Using a qualitative model to explore impacts of ecosystem and anthropogenic drivers upon declining marine survival in Pacific salmon

Kathryn L. Sobocinski[*,1,2], Correigh M. Greene[1], Michael W. Schmidt[2]

[1]Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
2725 Montlake Blvd. E
Seattle, WA 98112

[2]Long Live the Kings
1326 5th Ave. #450
Seattle, WA 98101

*Corresponding Author:
kathryn.sobocinski@noaa.gov
(206) 302-2466

Running Head: Salish Sea salmon qualitative network model

Word Count: 5,901, revised: 6,458

1 Summary

2 Coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*O. tshawytscha*), and steelhead (*O.*

3 *mykiss*) in Puget Sound and the Strait of Georgia have exhibited declines in marine survival over

4 the last 40 years. While the cause of these declines is unknown, multiple factors, acting

5 cumulatively or synergistically, have likely contributed. To evaluate the potential contribution

6 of a broad suite of drivers on salmon survival, we used qualitative network modeling (QNM).

7 QNM is a conceptually based tool that uses networks with specified relationships among the

8 variables. In a simulation framework, linkages are weighted and then the models are subjected

9 to user-specified perturbations. Our network had 33 variables, including: environmental and

10 oceanographic drivers (e.g., temperature, precipitation), primary production variables, food

11 web components from zooplankton to predators, and anthropogenic impacts (e.g., habitat loss,

12 hatcheries). We included salmon traits (survival, abundance, residence time, fitness, and size)

13 as response variables. We invoked perturbations to each node and to suites of drivers and

14 evaluated the responses of these variables. The model showed that anthropogenic impacts

15 resulted in the strongest negative responses in salmon survival and abundance. Additionally,

16 feedbacks through the food web were strong, beginning with primary production, suggesting

17 that several food web variables may be important in mediating effects on salmon survival

18 within the system. With this model, we were able to compare the relative influence of multiple

19 drivers on salmon survival.

20

21

Introduction

Problems of complex interactions are common in many fields, including medicine, economics, and ecology (Levins 1974). In ecology, much attention has been given to describing food webs and interactions among species (Paine 1966, May 1974, Pimm et al. 1991, Dunne et al. 2002a). But often, these food webs are nested within larger ecological or social-ecological contexts where exogenous forces influence components of the food web system. External forcings may include physical drivers, anthropogenic impacts, or ecosystem components that are not characterized within the focal network. In social-environmental systems, tools that incorporate ecological properties, abiotic variables, and management actions within the same analytical framework are needed to accurately understand the dynamics of complex systems and evaluate potential management actions (Liu et al. 2007). However, rarely are compatible datasets available for this type of analysis. Here we use a qualitative network model, a conceptually based modeling approach, and a suite of simulations to address questions about the relative impacts of human and natural influences on early marine survival of juvenile salmon.

In recent years, attention has turned to marine life-history stages of Pacific salmon (*Oncorhynchus* spp.) in an effort to understand population declines and the subsequent failure to rebound, given myriad conservation and restoration efforts in freshwater streams. In Chinook salmon, coho salmon, and steelhead (*O. tshawytscha*, *O. kisutch*, and *O. mykiss*, respectively), declines in marine survival have been evidenced within the Salish Sea (Puget Sound, WA, USA and the Strait of Georgia, BC, Canada) that have not been seen in coastal populations (Beamish et al. 2010, Johannessen and McCarter 2010, Zimmerman et al. 2015,

3

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

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

92

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

99

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 (Raymond et al. 2012)

148   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

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:

155
$$\frac{dx_i}{dt} = f_i(x_1, x_2, \ldots, x_n; \ c_1, c_2, \ldots, c_m)$$

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

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

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

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

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

161   Thomas et al. 2012).

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

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

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

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

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

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

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

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

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

171   10,000 stable simulated networks. We then assessed the proportion of model runs with

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

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

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

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

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

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

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

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

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

Invoking Perturbations

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

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

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

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

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

187   software functions to meet our analytical objectives.

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

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

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

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

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

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

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

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

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

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

198   query the relative impacts of each of these groups.

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

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

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

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

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

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

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

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

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

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

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

210   influence of many factors within one modeling framework.

211   Results

212   Model

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

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

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

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

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

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

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

220   related to information flow (Janssen et al. 2006). The most highly connected nodes were

221   temperature, diatoms, and (salmon) abundance with a total of 11 connections each; the other

222   salmon and zooplankton nodes were both highly connected (10 linkages) and highly influenced

223   by other variables (10 and 9 influencing nodes, respectively, Table 1). All nodes were a

224   minimum distance of four nodes or fewer from survival, but the range of feedback linkages

225   varied greatly, from 1 to 10. Each model node included a self-regulating feedback to better

226   represent ecological limits and to aid in model convergence; the exception was survival, which

227   was considered the primary variable of interest and was not constrained.

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

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

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

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

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

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

234   the model structure strongly confounded our results.

235 Perturbations

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

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

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

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

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

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

242 simulated outcomes were equally positive/negative in outcome.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

263 food web interactions for salmon survival.

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

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

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

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

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

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

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

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

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

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

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

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

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

277 times within the Salish Sea.

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

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

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

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

282   survival and growth than in the other regions, and were neutral for fitness and size, suggesting

283   that some of the oceanographic changes evidenced in Hood Canal may less detrimental for

284   salmon. Responses of other salmon were consistently positive in all three regions, reflecting

285   observed population trends (Fig. 1). Therefore, although our model is a generalization of the

286   processes occurring in the southern portion of the Salish Sea, it does replicate observed trends

287   in the region.

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

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

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

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

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

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

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

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

296   of disturbances.

Discussion

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

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

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

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

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

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

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

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

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

307   effects of individual drivers.

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

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

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

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

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

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

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

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

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

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

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

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

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

321   likely manifest in survival and population declines over time.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

337   apart this relationship.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

354   2001). The lack of explicit spatial or temporal components within the model limits our ability to

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

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

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

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

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

360   model is forming the conceptual basis for complex end-to-end modeling efforts and

361   multivariable time-series analyses related to this project, which will be undertaken with

362   available data.

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

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

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

366   efforts. Currently, development of statistical and ecosystem models is ongoing, via the Salish

367   Sea Marine Survival Project. The development of an Atlantis ecosystem model has been aided

368   by the conceptual underpinnings presented herein. And efforts have been made to develop

369   data streams where the conceptual model has shown important linkages (e.g., a sub-project

370   was initiated using satellite-derived data to better understand variability in primary production

371   in the system). In this way, the qualitative network model is foundational for continuing

372   quantitative modeling work, but is also an important tool for conveying the complexity of the

373   system and the problem to diverse audiences.

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

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

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

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

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

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

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

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

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

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

384   anthropogenic impacts, which warrant further examination.

Supplementary material

385

386 For supplementary material accompanying this paper, visit:

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

388

389

Acknowledgements

Financial Support

Conflict of Interest

None

Human and/or Animal Experimentation

None

Literature Cited

Beamish, R.J., D.J. Noakes, G.A. McFarlane, W. Pinnix, R. Sweeting, and J. King. 2000. Trends in coho marine survival in relation to the regime concept. *Fisheries Oceanography* 9:114–119.

Beamish, R.J., R.M. Sweeting, K.L. Lange, D.J. Noakes, D. Preikshot, and C.M. Neville. 2010. Early marine survival of coho salmon in the Strait of Georgia declines to very low levels. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 2: 424-439.

Beckman, B.R. 2011. Perspectives on concordant and discordant relations between insulin-like growth factor 1 (IGF1) and growth in fishes. *General and Comparative Endocrinology*, 170(2):233-252.

Burke, B.J., W.T. Peterson, B.R. Beckman, C. Morgan, E.A. Daly, et al. 2013. Multivariate models of adult Pacific salmon returns. *PLoS ONE* 8(1): e54134.doi:10.1371/journal.pone.0054134

Carey, M.P., P.S. Levin, H. Townsend, T.J. Minello, G.R. Sutton, T.B. Francis, C.J. Harvey, J.E. Toft, K.K. Arkema, J.L. Burke, C. Kim, A.D. Guerry, M. Plummer, G. Spiridonov, and M. Ruckelshaus. 2014. Characterizing coastal foodwebs with qualitative links to bridge the gap between the theory and the practice of ecosystem-based management. *ICES J Mar Sci* 71: 713–724.

Carpenter, S.R., and W.A. Brock. 2006. Rising variance: a leading indicator of ecological transition. *Ecology Letters*, 9(3), 311-318.

Christensen, V. and C.J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172:109-139.

DeAngelis, D.L. and J.C. Waterhouse. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* 57: 1:21.

Debertin, A.J., J.R. Irvine, C.A. Holt, G. Oka, and M. Trudel. 2017. Marine growth patterns of southern British Columbia chum salmon explained by interactions between density-dependent competition and changing climate. *Can. J. of Fish. and Aqua. Sci.* 10.1139/cjfas-2016-0265

Dunne, J. A., R.J. Williams, and N.D. Martinez. 2002a. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5: 558–567.

Dunne, J.A., R. J. Williams, & N.D. Martinez. 2002b. Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*. 99(20): 12917

447   Greene, C.M., L. Kuehne, C.A. Rice, K.L. Fresh, D. Penttila. 2015. Forty years of change in forage
448   fish and jellyfish abundance across greater Puget Sound, Washington (USA): anthropogenic and
449   climate associations. *Marine Ecology Progress Series* 525: 153-170.
450
451   Harvey, C.J., G.D. Williams, and P.S. Levin. 2012. Food web structure and trophic control in
452   central Puget Sound. *Estuaries and Coasts* 35: 821. doi:10.1007/s12237-012-9483-1
453
454   Harvey, C.J., J.C.P. Reum, M.R. Poe, G.D. Williams, and S.J. Kim. 2016. Using conceptual models
455   and qualitative network models to advance integrative assessments of marine ecosystems.
456   *Coastal Management.* 44: 486-503, DOI: 10.1080/08920753.2016.1208881
457
458   Hoekstra, J. M., K. K. Bartz, M. H. Ruckelshaus, J. M. Moslemi, and T. K. Harms. 2007.
459   Quantitative threat analysis for management of an imperiled species: Chinook salmon
460   (*Oncorhynchus tshawytscha*). *Ecological Applications* 17:2061–2073.
461
462   Hook, S., E. Gallagher, and G. Batley. 2014. The Role of Biomarkers in the Assessment of Aquatic
463   Ecosystem Health. *Integrated Environmental Assessment and Monitoring*. 10(3):327-41.
464
465   Holmes, E.E. 2001. Estimating risks in declining populations with poor data. *Proceedings of the*
466   *National Academy of Sciences of the United States of America.* 98: 5072-5077.
467
468   Irvine, J.R. and G.T. Ruggerone. 2016. Provisional estimates of numbers and biomass for
469   natural-origin and hatchery-origin pink, chum, and sockeye salmon in the North Pacific, 1952-
470   2015. NPAFC Doc. 1660. 45 pp. Fisheries and Oceans Canada, Pacific Biological Station and
471   Natural Resources Consultants, Inc. (Available at http://www.npafc.org).
472
473   Ives, A.R. and S.R. Carpenter. 2007. Stability and Diversity of Ecosystems. *Nature*. 317: 58-62.
474
475   Janssen, M. A., Ö. Bodin, J. M. Anderies, T. Elmqvist, H. Ernstson, R. R. J. McAllister, P. Olsson,
476   and P. Ryan. 2006. A network perspective on the resilience of social-ecological systems. *Ecology*
477   *and Society* 11: 15.
478
479   Johannessen, S.C. and B. McCarter. 2010. Ecosystem Status and Trends Report for the Strait of
480   Georgia Ecozone. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2010/010. vi + 45 p.
481
482   Kendall, N.W., G.W. Marston, and M.M. Klungle. 2017. Declining patterns of Pacific Northwest
483   steelhead trout (*Oncorhynchus mykiss*) adult abundance and smolt survival in the ocean. *Can. J.*
484   *of Fish. and Aqua. Sci.* 74(8): 1275-1290.
485
486   Levins, R. 1974. The qualitative analysis of partially specified systems. *Annals of the New York*
487   *Academy of Sciences* 231: 123–138.
488

489 Liu, J., T. Dietz, S.R. Carpenter, C. Folke, M. Alberti, C.L. Redman, S.H. Schneider, E. Ostrom, A.N.
490 Pell, J. Lubchenco, W.W. Taylor, Z. Ouyang, P. Deadman, T. Kratz, and W. Provencher. 2007.
491 Coupled human and natural systems. *AMBIO*. 236: 639–649.

493 Mauger, G.S., J.H. Casola, H.A. Morgan, R.L. Strauch, B. Jones, B. Curry, T.M. Busch Isaksen, L.
494 Whitely Binder, M.B. Krosby, and A.K. Snover, 2015. *State of Knowledge: Climate Change in*
495 *Puget Sound*. Report prepared for the Puget Sound Partnership and the National Oceanic and
496 Atmospheric Administration. Climate Impacts Group, University of Washington, Seattle.
497 doi:10.7915/CIG93777D

499 May, R. M. 1974. Stability and Complexity in Model Ecosystems. *Monographs in Population*
500 *Biology* 6, Princeton University Press, Princeton, New Jersey

502 Melbourne-Thomas, J., S. Wotherspoon, B. Raymond, and A. Constable. 2012. Comprehensive
503 evaluation of model uncertainty in qualitative network analyses. *Ecological Monographs*, 82(4):
504 505–519.

506 Ogden, A.D., J.R. Irvine, K.K. English, S. Grant, K.D. Hyatt, L. Godbout, and C.A. Holt. 2015.
507 Productivity (recruits-per-spawner) data for sockeye, pink, and chum salmon from British
508 Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* 3130: vi + 57 p.

510 O'Neill, S.M., and West, J.E. 2009. Marine distribution, life history traits, and the accumulation
511 of polychlorinated biphenyls in Chinook salmon from Puget Sound, Washington. *Transactions of*
512 *the American Fisheries Society* 138(3): 616-632.

514 Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-76.

516 Pearcy, W. G. 1988. Factors affecting survival of Coho Salmon off Oregon and Washington.
517 Pages 67–73 in W. J. McNeil, editor. *Salmon production, management, and allocation*. Oregon
518 State University Press, Corvallis.

520 Pimm, S. L., J.H. Lawton and J.E. Cohen. 1991. Food web patterns and their consequences.
521 *Nature* 350, 669–674.

523 Preikshot, D.B. 2008. *Public Summary—Computer Modelling of Marine Ecosystems: Applications*
524 *to Pacific Salmon Management and Research*. Vancouver, BC: Pacific Fisheries Resource
525 Conservation Council.

527 Puccia, C. J. and R. Levins. 1985. *Qualitative modeling of complex systems: An introduction to*
528 *loop analysis and time averaging*. Cambridge, MA: Harvard University Press.

530 Puget Sound Ecosystem Monitoring Program (PSEMP) Marine Waters Workgroup. 2016. *Puget*
531 *Sound Marine Waters: 2015 Overview*. S. K. Moore, R. Wold, K. Stark, J. Bos, P. Williams, K.

532   Dzinbal, C. Krembs and J. Newton (Eds). URL:
533   www.psp.wa.gov/PSEMP/PSmarinewatersoverview.php.
534
535   R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for
536   Statistical Computing, Vienna. www.r-project.org
537
538   Raymond, B., J. McInnes, J.M. Dambacher, S. Way, and D.M. Bergstrom. 2011 Qualitative
539   modelling of invasive species eradication on subantarctic Macquarie Island. *Journal of Applied*
540   *Ecology* 48: 181–191.
541
542   Raymond, B, J. Melbourne-Thomas, S. Wotherspoon. 2012. QPress: Qualitative Network
543   Analysis.
544
545   Reum, J.C.P., B.E. Ferriss, P.S McDonald, D.M. Farrell, C.J. Harvey, T. Klinger, and P.S. Levin.
546   2015. Evaluating community impacts of ocean acidification using qualitative network models.
547   *Marine Ecology Progress Series* 536: 11-24.
548
549   Roberts, M., T. Mohamedali, and B. Sackmann, T. Khangaonkar, and W. Long. 2014. *Puget*
550   *Sound and the Straits Dissolved Oxygen Assessment: Impacts of Current and Future Nitrogen*
551   *Sources and Climate Change Through 2070*. Washington Department of Ecology, Publication No.
552   14-03-007. Olympia, WA 151 pp.
553
554   Ruff, C.P., J.H. Anderson, I.M. Kemp, N.W. Kendall, P. Mchugh, A. Velez-Espino, C.M. Greene, M.
555   Trudel, C.A. Holt, K.E. Ryding, and K. Rawson. 2017. Salish Sea Chinook salmon exhibit weaker
556   coherence in early marine survival trends than coastal populations. *Fisheries Oceanography*.
557   DOI: 10.1111/fog.12222
558
559   Samhouri, J. F., K. S. Andrews, G. Fay, C. J. Harvey, E. L. Hazen, S. Hennessey, K. K. Holsman, M.
560   E. Hunsicker, S. I. Large, K. Marshall, A. C. Stier, J. Tam, and S. Zador. 2017. Defining ecosystem
561   thresholds for human activities and environmental pressures in the California Current.
562   *Ecosphere* 8(6):e01860. 10.1002/ecs2.1860
563
564   Scheffer, M., S. Carpenter, J.A. Foley, C. Folke and B. Walker. 2001. Catastrophic shifts in
565   ecosystems. *Nature* 413: 591-596.
566
567   Sih, A., S.F. Hanser, and K.A. McHugh. 2009. Social network theory: new insights and issues for
568   behavioral ecologists. *Behavioral Ecology and Sociobiology* 63: 975.
569
570   Teo, S. L. H., L. W. Botsford, and A. Hastings. 2009. Spatio-temporal covariability in Coho Salmon
571   (*Oncorhynchus kisutch*) survival, from California to southwest Alaska. *Deep Sea Research Part II:*
572   *Topical Studies in Oceanography* 56: 2570–2578.
573

574   Zimmerman, M., J. R. Irvine, M. O'Neill, J. H. Anderson, C. M. Greene, J. Weinheimer, M. Trudel,
575   K. Rawson. 2015. Spatial and temporal patterns in smolt survival of wild and hatchery coho
576   salmon in the Salish Sea. *Marine and Coastal Fisheries* 7(1):116-134.

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.
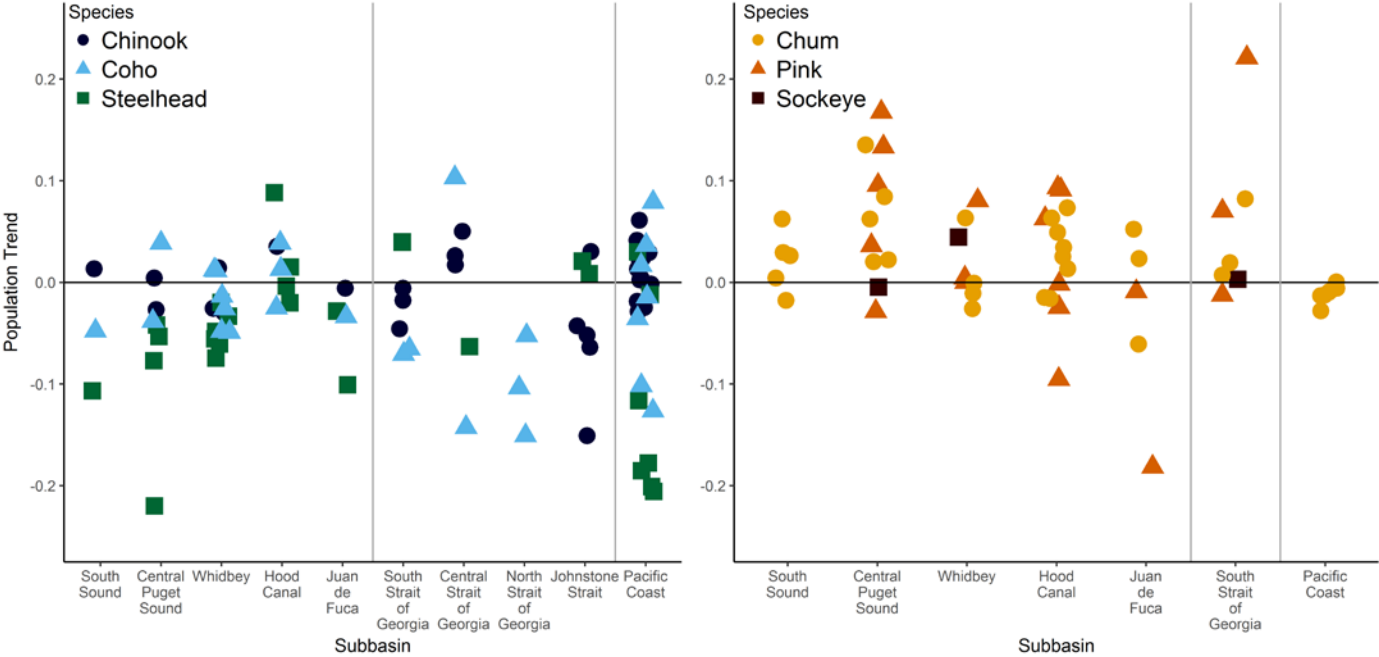
Figure 2. Conceptual model of the Salish Sea related to salmon survival. Model variables (shapes) represent food web components (ovals), physical drivers (rectangles), anthropogenic impacts (diamonds) and salmon traits of interest (triangles). Survival is shown as a hexagon and was the primary variable 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.
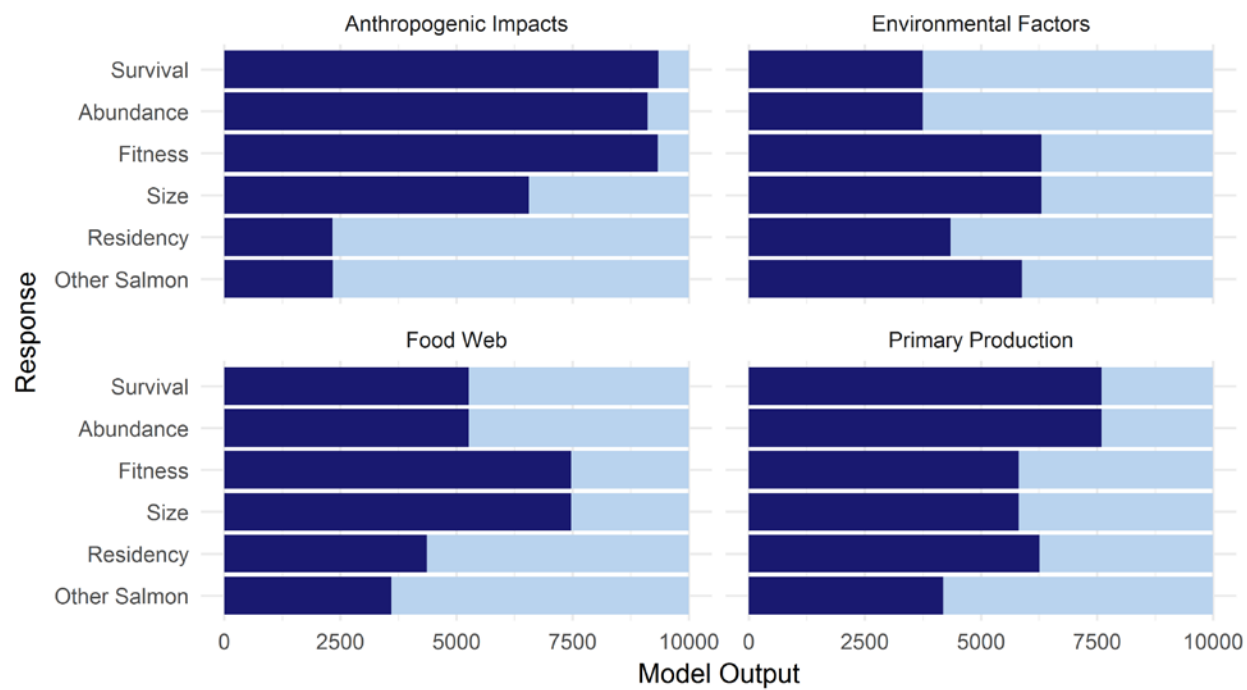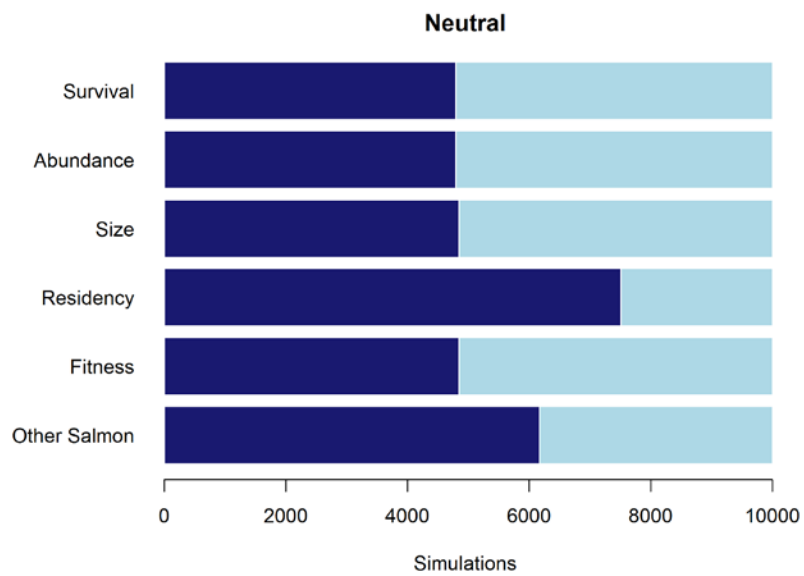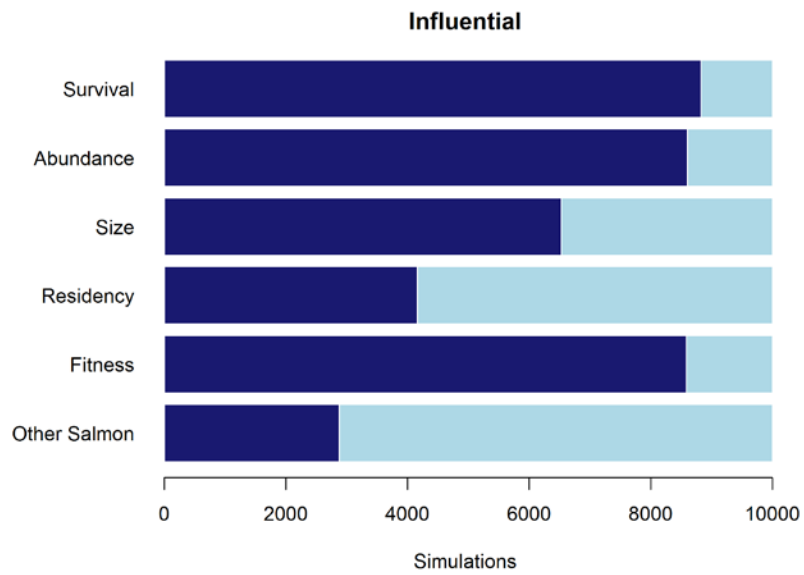
613

614

615

Positive interaction in the direction of the arrow
Negative interaction in the direction of the dot
Bi-directional interaction
Positive feedback
Self-regulating loop

616

29

617

Influential

Neutral

618

31
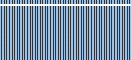
Drivers	Variables	Total # of Connected Nodes	Number of Influencing	Minimum Nodal Distance to Survival	Description
Environmental	Sunlight	4	2	3	Solar radiation
	Winter Storms	5	1	4	Commonly occurring winter storm events
	Precipitation	5	2	3	Annual total precipitation
	Upwelling	5	2	3	Oceanographic upwelling 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

619

Response Variables

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

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)

620

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*

621

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		Responses	South Sound	Hood Canal	Central Basin
Strong Neg. Effect (>80% of runs were negative)	■	Survival	■ Strong Neg.	■ Weak Neg.	■ Strong Neg.
Weak Neg. Effect (60-80% of runs were negative)	■	Abundance	■ Strong Neg.	■ Weak Neg.	■ Strong Neg.
Neutral (40-60% of runs positive/negative)	■	Fitness	■ Strong Neg.	■ Neutral	■ Strong Neg.
Weak Pos. Effect (60-80% of runs were positive)	▥	Size	■ Weak Neg.	■ Neutral	■ Weak Neg.
Strong Pos. Effect (>80% of runs were positive)	■	Residency	■ Strong Pos.	■ Weak Neg.	▥ Weak Pos.
		Other Salmon	■ Strong Pos.	▥ Weak Pos.	▥ Weak Pos.

622

35

Supplementary Material—Salish Sea Salmon Qualitative Network Model

624 Appendix 1. Methods and Data Supporting Figure 1.

625 Methods

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

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

638 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. 2015	North Strait of Georgia	-0.052	0.021
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

639

Appendix 2. Model Sensitivity Analysis

641   Methods

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

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

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

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

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

647   Results

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

666

667

668
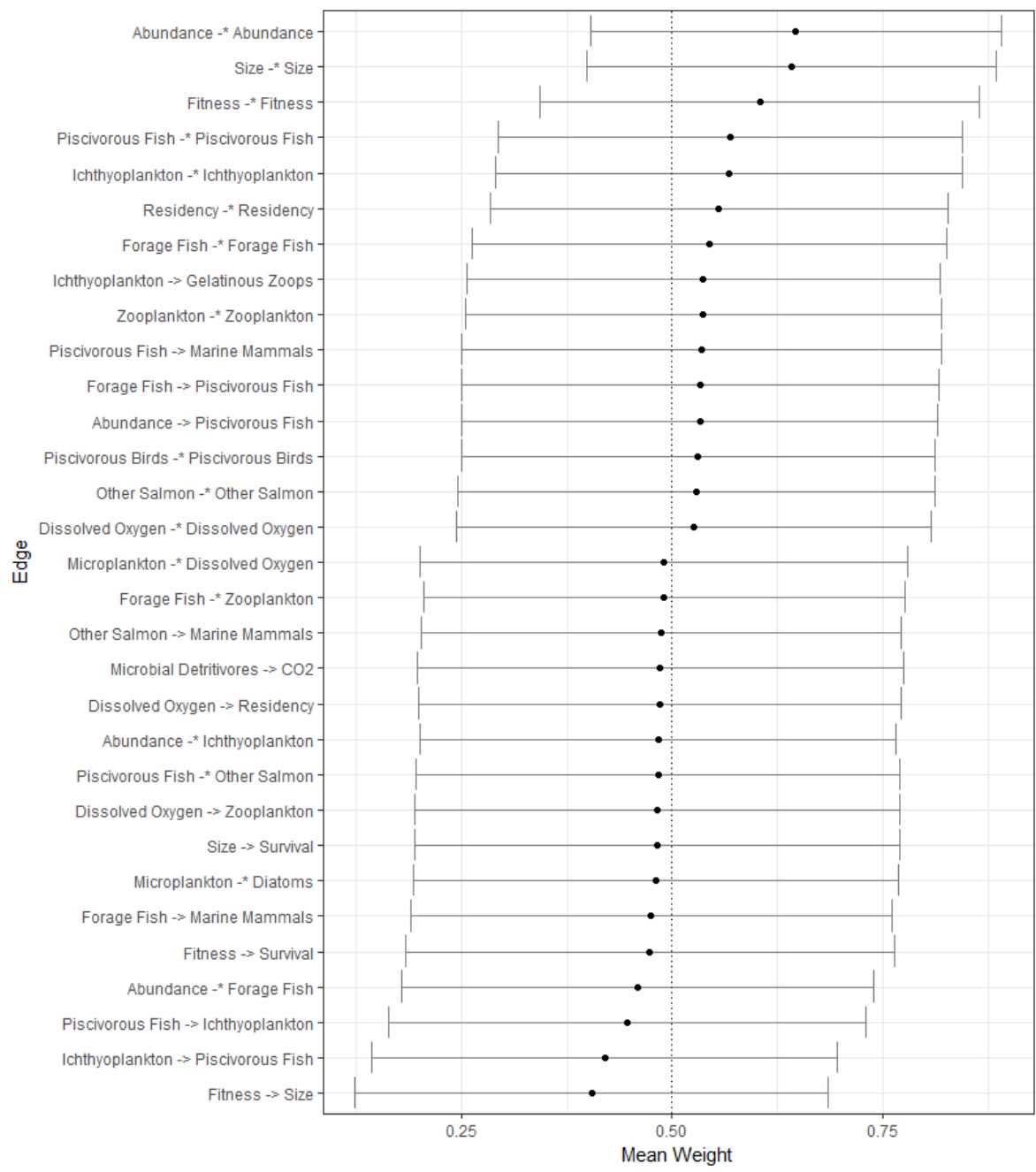
Figure A2.1. Calculated means and standard deviations from all model runs for edges (model linkages) with mean values different from the expected mean (0.5). The expected mean is denoted by the black dashed line. Positive linkages are indicated by an arrow and negative linkages are indicated by a dash and asterisk.

673

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	↑

---

[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

676   Anderson, E.M., Bower, J.L., Nysewander, D.R., Evenson, J.R. and Lovvorn, J.R. 2009. Changes
677   in avifaunal abundance in a heavily-used wintering and migration site in Puget Sound,
678   Washington during 1966–2007. *Marine Ornithology* 37: 19-27.
679
680   Burke, B. J., B. R. Beckman, W. T. Peterson, C. Morgan, E. A. Daly, M. Litz. 2013. Multivariate
681   methods to forecast Pacific salmon returns. *PLoS ONE* 8(1): e54134.
682
683   Chasco, B. I. Kaplan, A. Thomas, A. Alejandro-Gutiérrez, D.P. Noren, M.J. Ford, M.B. Hanson, J.
684   Scordino, S.J. Jeffries, S.F. Pearson, K. Marshall, E.J. Ward. 2017. Estimates of Chinook salmon
685   consumption in Washington State inland water by four marine mammal predators from 1970-
686   2015. *Can. J. of Fish. and Aqua. Sci. 10.1139/cjfas-2016-0203*
687
688   Christie, M.R., M.L. Marine, R.A. French, R.S. Waples and M.S. Blouin. 2012. Effective size of a
689   wild salmonid population is greatly reduced by hatchery supplementation. *Heredity* 109: 254-
690   260.
691
692   Crecilius, E.A., V.I. Cullinan, L.F. Lefkovitz and C. Peden. 1995. Historical trends in the
693   accumulation of chemicals in Puget Sound. 825-831, in Volume 2, Puget Sound Research '95
694   Proceedings, Puget Sound Water Quality Authority, Olympia.
695
696   Feely, R. A., S. R. Alin, J. Newton, C. L. Sabine, M. Warner, A. Devol, C. Krembs, and C. Maloy.
697   2010. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate
698   saturation in an urbanized estuary. *Estuarine, Coastal and Shelf Science*, 88, 442-449,
699   doi:10.1016/j.ecss.2010.05.004
700
701   Field, D., D. Cayan, and F. Chavez. 2006. Secular warming in the California current and North
702   Pacific. *California Cooperative Oceanic Fisheries Investigations Reports*, 47, 92-108.
703
704   Hoekstra, J. M., K.K. Bartz, M.H. Ruckelshaus, J.M. Moslemi, and T.K. Harms. 2007. Quantitative
705   threat analysis for management of an imperiled species: Chinook salmon (*Oncorhynchus
706   tshawytscha*). *Ecological Applications*, 17: 2061-2073.
707
708   Hollowed, A. B., S. R. Hare, and W. S. Wooster. 2001. Pacific Basin climate variability and
709   patterns of Northeast Pacific marine fish production. *Progress in Oceanography*, 49, 257-282,
710   doi:10.1016/S0079-6611(01)00026-X.
711
712   Gaydos, J.K. and S.F. Pearson. 2011. Birds and mammals that depend on the Salish Sea: A
713   compilation. *Northwest Naturalist*: 92:79–94.
714
715   Intergovernmental Panel on Climate Change. 2014. Climate Change 2014: Synthesis Report.
716   Contribution of Working Groups I, II and III to the Fifth Assessment Report of the

717 Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer
718 (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
719
720 Li, L., D. Mackas, B. Hunt, J. Schweigert, E. Pakhomov, I. Perry, M. Galbraith, T.J. Pitcher. 2013.
721 Zooplankton communities in the Strait of Georgia, British Columbia, track large-scale climate
722 forcing over the Pacific Ocean. *Progress in Oceanography*.
723 doi:http://dx.doi.org/10.1016/j.pocean.2013.05.025
724
725 Littell, J.S., M. McGuire Elsner, L.C. Whitely Binder, and A.K. Snover (eds). 2009. *The*
726 *Washington Climate Change Impacts Assessment: Evaluating Washington's Future in a*
727 *Changing Climate.* Climate Impacts Group, University of Washington, Seattle, Washington.
728 Available at: www.cses.washington.edu/db/pdf/wacciaexecsummary638.pdf
729
730 Mauger, G.S., J.H. Casola, H.A. Morgan, R.L. Strauch, B. Jones, B. Curry, T.M. Busch Isaksen, L.
731 Whitely Binder, M.B. Krosby, and A.K. Snover. 2015. State of Knowledge: Climate Change in
732 Puget Sound. Report prepared for the Puget Sound Partnership and the National Oceanic and
733 Atmospheric Administration. Climate Impacts Group, University of Washington, Seattle.
734 doi:10.7915/CIG93777D
735
736 Meador, J.P., F.C. Sommers, G.M. Ylitalo, C.A. Sloan. 2006. Altered growth and related
737 physiological response in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from dietary
738 exposure to polycyclic aromatic hydrocarbons (PAHs). *Can. J. of Fish. and Aqua. Sci.* 63: 2364-
739 2376.
740
741 Moore, S.K. et al., 2011. Past trends and future scenarios for environmental conditions favoring
742 the accumulation of paralytic shellfish toxins in Puget Sound shellfish. *Harmful Algae*, 10, 521-
743 529.
744
745 Moore, S.K. et al., 2015. Present-day and future climate pathways affecting the harmful algal
746 blooms species *Alexandrium catenella* in Puget Sound, WA, USA. *Harmful Algae*, 48, 1-11. 25
747
748 O'Neill, S.M., and West, J.E. 2009. Marine Distribution, Life History Traits, and the Accumulation
749 of Polychlorinated Biphenyls in Chinook Salmon from Puget Sound, Washington*. Transactions of*
750 *the American Fisheries Society* 138(3): 616-632.
751
752 Pacific Fishery Management Council. 2016. Review of 2015 Ocean Salmon Fisheries: Stock
753 Assessment and Fishery Evaluation Document for the Pacific Coast Salmon Fishery
754 Management Plan. Pacific Fishery Management Council, Portland, Oregon.
755 http://www.pcouncil.org/wp-
756 content/uploads/2016/02/Review_of_2015_Salmon_Fisheries_FullDocument.pdf
757
758 Palsson, W.A., T.J. Northrup, and M.W. Baker. 1998. Puget Sound Groundfish Management
759 Plan. Washington Department of Fish and Wildlife. Olympia, WA.
760

761   PSEMP Marine Waters Workgroup. 2016. Puget Sound marine waters: 2015 overview. S. K.
762   Moore, R. Wold, K. Stark, J. Bos, P. Williams, K. Dzinbal, C. Krembs and J. Newton (Eds). URL:
763   www.psp.wa.gov/PSEMP/PSmarinewatersoverview.php.
764

765   Puget Sound Water Quality Action Team. 2002. *2002 Puget Sound Update: Eighth Annual*
766   *Report of the Puget Sound Ambient Monitoring Program*. Puget Sound Water Quality Action
767   Team. Olympia, Washington.
768

769   Roberts, M., T. Mohamedali, B. Sackmann, T. Khangaonkar, W. Long. 2014. Puget Sound and
770   the Straits Dissolved Oxygen Assessment Impacts of Current and Future Human Nitrogen
771   Sources and Climate Change through 2070. Washington State Department of Ecology,
772   Publication No. 14-03-007. Olympia, WA.
773

774   Roon, S.R., J.D. Alexander, K.C. Jacobson, and J.L. Bartholomew. 2015. Effect of *Nanophyetus*
775   *salmincola* and bacterial co-infection on mortality of juvenile Chinook salmon. *Journal of*
776   *Aquatic Animal Health*, 27:4, 209-216.
777

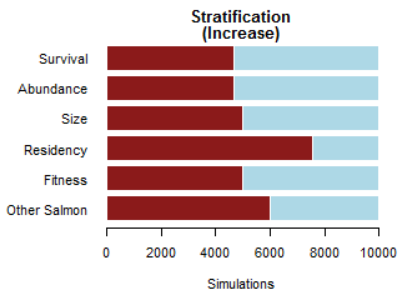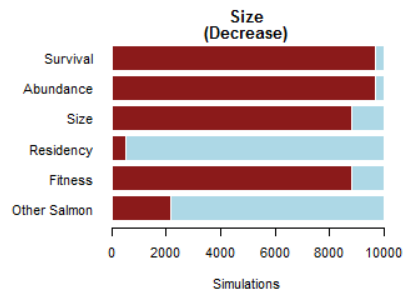778   Waples, R.S. 1999. Dispelling some myths about hatcheries. *Fisheries* 24: 12–21.
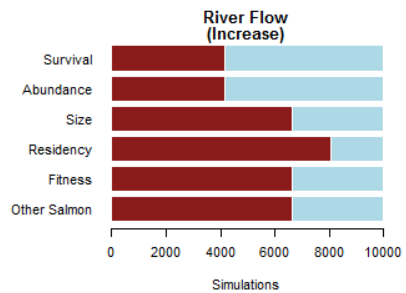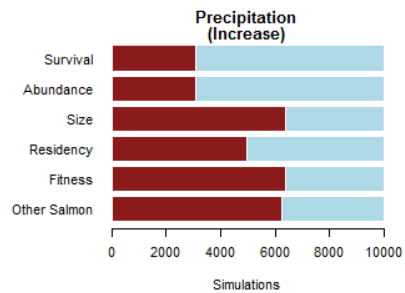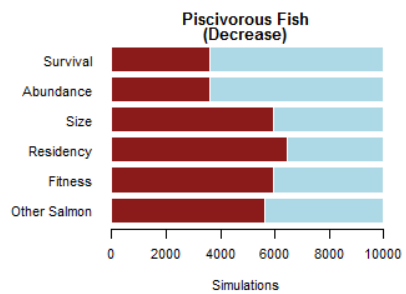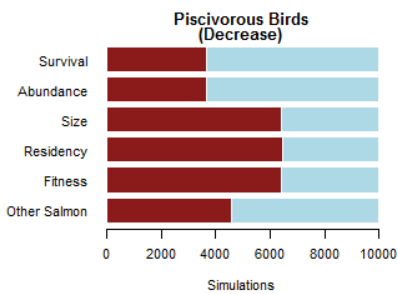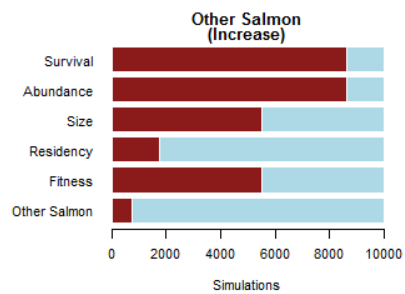779

780   WADOE. 2017. Marine Waters Program, Washington Department of Ecology.
781   http://www.ecy.wa.gov/programs/eap/mar_wat/
782

783

785   Model output showing 6 model nodes of interest: salmon survival, abundance, size, residency,
786   fitness and other salmon. Other salmon refers to the populations (chum, pink, and sockeye)
787   which have not seen a noticeable decline in survival in recent decades. In each plot box, the
788   model node that was perturbed is shown in the title, with the direction of the press (increase or
789   decrease) shown below. The bar graphs indicate the proportion of model simulations with
790   negative (red bars) and positive (blue bars) outcomes for that model node, given the invoked
791   press perturbation. Where the bars are dark gray, there was no impact to those nodes.

792
793
794

795
796

Global Warming (Increase)

Habitat Loss (Increase)

Harvest (Increase)

Hatcheries (Increase)

Ichthyoplankton (Decrease)

Marine Mammals (Increase)

Microbial Detritivores (Increase)

Microplankton (Increase)

Nutrients (Increase)

797

798
799
800
801

802