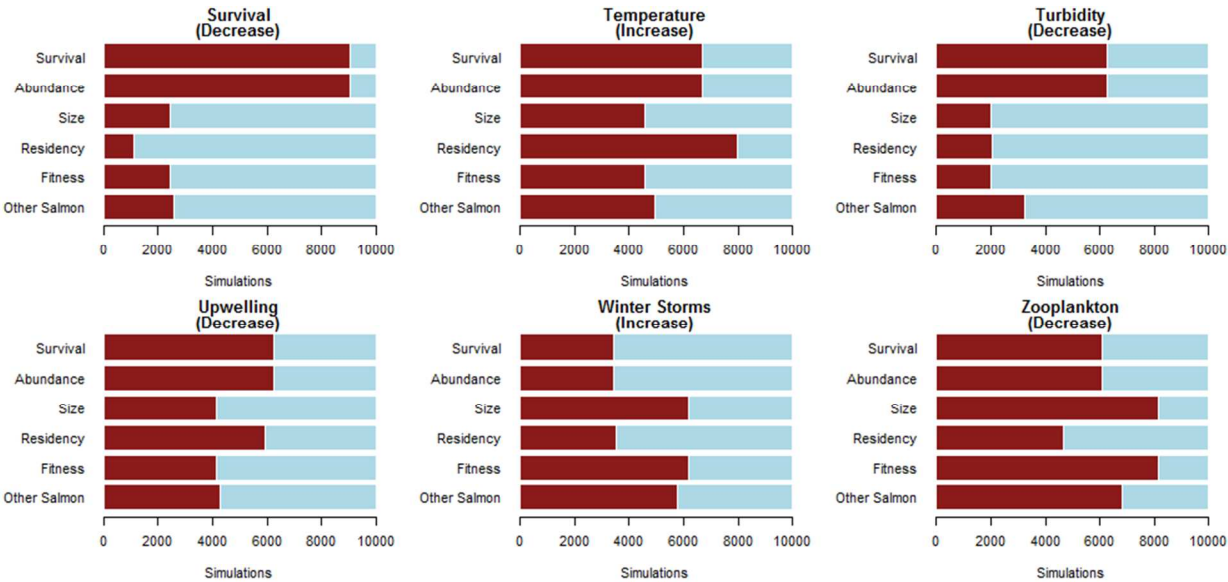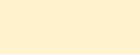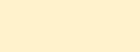
Drivers	Variables	Total # of Connected Nodes	Number of Influencing	Minimum Nodal Distance to Survival	Description
Environmental	Sunlight	4	2	3	Solar radiation
	Winter Storms	5	1	4	Commonly occurring winter storm events
	Precipitation	5	2	3	Annual total precipitation
	Upwelling	5	2	3	Oceanographic upwelling driven by wind and currents in the coastal waters
	Stratification	8	6	3	Formation of layers in the water column resulting from ocean conditions
	Temperature	11	5	2	Water temperature within the Salish Sea (generalized, but upper portion of the water column where salmon occur)
	River Flow	4	2	2	Annual streamflow
	Turbidity	4	3	1	Relative clarity of the water within the Salish Sea
	Dissolved Oxygen	9	7	2	Amount of oxygen available in Salish Sea waters
Production	Nutrients	5	5	4	Total nutrients (generalized to be anthropogenic sources of N)
	Microplankton	9	6	4	Dinoflagellates, e.g. *Noctiluca* spp.
	Microbial Detritivores	7	6	3	Generalized microbes, including bacteria
	Diatoms	11	9	3	Autotrophic phytoplankton
Food web	Zooplankton	10	9	2	Energy-rich zooplankton (e.g., copepods, krill, amphipods)
	Gelatinous Zooplankton	6	5	3	Zooplankton including ctenophores, medusae, and salps
	Forage Fish	9	9	2	Herring, smelt, and other small-bodied fishes
	Ichthyoplankton	7	6	2	Immature stages of fish, residing in the water column
	Other Salmon	10	10	2	Chum, Pink, and Sockeye Salmon
	Piscivorous Fish	7	6	1	Any fish-eating fish; characterized by gadids and scorpaenids in the Salish Sea
	Piscivorous Birds	5	4	1	Any fish-eating bird, such as cormorants and auklets
	Marine Mammals	7	6	1	Generally harbor seals, sea lions, orcas, and dolphins
Anthropogenic	Hatcheries	4	1	2	Production, through human intervention, of large numbers of juvenile fish through breeding programs, specifically salmon
	Harvest	2	1	3	Catch of fish, specifically Steelhead, Coho, and Chinook salmon; generalized to include both recreational and commercial take
	Habitat Loss	5	1	2	Loss on intertidal and subtidal habitats for spawning or rearing
	CO2	5	5	4	Input of carbon dioxide via anthropogenic activities
	Global Warming	3	1	2	The general warming trend of the earth's atmosphere
	Contaminants	6	1	2	Exposure to common toxins like PCBs, PBDE, etc., as well as contaminants of emerging concern (e.g. pharmaceuticals)
	Disease	3	2	2	Exposure to diseases such as *Nanophyetus* and bacterial kidney disease
Salmon Traits	Residence Time	6	5	1	The amount of time an outmigrating salmon spends in the Salish Sea
	Size	6	5	1	Overall size of salmon
	Fitness	7	6	1	Overall health of salmon
	Abundance	11	4	2	Number or biomass of salmon
	Survival	8	7	-	Successful completion of the marine life stage by individuals of a population

Drivers	Variables	Invoked Perturbation	Response Variables					
			Survival	Abundance	Fitness	Size	Residence	Other Salmon
Environmental	Sunlight	↑						
	Winter Storms	↑						
	Precipitation	↑						
	Upwelling	↓						
	Stratification	↑						
	Temperature	↑						
	River Flow	↑						
	Turbidity	↓						
	Dissolved Oxygen	↓						
Production	Nutrients	↑						
	Microplankton	↑						
	Microbial Detritivores	↑						
	Diatoms	↓						
Food web	Zooplankton	↓						
	Gelatinous Zooplankton	↑						
	Forage Fish	↓						
	Ichthyoplankton	↓						
	Other Salmon	↑						
	Piscivorous Fish	↓						
	Piscivorous Birds	↓						
	Marine Mammals	↑						
Anthropogenic	Hatcheries	↑						
	Harvest	↑						
	Habitat Loss	↑						
	CO2	↑						
	Global Warming	↑						
	Contaminants	↑						
	Disease	↑						

Legend:
- Strong Neg. Effect (>80% of runs negative)
- Weak Neg. Effect (60-80% of runs negative)
- Neutral (40-60% of runs positive/negative)
- Weak Pos. Effect (60-80% of runs positive)
- Strong Pos. Effect (>80% of runs positive)

Variable	Driver Group			
	Environmental	Primary Production	Food web	Anthropogenic
Winter Storms	↑			
Precipitation	↑			
Temperature	↑			
Dissolved Oxygen	↓			
Nutrients		↑		↑
Microplankton		↑		
Microbial Detritivores		↑		
Diatoms		↓		
Gelatinous Zooplankton			↑	
Forage Fish			↓	
Piscivorous Fish			↓	
Marine Mammals			↑	
Hatcheries				↑
Habitat Loss				↑
Contaminants				↑
Total Nodal Distance	*11*	*14*	*8*	*11*

Drivers	Perturbations	References	South Sound	Hood Canal	Central Basin
Oceanographic	Nutrients	Roberts et al. 2014	↑		
	Stratification	Mauger et al. 2015		↑	
	Dissolved Oxygen	Roberts et al. 2014		↓	
	Turbidity	PSEMP 2016		↓	
	Temperature	PSEMP 2016		↑	
Food web	Diatoms	PSEMP 2016			↓
	Gelatinous Zooplankton	Greene et al. 2015	↑		↑
	Forage Fish	Greene et al. 2015	↓		↓
	Other Salmon	Fig. 1, this paper		↑	
Anthropogenic Impacts	Contaminants	O'Neill et al. 2009	↑		↑
	Habitat Loss	Hoekstra et al. 2007			↑
	Hatcheries	Hoekstra et al. 2007	↑		

Response Key

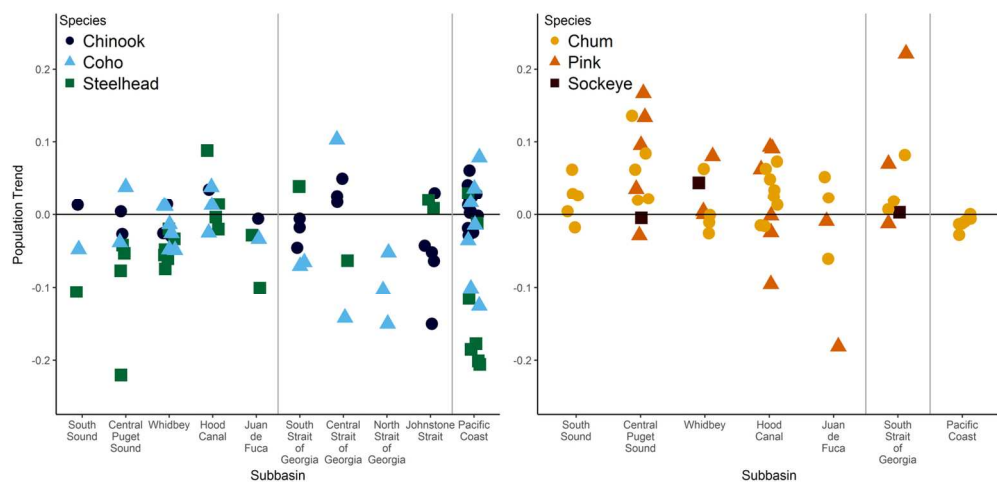| Response Key		Responses	South Sound	Hood Canal	Central Basin
Strong Neg. Effect (>80% of runs were negative)	[dark red]	Survival	Strong Neg.	Weak Neg.	Strong Neg.
Weak Neg. Effect (60-80% of runs were negative)	[orange]	Abundance	Strong Neg.	Weak Neg.	Strong Neg.
Neutral (40-60% of runs positive/negative)	[light]	Fitness	Strong Neg.	Neutral	Strong Neg.
Weak Pos. Effect (60-80% of runs were positive)	[hatched]	Size	Weak Neg.	Neutral	Weak Neg.
Strong Pos. Effect (>80% of runs were positive)	[dark blue]	Residency	Strong Pos.	Weak Neg.	Weak Pos.
		Other Salmon	Strong Pos.	Weak Pos.	Weak Pos.

Figure 1. Salmon population trends within Puget Sound (left most subbasins), the Strait of Georgia (center subbasins) and the Pacific Coast (right) for species with generally decreasing trends (Chinook, coho, and steelhead, left) and increasing or stable populations trends (chum, pink, and cockeye, right). Two abnormally high Pink salmon runs were omitted from the right panel for ease of presentation—these runs had trends of 1.05 and 0.43 and were both from Puget Sound subbasins. Data are from Washington Department of Fish and Wildlife, Pacific States Marine Fisheries Commission, Ogden et al. 2015, and Zimmerman et al. 2015.

139x66mm (300 x 300 DPI)

Figure 2. Conceptual model of the Salish Sea related to salmon survival. Model variables (shapes) represent food web components (ovals), physical drivers (rectangles), anthropogenic impacts (diamonds) and salmon traits of interest (triangles). Survival is shown as a hexagon and was the primary variable of interest.
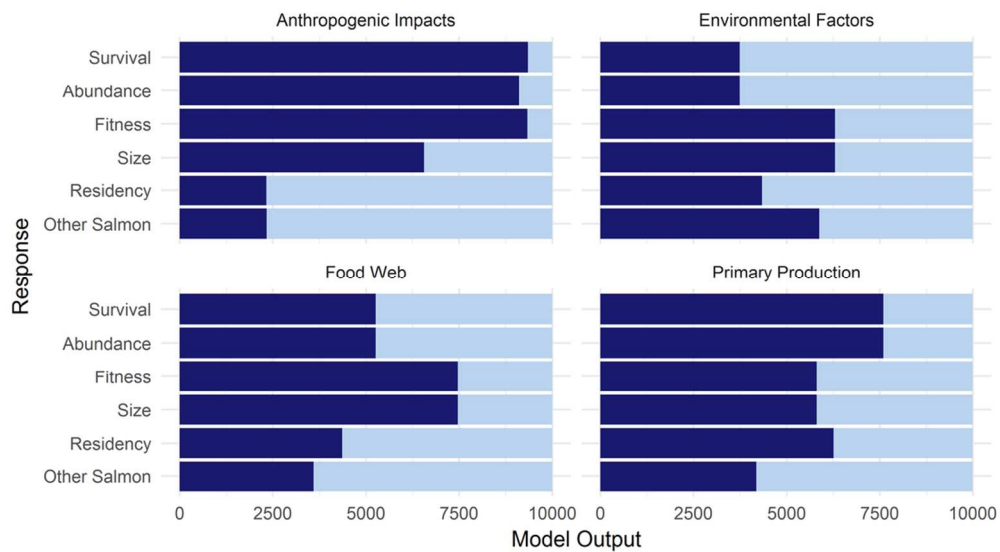
Figure 3. Results for the primary response variables for each of the four groups of drivers. Perturbations were according to Table 3 and in all four figures, bars represent the number of runs resulting in negative (dark bars) or positive (light bars) response in the response variable.
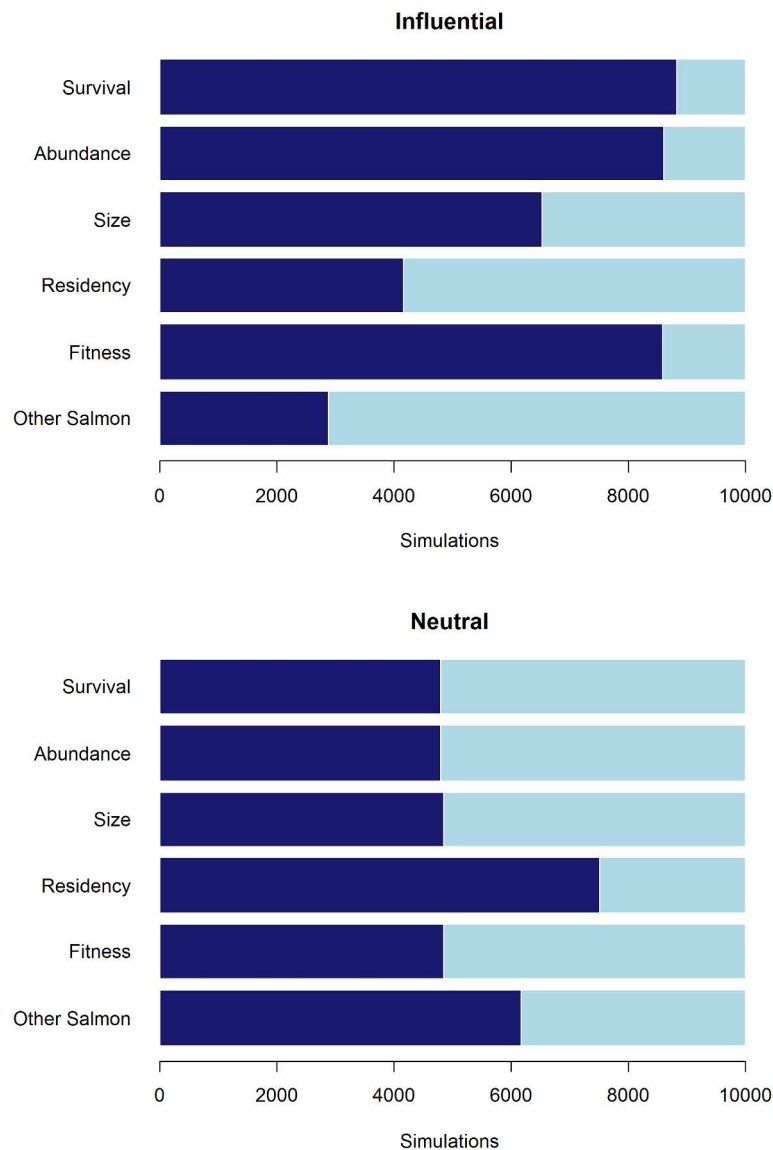
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Figure 4. Comparison of multiple (n=10) strongly influential (top) and neutral (bottom) variables on salmon survival. The influential variables (resulting from the analysis presented in Table 2) were: CO2, contaminants, diatoms, disease, gelatinous zooplankton, habitat loss, hatcheries, other salmon, temperature, and zooplankton. The neutral variables were: global warming, forage fish, ichthyoplankton, marine mammals, microbial detritivores, nutrients, precipitation, stratification, sunlight, and upwelling. The variables in each set were perturbed simultaneously to simulate cumulative impacts and assess model response. Dark bars show negative impacts to the response variable and light bars show positive responses.

177x266mm (300 x 300 DPI)