1 **Connectivity between spawning and nursery areas for Pacific cod (*Gadus***

2 ***macrocephalus*) in the Gulf of Alaska**

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23

24   **ABSTRACT**

25

26   We present the results of a study of the connectivity between Pacific cod spawning and

27   nursery areas, and settlement of Pacific cod in the Gulf of Alaska. This work was conducted to

28   address the hypothesis that spatial and temporal patterns of recruitment are related to variability

29   in connectivity between spawning and nursery areas. To examine this hypothesis, we developed

30   a Lagrangian, biophysical, individual-based model of Pacific cod early life history and dispersal

31   using the Dispersal Model for Early Life Stages (DisMELS) framework. This model is driven by

32   currents and scalars such as temperature from a version of the Regional Oceanographic Model

33   System (ROMS) developed for the Gulf of Alaska. Results of our study show connectivity

34   patterns predicted by the model that agree with our understanding (based on genetic analyses)

35   that there is a high degree of localized retention in Pacific cod. The results indicate that the

36   Shumagin Islands and Prince William Sound regions may serve as important collectors of Pacific

37   cod recruits from upstream spawning areas. We also find correlations between individual-based

38   model outputs and several large-scale climate indicators that appear to show settlement in several

39   important nursery areas, and recruitment overall, are positively affected by slower gyre

40   circulation in the Gulf of Alaska. We hypothesize that this is due to enhancement of retention,

41   settlement in the Shumagin Island region, and reduction of transport of young cod out of the Gulf

42   of Alaska to the southwest.

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44   Keywords: USA, Alaska, Gulf of Alaska; *Gadus macrocephalus*, Pacific cod, Recruitment;

45   Modelling

46

1. Introduction

The Gulf of Alaska Integrated Ecosystem Program (GOAIERP) was a vertically-integrated study of the physics, fisheries and ecosystem of the Gulf of Alaska (GOA). The goal of the GOAIERP was to identify how physical and biological variability affect recruitment of five commercially-important groundfish species in the Gulf. The main hypothesis of the GOAIERP was that survival of young fish during transport from spawning to nursery areas influences recruitment variability. Successful recruitment depends on many interrelated physical (runoff, mixing, water temperature, and wind speed and direction) and biological (predation, food supply, and competition) factors along the transport pathways. We refer to the biophysical environment that individuals have to navigate during the first year of life as "the gauntlet."

This paper focuses on Pacific cod (*Gadus macrocephalus*), one of GOAIERPs five focal groundfish species. Pacific cod is a commercially important species in the GOA, accounting for 318,870 t or 14.7% of the total catch of Alaska groundfish in 2013 (Alaska Fisheries Science Center, Seattle, WA, http://www.afsc.noaa.gov/species/Pacific_cod.php). Pacific cod are also a key predator species in the GOA, especially on walleye pollock (Aydin et al., 2007). Cod are opportunistic predators, and as such have a varied diet, feeding on fish and invertebrate species, including commercially important crabs. They appear to be sensitive to bottom up effects from both pelagic and benthic pathways (Aydin et al., 2007). Fishing, along with predation by groundfish and marine mammals, accounts for most of the Pacific cod mortality in the GOA.

The abundance of Pacific cod in Alaskan waters has been highly variable. Spawning stock biomass (SSB, Fig. 1) was high during the early 1980s due to a year of very high recruitment of Pacific cod in 1977 (Barbeaux et al., 2018). SSB declined from the mid-1980s

70   until 2009, and then increased until 2014 when it experienced a significant decline during a

71   marine heat wave in the GOA (Di Lorenzo and Mantua, 2016). The cohorts of 1977 and 2012

72   were the strongest in recent decades, although the factors driving those recruitment events, and

73   recruitment variability in general, are not well understood. It has been recognized since the work

74   of Hjort (1914) that there is rarely a good relationship between spawning stock biomass of marine

75   fish species and recruitment, and that recruitment levels are the result of complex interrelationships

76   of physical and biological variables affecting early life stages (Houde, 2009). We hypothesize that

77   variability in patterns of connectivity, i.e. transport between spawning and nursery areas,

78   underlies variability in Pacific cod recruitment and we use a Lagrangian, spatially-explicit,

79   Individual Based Model (IBM) for Pacific cod to test it. The term "recruitment" (or "recruits") in

80   this study refers to the number of age-0 Pacific cod at the end of their first year of life estimated

81   by the stock assessment model, as reported in the SAFE (Stock Assessment and Fisheries

82   Evaluation) document (Barbeaux et al., 2018).

83   Relative to their congener Atlantic cod (*Gadus morhua*), very little is known about the

84   dispersal and connectivity patterns of Pacific cod. Spawning Pacific cod are found in the GOA

85   between February and July (Dunn and Matarese, 1987). Eggs are demersal and semi-adhesive

86   (Laurel et al., 2008), which has been hypothesized to limit dispersal compared to the pelagic

87   eggs of Atlantic cod. Eggs are also stenothermal, euryhaline and euryoxic, with optimum

88   temperatures for development between 3.5 and 4ºC (Alderdice and Forrester, 1971). At 4ºC,

89   hatching occurs at 21-26 days after fertilization and newly hatched yolk-sac larvae are 3.8-5.3

90   mm SL (Laurel et al., 2008). The yolk-sac larval stage duration is between 3 and 12 days

91   depending on temperature (Laurel et al., 2008). Larvae are pelagic and yolk-sac larvae show a

92   strong surface orientation as early as 1 day post-hatch (Hurst et al., 2009). Larvae occur

93   primarily in the upper 45 m; however larval depths are highly variable. Flexion occurs at 20-35

94   days after hatch at 8° C (Narimatsu et al., 2007). After flexion (10-17 mm), larvae respond to

95   light variation with vertical movements reflecting a diel vertical migration with greater occupied

96   depths during the day (Hurst et al., 2009), although this pattern was not observed by Brodeur and

97   Rugen (1994). Transformation to the juvenile stage occurs at around 25-35 mm SL, about 70-75

98   days after hatch at 8° C. Although maturity occurs at 4-5 years of age, for our purposes,

99   "juvenile" explicitly refers to fish during their first year of life. By July of their first year,

100   individuals have been transported towards shore (Rugen and Matarese, 1988), and have begun to

101   settle to the bottom. Juvenile nursery areas are primarily shallow coastal embayments (Abookire

102   et al., 2007; Laurel et al., 2007). Although juveniles have been caught at depths to 70 m (Smith

103   et al., 1984), densities are generally highest in waters shallower than 20 m during the summer

104   and fall (Laurel et al., 2009). Within this depth region, juvenile cod show a preference for high

105   salinity water (Abookire et al., 2007) and structured habitat features (e.g. sea cucumber mounds,

106   eelgrass and kelp; Laur and Haldorson, 1996; Dean et al., 2000; Laurel et al., 2007). Pacific cod

107   are known to make annual feeding migrations and return to prior spawning locations, but some

108   stock components may be non-migratory. Genetic studies indicate that dispersal distances of

109   Pacific cod between birth and reproduction may be less than 30 km (Cunningham et al., 2008).

110   Mean circulation in the GOA is predominantly east to west. Along the continental shelf

111   break the Alaskan Stream is a westward flowing boundary current with flow rates up to 80-100

112   cm s^{-1} (Reed and Schumacher, 1984). On the shelf, within about 50 km of the coast, the Alaska

113   Coastal Current is a westward-flowing, wind-driven current (Royer, 1998; Stabeno et al., 2016)

114   with a low salinity core and flow rates of 25 to 175 cm s^{-1} (Stabeno et al., 1995). Both current

115   systems meander and shed eddies, which affect the trajectories and mixing of water masses

116 (Janout et al., 2009; Ladd and Stabeno, 2009; Ladd et al., 2005; Okkonen, 2003). Storms

117 associated with the Aleutian Low atmospheric pressure system promote onshore advection of

118 surface water (Cooney, 1986), and the coastal mountain range constrains these pressure systems

119 resulting in elevated precipitation and runoff (Royer, 1982). Variation in the storms and runoff

120 result in interannual variability in many aspects of the circulation including onshore advection

121 (Stabeno et al., 2004).

122 IBMs, such as that used here, are biophysical models that have been used in studies of

123 recruitment (Hinckley et al., 1996, Stockhausen and Lipcius, 2003), marine reserves

124 (Stockhausen and Hermann, 2007; Stockhausen and Lipcius, 2001; Stockhausen et al., 2000;

125 Pelc et al., 2010; Paris et al., 2004), and connectivity (Cowen et al., 2006, Cowen et al., 2007,

126 Cooper et al., 2013, Parada et al., 2010), and for other applications in marine ecology and

127 fisheries. These models generally include several pelagic early life history stages, with biological

128 processes that differ among the stages. IBMs are typically coupled to regional three-dimensional

129 oceanographic models to simulate the environmental factors that affect development and

130 transport of each life stage such as temperature, salinity, and currents. IBMs can be simple,

131 accounting for only a few base variables, or relatively complex, to include a full suite of

132 processes such as feeding, bioenergetics, growth and movement (e.g. Werner et al., 2001, North

133 et al., 2009, Hinckley et al., 1996; Hinckley et al., 2001; Megrey and Hinckley, 2001, Kim et al.,

134 2015, Parada et al., 2010). The degree of complexity often reflects the data available for a

135 particular species as well as the research question or focus.

136 Using a model-based approach to explore ways in which environmental variability in the

137 GOA affects recruitment of Pacific cod, we specifically address the hypothesis that *Recruitment*

138 *variability of Pacific cod is primarily influenced by variability in the proportion of young fish*

139 *transported from (offshore) spawning areas to nearshore nursery areas (connectivity) due to*

140 *interannual differences in the characteristics of the physical regime in the GOA.* To address our

141 hypothesis, we initially examine connectivity between potential Pacific cod spawning and

142 nursery areas and patterns of settlement, and then develop model-based indices of connectivity to

143 compare with indices of environmental variables that could impact young Pacific cod. These

144 potential indices are then compared to variability in recruitment estimates from the stock

145 assessment of Pacific cod.

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147

148 **2. Methods**

149

150 *2.1. Model descriptions and simulations*

151

152   We used a species-specific IBM coupled to a hydrodynamic model of the region to

153 explore Pacific cod connectivity in the Gulf of Alaska. The structure of the IBM is similar to

154 those developed for walleye pollock (Hinckley et al., 1996; Hinckley et al., 2016; Parada et al.,

155 2016) and for snow crab (Parada et al., 2010) in that it is driven by a 3-dimensional (3D)

156 hydrodynamic model and describes biophysical processes happening during early life history

157 stages. However, it uses a different modeling framework than the earlier models, and stage

158 processes and parameters are specific to Pacific cod. The walleye pollock and snow crab models

159 used the Ichthyops framework (Lett et al., 2008). The current model was developed within the

160 Dispersal Model for Early Life Stages (DisMELS) framework that uses the output of a coupled,

161 biophysical, Regional Oceanographic Model System (ROMS) to provide information on the

162   physical and lower trophic level environment. The coupled model simulation years were 1997 to

163   2013. This time span includes the field sampling years of the GOAIERP (2011-2013), years of

164   high and low recruitment of Pacific cod, and years representing different climate conditions

165   (including the 1997-1998 El Nino).

166

167   *2.1.1. ROMS Hydrographic Model*

168   We employed two model domains: a 3-km resolution model of the GOA, embedded

169   within an 11-km resolution model of the Northeast Pacific. The hydrodynamic models are based

170   on ROMS (Shchepetkin and McWilliams, 2005; Haidvogel et al., 2008), version 3. ROMS is a

171   hydrostatic, primitive equation ocean model that utilizes sigma-coordinates in the vertical and

172   curvilinear orthogonal coordinates in the horizontal. The 3-km and 11-km regional models each

173   utilized 42 vertical layers, with refinement for tighter spacing to resolve the surface boundary

174   layer.

175   The 3-km grid extends from northern British Columbia in the east to west of the

176   Shumagin Islands off the Alaska Peninsula in the west, and from the coast to approximately 1200

177   km offshore, with ~500 x 500 grid points. The 11-km model domain covers the region from Baja

178   California to the Chukchi Sea, from the coast to approximately 2000 km offshore, for a total of

179   ~200 x 500 grid points. Fine-scale bathymetry is based on ETOPO5, a gridded data set of land

180   and sea-floor elevations (NOAA, National Geophysical Data Center, Boulder, Colorado, 1988)

181   and supplementary datasets as described in Danielson et al. (2011); smoothing of the bathymetry

182   was utilized for numerical stability. The layered coordinate system of ROMS required that

183   regions shallower than 10 m be set to a depth of 10 m to ensure numerical stability (which would

184   be violated for overly thin layers, given a fixed model time step). Vertical mixing in both the 3-

185   km and 11-km models was based on the algorithms of Large et al. (1994). Tidal dynamics are

186   included in the 3-km ROMS model; the explicit inclusion of tidal flows allows tidally-generated

187   mixing and tidal residual flows to develop. Tides are included in the 11-km model simulation.

188   The models were forced by 6-hourly atmospheric (for surface forcing) and monthly

189   oceanic (for initial and boundary conditions) reanalysis output from NOAA's global Climate

190   Forecast System Reanalysis (CFSR; Saha et al., 2010), and subsequent operational analyses,

191   spanning the years 1995-2013. Horizontal resolution of the CFSR atmospheric and oceanic

192   reanalyses is ~ 40 km; these were interpolated to the regional grids. Bulk forcing, based on the

193   algorithms of Large and Yeager (2008), was used to relate the 6-hourly CFSR atmospheric

194   variables (wind velocities, air temperature, rainfall rate, absolute humidity, downward shortwave

195   and longwave radiation) to surface stress and the net transfers of sensible heat, latent heat,

196   shortwave and longwave radiation through the sea surface, as well as surface freshening by the

197   rainfall.

198   The oceanic boundary conditions were enforced using the hybrid nudging/radiation

199   scheme of Marchesiello et al. (2001). The 11-km model initial and boundary conditions were

200   derived from the CFSR, while these conditions for the 3-km model were derived from weekly

201   averages of the 11-km model physical output, spatially interpolated onto the 3-km model

202   boundaries (one-way nesting with no feedback to the outer model). The 11-km model was run

203   for one year prior to its use for initialization of the 3-km model.

204   Freshwater runoff was applied to the northern Gulf of Alaska simulations by freshening

205   surface salinity within a few grid points of the coastline using an exponential taper based on

206   squared distance from the coastline, with an e-folding distance of ~30 km. This technique

207   minimized the runaway stratification artifact, which has been observed using continuous

208 horizontal input of freshwater along broad stretches of the coastline (Dobbins et al., 2009; Vaz

209 and Simpson, 1994). The alongshore spatial pattern of the runoff for the 11-km NEP grid for

210 1995 – 2007 came from Dai et al. (2009). After 2007, a climatology based on Dai et al. (2009)

211 was used to set the NEP grid runoff. Runoff for the 3-km CGOA grid was generated from a high-

212 resolution freshwater discharge model for the Gulf of Alaska (Hill et al., 2015; Beamer et al.,

213 2016) as described in Coyle et al. (in press, this volume).

214 Output from the 3-km model was lowpass-filtered to eliminate tidal and inertial

215 oscillations, and stored as 1-day averages for subsequent use by the IBMs. Validation studies and

216 descriptions of related versions of the 11-km NEP model are available in Danielson et al. (2011)

217 and Hermann et al. (2009a). Validation studies and descriptions of related versions of the 3-km

218 biogeochemical and physical GOA model are described in Hermann et al. (2009b), Hinckley et

219 al. (2009), Dobbins et al. (2009), and Coyle et al. (2012, 2013).

220

221 *2.1.2. DisMELS framework*

222 DisMELS was developed at the Alaska Fisheries Science Center (NOAA/NMFS) to

223 provide a framework to develop and run IBMs simulating the early life stage development and

224 dispersion of marine fishes and invertebrates with pelagic egg and larval stages. It couples an

225 IBM framework with stored output from a ROMS model to provide a time-varying, 3D physical

226 environment in which to simulate the dispersal trajectories of thousands of simulated eggs and

227 larvae from natal locations up to early juvenile life stages. DisMELS also provides a graphical

228 user interface to facilitate defining life stage sequences, stage-specific characteristics, and initial

229 conditions, as well as to run models and analyze results.

230

231 *2.1.3. The Pacific cod IBM*

232   A conceptual model of Pacific cod early life history is shown in Fig. 3. Six life stages were

233 included in the IBM (eggs, yolk-sac larvae, pre-flexion feeding larvae, post-flexion feeding

234 larvae, epipelagic juveniles and settled juveniles). Processes such as growth and development,

235 depth distribution, and diel migration differed by life stage. To accommodate the complexity of

236 Pacific cod life history, changes and additions were made to the basic DisMELS model code to

237 include parameters and algorithms specific to Pacific cod egg, larval and juvenile (less than one-

238 year old) stages. The stage-specific parameterization of the IBM is described below.

239

240 *2.1.3.1. Egg stage*

241   Pacific cod spawn at the sea bottom over the continental shelf; therefore, eggs were

242 considered to be attached to the bottom and do not move from their spawning location. The

243 initial size of embryos in the model was assumed to be 0 mm, and using growth rates for

244 embryos (Hurst et al., 2010) resulted in size at hatch averaging between 4 and 5 mm (Laurel et

245 al., 2008; Doyle and Mier, 2016). Egg stage duration was modeled as a function of temperature

246 (Laurel et al., 2008) with a minimum set to 8 d and an average of 20-25 d.

247

248 *2.1.3.2. Yolk-sac stage*

249   Upon hatching, yolk-sac larvae move quickly to the surface (Matarese et al., 1989;

250 Mecklenburg et al., 2002; Hurst et al., 2009, Doyle and Mier, 2016). The depths for yolk-sac

251 larvae were restricted to 0-40 m (Brodeur and Rugen, 1994). Yolk-sac larvae were assumed to

252 move vertically in a random manner with a mean vertical velocity of 1×10^{-4} m s^{-1}. Progress

253 through the yolk-sac larval stage was modelled similar to walleye pollock (Hinckley et al.,

254   1996). The number of days to the point of no return (PNR), the time at which a larva cannot

255   recover from starvation, was a function of temperature (Laurel et al., 2008), as were days to

256   yolk-sac absorption (YSA) or first-feeding readiness. If larval time in the stage was less than

257   YSA, larval age and growth were incremented and feeding did not occur. Once a larva was ready

258   to feed (past YSA), the probability of feeding on each day was set to a random variate between 0

259   and 1, which increased linearly with age. If it did feed, larval age and growth were incremented

260   using the growth algorithm for the yolk-sac stage, and the larva passed into the pre-flexion

261   feeding larval stage. If it did not feed, age and growth were incremented, but it did not pass into

262   the next stage. If PNR was reached without feeding, the larva died of starvation. The duration of

263   the yolk-sac larval stage was constrained to 2 – 15 days.

264

265   *2.1.3.3.   Pre-flexion feeding larvae through benthic juvenile stages*

266   During the pre-flexion feeding larval stage, the individual's depth was constrained to

267   between 0 and 40 m, and there was no diel migration (Brodeur and Rugen, 1994; Hurst et al.,

268   2009). Vertical velocity was a function of length and temperature (Ottmar and Hurst, 2012).

269   Growth rates for pre-flexion stages were based on measurements in Hurst et al (2010). In that

270   paper, the authors acknowledge the potential for underestimation of growth rates due to the use

271   of rotifers instead of natural copepods as prey. However additional runs of our model applying

272   elevated pre-flexion growth rates led to similar patterns of connectivity between spawning and

273   nursery areas.

274   Each larva passed into the post-flexion feeding larval stage after reaching a length of 13.5

275   mm (Matarese et al., 1989). Growth rate for the post-flexion feeding larval stage differed from

276   that of the previous stage (Hurst et al., 2010) and diel migration was initiated. Daytime depth

277   varied between 20 and 40 m, whereas nighttime depth was between 0 and 20 m. The day-night

278   depth pattern was based on maintaining the 0-40 m depth range observed for pre-flexion larvae

279   (Brodeur and Rugen, 1994) as well as the vertical migration behavior observed in lab

280   experiments (Hurst et al., 2009). Each larva grew until it reached the length of transformation (25

281   mm, Dunn and Matarese, 1987), when it passed into the epipelagic juvenile stage. Larvae in this

282   developmental stage exhibited a similar pattern of day and night depths and vertical velocity as

283   the preceding stage, but could settle if they reached an area where the depth was less than 70 m

284   (Smith et al., 1984). Individuals in the benthic juvenile stage were constrained to one location

285   (although they actually move horizontally in an unknown manner). The goal of this study was to

286   model transport to potential settlement regions, and was not focused on fine-scale post-

287   settlement habitat selection, hence the lack of movement after settlement.

288   Growth rates for all life stages were functions of temperature and were taken from Hurst

289   et al. (2010); these growth rates differed by life stage (Table 1). Except for starvation during the

290   first-feeding stage, there was no explicit mortality included in the IBM. This is because there are

291   insufficient data on predator feeding habits, distribution and abundance, or on the total

292   abundance of cod early life stages necessary to parameterize predation mortality. This

293   simplification implies that the connectivity shown here represents maximum connectivity

294   between potential spawning and nursery areas. However, the main purpose of this study was to

295   examine stability and variation in the oceanographic drivers of dispersal and connectivity

296   patterns. Parameters and algorithms used in the IBM are listed in Table 1.

297

298   *2.2. Connectivity*

299

300   Connectivity between zones was defined as the fraction of fish initiated in a specific

301   spawning area that ended in each zone. We divided the GOA into geographical zones

302   representing source (spawning, zones 102-113, 202-213) and sink or ending (nursery, zones 101-

303   113, and other non-nursery (0-12, 201-213) areas (Fig. 2), to assess the connectivity between

304   spawning and nursery (or other) areas. Individuals that left the ROMS grid were classified as

305   ending in zone 998. The GOA was divided into 12 alongshore zones, and several depth zones.

306   These zones, by discretizing space in the GOA, help us define where each individual spawns,

307   zones that it may travel through, and the zone where it settles. The zones also facilitate the

308   analysis of connectivity by grouping the locations of individuals. The alongshore zones were

309   defined based on several criteria, including topography and geographic region (e.g. Cook Inlet or

310   West Shumagins). The depth zones represented depths significant to Pacific cod life history.

311   Pacific cod spawning zones were considered to be between 20 and 200 m depth (Dunn and

312   Matarese, 1987) while nursery areas were assumed to be regions where the depth was less than

313   70 m (Smith et al., 1984).

314

315   *2.3. Initial conditions*

316

317   Little information on specific locations of Pacific cod spawning or egg distribution exists.

318   Pacific cod spawning distribution is known to be patchy, but the specific locations of these

319   patches are not known. The few studies of distribution of Pacific cod spawning adults in the Gulf

320   of Alaska (Stark, 2007; Hirschberger and Smith, 1983; Fisheries Monitoring and Analysis

321   Division, Alaska Fisheries Science Center, NMFS, Seattle, unpublished data) have narrow

322   spatial and temporal coverage. Commercial catch between February and June (the spawning

323   period) occurs throughout the Gulf of Alaska and is not specifically targeted on the spawning

324   aggregations, so could not be used to delineate spawning patches. Furthermore, because of their

325   demersal nature, Pacific cod eggs are not caught in ichthyoplankton surveys which use pelagic

326   nets (Dunn and Matarese, 1987). Due to this paucity of information, cod eggs were released over

327   all suitable locations in the GOA where the water depth was shallower than 200 m.

328   A sensitivity analysis was performed to determine the optimal spatial resolution for

329   initialization of individuals. For this test, we released eggs from two connectivity zones

330   (different zones from those shown in Fig. 2) in Southeast Alaska, a shallow (<70 m) spawning

331   zone and a deep (70-200 m) spawning zone. Within these zones, eggs were released on grids

332   with spatial resolutions of 1, 2.5, 5, 7 and 10 km, with a single egg released at each grid point.

333   Eggs were released on 15 March at the bottom, and individuals were tracked until 1 November.

334   At the end of each simulation, the final connectivity zone of individuals was determined and

335   connectivity zones were ranked by the number of individuals they contained. The top ten final

336   zones (of 36) and the total number of individuals simulated (which is determined by the grid

337   size) were compared for each grid size (Table 2). Grids with larger spatial resolutions were

338   compared to the 1 km grid. Grids with spatial resolutions of 1 km and 2.5 km resulted in the

339   same top 10 final zones, although these were in a somewhat different order. Nine zones were the

340   same (out of the top 10) for the 5- and 7-km grids as were found for the 1-km grid, and the 10-

341   km grid resulted in eight zones that were the same as the 1-km grid. The simulations with the 1-

342   km and 2.5-km grids required substantially more modelled individuals than the coarser grids.

343   Final models were run releasing eggs on a 5-km grid, which provided agreement with the finer 1-

344   km grid results with markedly reduced computation time.

345   Individuals were released mid-month from February to June on the 5-km grid. The June

346   release resulted in no settlers by the end of the simulation (31 October), so this release time was

347   removed from further analysis. Due to the narrow shelf and small areal extent of potential

348   spawning areas in regions 101 and 201, no eggs were released in these zones.

349

350   *2.4. Analysis methods*

351

352   *2.4.1.   Connectivity matrices*

353   Connectivity matrices were computed for each year of the simulation. The cells of the

354   matrices show the probability of modelled individuals from each spawning zone dispersing to

355   any connectivity zone by the end of the simulation (so that the sum of the probabilities over each

356   row of the matrix (spawning areas) is 1.0). The ending zones (columns of the matrix) could be

357   nursery areas (<70 m), or any other zone. Individuals that exited the 3-km grid (designated as

358   Zone 998) were also recorded. The average probability of transport from a specified start zone to

359   a specific end zone and the standard deviation (SD_{conn}) of these probabilities over all simulated

360   years (1996-2011) were calculated. The average and SD_{conn} were plotted as matrices, and the

361   spawning areas for settlement regions of interest were plotted to clarify some of the observed

362   patterns.

363   We hypothesize that variability in annual recruitment is related to variability in

364   connectivity. We used a Normalized Difference Index (*NDI*) and an Overlap Coefficient (*OC*) to

365   examine this hypothesis. The *NDI* and the *OC* have been applied to compare modelled

366   distributions with observed field distributions of young fish (Hinckley et al., 2016).

367

368   *2.4.2. Normalized difference index*

369   The normalized difference index (*NDI*) was adapted from Hinckley et al. (2016),

370   Berntsen et al. (1996) and Søiland and Skogen (2000), and used to examine variation among

371   annual connectivity matrices. We calculated the normalized difference between modelled

372   connectivity matrix probabilities for each *i*-th cell for each year *t* ($P_{i,t}$) and the average modelled

373   connectivity matrix values for all years for each *i*-th cell ($\bar{P}_i$), divided by the standard deviation

374   (SD_i) of modelled connectivity output for all years for each cell. Following Søiland and Skogen

375   (2000), we used the maximum of either the SD_i or 0.01 to avoid division by a very small number.

376   The resulting cost function field $NDI_{i,t}$ is defined by:

377           $$NDI_{i,t} = (P_{i,t} - \bar{P}_i)/max(SD_i, 0.01) \qquad (10)$$

378   Negative values of $NDI_{i,t}$ indicate that the connectivity probability for that cell/year was less than

379   the mean connectivity probability for that cell, whereas positive values of $NDI_{i,t}$ indicate that the

380   connectivity probability for that cell/year was greater than the mean. The NDI_t for each year is

381   the sum of the absolute values over all cells with higher NDI_t values indicate greater differences

382   from the overall mean pattern in connectivity. The time series of NDI_t values was compared to

383   the recruitment time series for Pacific cod.

384

385   *2.4.3. Overlap coefficient*

386   An overlap coefficient (*OC*) was used to examine the overlap of each year's connectivity

387   matrix with the average (1997-2013) connectivity matrix. This type of coefficient is normally

388   used to examine the overlap of spatial distributions (Hinrichsen et al., 2005); here we apply it to

389   connectivity matrices calculated as:

390           $$OC_t = 2 \sum_{i=1}^{n}\left(P_{i,t}.\bar{P}_i\right)/(\sum_{i=1}^{n} P_{i,t}^2 + \sum_{i=1}^{n} \bar{P}_i^2)$$

391   for year *t* and cell *i*. The *OC* is 0 when there is no overlap and 1 when the two matrices are

392   identical. Hinckley et al. (2016) used this index to compare modelled distributions of pollock

393   larvae with survey distributions. Hinrichsen et al. (2005) applied *OC* to determine how many

394   modelled larvae and prey were simultaneously present in the subareas of the central Baltic Sea.

395

396   *2.4.4.   Settlement analysis, physical indices and recruitment*

397   We examined several other metrics: (1) the fraction of the total number of simulated

398   individuals that settled by year, (2) the fraction settling in each nursery zone, and (3) the fraction

399   settling from each spawning zone. Several model-derived time series were compared to Pacific

400   cod recruitment (Barbeaux et al., 2018) using Pearson's correlation coefficient. We examined the

401   correlations (Pearson's r) between the fraction settling in each nursery zone and several large-

402   scale climate indices. An average of three winter months (December-February), just prior to

403   spawning, was used for each index. The Multivariate ENSO index (MEI, Wolter and Timlin,

404   1993, 2011) reflects the El Niño/La Niña state with positive values representing stronger gyre

405   circulation associated with El Niño, and vice-versa for La Niña. The North Pacific Index (NPI,

406   Trenberth and Hurrell, 1994, 1995) is the area-weighted sea level pressure over the region

407   between 30°N and 65°N with positive NPI values reflecting a weaker Aleutian Low and reduced

408   gyre circulation. The Pacific Decadal Oscillation (PDO, Mantua et al., 1997; Zhang et al., 1997;

409   Bond and Harrison, 2000) represents Sea Surface Temperature (SST) anomalies in the North

410   Pacific. Lastly, the Arctic Oscillation (AO, Higgins et al., 2001, 2002) reflects the strength of

411   counterclockwise winds at ~55°N latitude, with negative AO values associated with increasing

412   storminess in mid-latitudes. The MEI, NPI and AO indices were chosen because they relate to

413   different drivers of circulation, and therefore larval transport, in the Gulf of Alaska. Stachura et

414   al. (2014) found that the NPI may be a good predictor of recruitment for fish species in the GOA.

415   The PDO was chosen because temperature affects growth of individuals in the Pacific cod IBM.

416   Growth determines larval life stage and therefore depth, which affects transport in a vertically

417   stratified ocean.

418

419

420   **3. Results**

421

422   *3.1.Connectivity*

423

424   The average annual connectivity for Pacific cod between spawning areas and ending

425   areas (including nursery and non-nursery areas) for the years 1997-2013 is shown in Fig. 4. For

426   modelled individuals initialized in the shallow (< 70 m) spawning areas, retention (i.e. settlement

427   in the same areas as release) of modelled individuals was the dominant pattern (average

428   probability =0.41). This pattern is indicated by the lower diagonal white line in Fig. 4. Some

429   young Pacific cod moved from their spawning areas to nearby areas downstream, as shown by

430   the shaded cells immediately left of the diagonal. Another important pattern was the movement

431   of individuals from deep spawning areas to adjacent inshore nursery areas (upper diagonal white

432   line in Fig, 4). However, the probabilities of such shoreward transport were less than the

433   probabilities of retention. For the most part, the early life stages of Pacific cod were not

434   transported great distances between spawning zones and nursery areas. Despite the general

435   pattern of retention, a high proportion of individuals were transported out of the GOA model

436   domain (designated as zone 998 on the connectivity matrices). The probability of loss was

437 between 0.01 and 0.91 (depending on the start zone) and was greatest for fish spawned to the

438 west of Kodiak Island (especially the deeper spawning areas 209-212; Fig. 2). Most of these

439 individuals were transported out of the model domain to the southwest; however, some were

440 transported out of the model grid to the southeast.

441 The largest standard deviation (SD_{conn}) in the probability of transport between start/end

442 pairs over the modelled years was 0.10 (Fig. 5). The highest variability in connectivity was seen

443 in the transport of individuals released in areas 112, 113, and 212 near the Shumagin Islands and

444 in fish transported out of the southwest corner of the grid.

445 The spawning areas for several of the nursery or ending regions and for the modelled

446 individuals that left the GOA are plotted to reflect an alternate perspective on dispersal (Fig. 6).

447 Retention in the spawning area is clearly the most important source for settling individuals in

448 each nursery area. The contribution of spawning zones to the east of the nursery area (102 and

449 202 being the farthest east) decreased rapidly with distance from the nursery area. Individuals

450 generally did not come from zones west of the settlement area (112 and 212 being the farthest

451 west). Area 106 (Prince William Sound) was more strongly connected to multiple spawning

452 areas upstream and offshore than other nursery areas. This was also true for nursery area 112

453 (West Shumagins). It is also clear from Fig. 6 that most individuals exiting the grid (Area 998)

454 came from the southwesterly spawning areas (112, 211,212) closest to the southwestern grid

455 boundary.

456

457 *3.2.Normalized difference index and overlap coefficient*

458

459   The year with the lowest *NDI*, i.e. the year in which connectivity patterns were most

460   similar to the mean, was 2000 (*NDI* = 20.50, Fig. 7). The year with the highest overall *NDI* (i.e. a

461   connectivity matrix most divergent from the mean) was 1998 (*NDI* = 36.45). The range of the

462   *OC* index was small. The year with the lowest *OC* (Fig. 7) was 1998 (*OC* = 0.94), and 2000 was

463   the year with the highest *OC* (0.98). *NDI* and *OC* were inversely correlated with r = -0.84 (p <

464   0.001).

465   The largest differences in 1998 from the annual mean were that more simulated

466   individuals exited the model domain (sink area 998) from areas 110 (Chirikof) and areas 207-211

467   (Kenai to East Shumagins, deep spawning areas) (Fig. 8). There was also higher than average

468   retention within area 103 (Cross Sound), and fewer individuals ending in area 112 (West

469   Shumagins) in that year. Recruitment of Pacific cod in 1998 was the second lowest of the

470   modelled period.

471

472   *3.3. Settlement, physical indices and recruitment*

473

474   The analysis of settlement fractions in each nursery zone must be considered preliminary,

475   as there is little information about initial spawning distributions. However, given this constraint,

476   settlement fractions (of the total number of simulated individuals) generally increased from east

477   to west with a peak in area 112 (West Shumagins, Fig.9A). The lowest fractions settled were in

478   Southeast Alaska (areas 101-103) and Yakutat/Icy Bay in East Central GOA (104-105).

479   Fractions settled in the central GOA from Prince William Sound (106) to Chirikof (110) regions

480   were similar and higher than those farther east.

481   The patterns of settlement for fish starting from the shallow and deep spawning areas

482   (Figs. 9B, C) were similar, and were quite high except for area 112 and 212 (West Shumagins).

483   The latter is probably because (as was mentioned in the connectivity results) Pacific cod are

484   mostly either retained in their spawning areas, or they disperse a short distance from their

485   starting location; in the case of area 212 they can easily move out of the grid to the southwest, as

486   the prevailing currents take them in this direction. Settlement fractions for individuals from

487   spawning areas 102-108 and 203-208 (Sitka to North Kodiak) were above 70%. Settlement

488   fractions decline from North Kodiak Island to the West Shumagins (areas 109-112 and 209-212).

489   Settlement of modelled individuals released in Cook Inlet (areas 113 and 213) was high (>80%).

490   It is unknown whether there is a high abundance of Pacific cod spawning in Cook Inlet. Of the

491   simulated years, 1998 had the lowest fraction settled (Fig. 9D) with 2003 and 1997 showing the

492   highest fraction settled.

493   Most of the model-derived time series that were compared to actual Pacific cod

494   recruitment from the NMFS stock assessments showed very low correlation coefficients (Table

495   3). However, the fraction settled in area 105 (Icy Bay) was positively correlated with observed

496   Pacific cod recruitment (as estimated by Barbeaux et al., 2018). Recruitment was negatively

497   correlated with settlement in areas 101 (Pt. Wales Island), 107 (Kenai), and 108 (North Kodiak).

498   Settlement in area 112 (West Shumagins) was negatively correlated with the MEI and NPI,

499   whereas settlement in area 105 was negatively correlated with the PDO. The AO index was not

500   significantly correlated with settlement in any of the nursery zones.

501

502

4. Discussion

Knowledge of connectivity, the linkage between spawning areas and settlement areas, can increase our understanding of the fate of fish spawned in particular regions, of the potential importance of different spawning and nursery areas, of stock structure, and of the impacts of larger scale climate forcing on recruitment patterns. It can also give insight into how these patterns may differ between the eastern and the western GOA, or of how these two regions may be linked via larval transport. We hypothesized that variation in annual recruitment is related to patterns of dispersal and connectivity throughout the Gulf of Alaska. Lagrangian IBMs are one of the few available tools for studying connectivity, with their ability to follow modelled individuals along transport pathways.

This study of connectivity and settlement patterns of Pacific cod in the Gulf of Alaska revealed some general patterns that are in accordance with what is known about Pacific cod early life history, and that also extend our understanding of potential transport and settlement patterns. Some possible causes of variability in these patterns due to large-scale climate factors, and consequences of these patterns and their interannual variability on recruitment were also examined.

The results of modelled connectivity patterns indicate that the early life history stages of Pacific cod generally do not disperse far from their natal areas. Retention of modelled individuals in areas where they were spawned was the strongest connectivity pattern seen. This result agrees with patterns of genetic variation suggesting limited dispersal rates in this species (Cunningham et al., 2008). We also found that individuals spawned in shallower spawning areas nearer to shore or in areas where the circulation is weaker are more likely to be retained than

526 those released in deeper shelf areas where strong directed currents such as the Alaska Current are

527 dominant, as might be expected. Many cod that were spawned to the west of Kodiak in the

528 model, especially in the Shelikof Strait sea valley (with its strong westward currents), were

529 transported out of the GOA. However, many modelled individuals were also transported from

530 the deeper shelf spawning regions to nearby nearshore settlement regions, indicating the

531 importance of cross-shelf transport. The variability in connectivity for Pacific cod was not as

532 high as for other, long-distance dispersing species such as sablefish (*Anoplopoma fimbria*,

533 Gibson et al., in press, this volume), Pacific Ocean perch (*Sebastes alutus,* Stockhausen et al., in

534 press, this volume) or arrowtooth flounder (*Atheresthes stomias*, Stockhausen et al., in press, this

535 volume). The highest variability was in the patterns that showed the strongest connections, such

536 as retention and transport out of the GOA. This restricted transport of early life stages of Pacific

537 cod has consequences for east vs. west differences. Cod spawned in southeast Alaska that were

538 not retained in that area, for example, were not likely to be transported much farther west than

539 Prince William Sound.

540   The retention and limited transport in our model results is partially because (in the model

541 and *in situ*) Pacific cod eggs are attached or semi-attached to the bottom for nearly a month of

542 their early life. This trait, which is unique among species in the genus may, among other things,

543 be an adaptation to restrict larval dispersal. In the model, we also assumed that once the

544 modelled individuals settle as benthic juveniles, they do not move from their settlement location.

545 Benthic juveniles cod are likely to move horizontally to some degree. However, it is thought that

546 they may not move far based on nearshore settlement dynamics of Atlantic cod (Laurel et al.,

547 2003).

548   The fraction of settling Pacific cod in these simulations was higher than that observed for

549   sablefish (Gibson et al., in press, this volume), Pacific Ocean perch and arrowtooth flounder

550   (Stockhausen, et al., in press, this volume). Walleye pollock settlement fractions are generally

551   between those for Pacific cod and the other species (Parada et al., 2016). We did not have precise

552   locations of Pacific cod spawning or information on the spatial pattern of predation on egg and

553   larval stages, so the number of individuals settling in each modelled nursery area may differ from

554   the dispersal patterns reflected here. However, the modelling results indicate that the area around

555   and just west of the Shumagin Islands could represent a significant nursery area for Pacific cod

556   in the Gulf of Alaska because this area received settling fish from a wide range of potential

557   spawning locations. Doyle and Mier (2016) show that many late larval Pacific cod concentrated

558   in this region in May. High commercial catches of adult Pacific cod are also found in this region

559   (http://www.afsc.noaa.gov/maps/FMA/datamap/obsmap.html).

560   Nursery areas in southeast Alaska and the east central GOA had the lowest settlement

561   rates and the highest likelihood of individuals spawned there being dispersed downstream or

562   offshore. This is likely due to the narrowness of the continental shelf, and the impingement of the

563   Alaska Current and oceanic eddies. A high proportion of modelled fish released in Cook Inlet

564   reached suitable settlement sites, but little is known about the magnitude of spawning activity

565   occurring there. Prince William Sound and the West Shumagins seem to act as collection areas

566   for fish transported from upstream areas. Individual fish from southeast Alaska to Prince William

567   Sound settled in Prince William Sound, as well as being retained in their spawning areas.

568   Individuals from Kodiak to the West Shumagins settled in the West Shumagins, as well as being

569   retained near their spawning areas. These results may indicate that if recruitment of Pacific cod is

570   determined in the early life stages, the eastern and western regions could show different

571   recruitment patterns. We were unable to examine this hypothesis however, because estimates of

572   recruitment for this species are made Gulf-wide, not for specific regions.

573   The year 1998 exhibited the highest divergence (using the *NDI*) from the mean

574   connectivity pattern, and had the lowest fraction settled of all years in our time series.

575   Recruitment in 1998 was also the third lowest of our modelled period. More modelled

576   individuals exited the GOA, and fewer individuals settled in West Shumagins in 1998.

577   Settlement in the east central GOA was positively correlated with recruitment, whereas

578   settlement around North Kodiak and the Kenai area was inversely correlated with recruitment,

579   although the reasons for the latter are unclear.

580   Several hypotheses arise from this work that require further exploration. For example,

581   settlement and recruitment success for Pacific cod may increase when the GOA gyre circulation

582   is slow, enhancing retention and short-distance transport, and minimizing transport out of the

583   GOA. A negative MEI (the Multivariate ENSO index) indicates La Niña conditions (weak

584   circulation) whereas a positive MEI indicates El Niño conditions (strong circulation; Comes and

585   DiLorenzo, 2007). NPI is area-weighted sea level pressure over the region between 30°N and

586   65°N with a positive NPI reflecting a weaker Aleutian Low and slower gyre circulation. During

587   the examined period, Pacific cod recruitment in the GOA was positively correlated with NPI ($r =$

588   0.496, $p = 0.043$) and negatively associated with the MEI ($r = -0.421$, $p = 0.092$). These patterns

589   basin-scale patterns appear to be associated with climate-related patterns of delivery of Pacific

590   cod larvae to specific nursery regions. For example, settlement in both the West Shumagin area

591   (the nursery area with the greatest fraction of settling fish) and Prince William Sound (important

592   for collection of upstream larvae as well as retention) were positively correlated with the NPI

593   and negatively correlated with the MEI.

594   It is difficult to isolate the specific mechanisms linking regional climate indices to

595   population connectivity and recruitment as aspects of climate and ocean conditions are generally

596   linked. For example, overall recruitment was also negatively correlated ($r = -0.505$, $p = 0.039$)

597   with the PDO, which could suggest a positive effect on cod survival of low temperatures or

598   central GOA wind events (Ladd et al. 2016). However, the PDO was only weakly correlated with

599   settlement in the West Shumagin area and not correlated with settlement in Prince William

600   Sound. The lack of consistent correlations between the PDO and settlement in the model could

601   be due to the focus on transport-related processes in the model. While growth and development

602   of cod early life stages were driven by temperature, other potentially temperature-mediated

603   biological processes such as prey availability and mortality were not incorporated throughout the

604   model. Interestingly, the AO showed virtually no correlation with recruitment or settlement into

605   any specific region.

606   Trust in the results of modelling studies generally requires some degree of validation of

607   the models. The ROMS model is able to reproduce currents and temperature in the GOA (Coyle

608   et al., 2012). Details of the circulation, such as the precise locations of medium- and large-scale

609   eddies at specific times (which may affect dispersal and recruitment of young fish, Parada et al.,

610   2016) cannot be expected to be exact due to the stochastic nature of these flow features.

611   Empirical observations to corroborate the Pacific cod IBM are currently limited. Data on larval

612   distribution exist (Doyle and Mier, 2016), but observations are concentrated in the western GOA.

613   Our model also showed juvenile cod settlement all around the GOA and is generally supported

614   by data from the NOAA Nearshore Fish Atlas (Johnson et al., 2012) showing that juvenile cod

615   were caught in every area surveyed around the coastal GOA.

616   To some degree, this latter pattern of settlement was a result of the uniform egg releases

617   that we used to initialize the model, due to the lack of information about specific spawning

618   locations of Pacific cod in the GOA. Also, our settlement criterion was very simple, i.e.

619   epipelagic juveniles were allowed to settle when they first encountered water depths less than 70

620   m. The decision to settle is undoubtedly much more complex. For example, studies have found

621   young cod in eelgrass beds and other emergent vegetation, and associated with mounds of sea

622   cucumbers. These associations may represent post-settlement habitat selection. It was not

623   possible to include these complex factors, as knowledge of settling behavior, and comprehensive

624   maps of potential habitat such as emergent vegetation are not available. However, a coordinated

625   effort to look at spatial variation in abundance and distribution of juvenile Pacific cod in western

626   GOA nurseries is currently underway (Ben Laurel, pers. comm.), which should provide more

627   detailed information to support examination of specific patterns of connectivity.

628   The success of transport from spawning to nursery areas undoubtedly depends on factors

629   other than physical dispersal and temperature effects, which are the main processes included in

630   this model. Predation mortality was not included and it was also not possible to include more

631   complex processes of feeding or bioenergetics due to the lack of data and rates. In the future, the

632   Pacific cod IBM would be greatly improved with better understanding of spawning locations,

633   settling behavior and habitat, and additional data on the distributions of the early life stages of

634   cod throughout the GOA. Information on spatial variation in prey availability, foraging success,

635   and predation vulnerability of these life stages would further improve the model, and allow

636   integration of the suite of processes influencing population connectivity and recruitment. A

637   clearer understanding of these integrated processes would aid in predicting how the Pacific cod

638   stock in the Gulf of Alaska will respond under varying environmental conditions in the short and

639 long term. However, the results of this study show intriguing potential relationships between

640 patterns of connectivity and large-scale climate indices with recruitment of Pacific cod in the

641 GOA.

642

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644

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658 **References**

659

660 Abookire, A. A., J. T. Duffy-Anderson and C. M. Jump. 2007. Habitat associations and diet of

661 young-of-the-year Pacific cod (*Gadus macrocephalus*) near Kodiak, Alaska. Mar. Biol.

662 150, 713-726.

663 Alderdice, D. F. and C. R. Forrester. 1971. Effect of salinity, temperature, and dissolved oxygen

664 on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Bd. Can.

665 28, 883-902.

666 Aydin, K., S. Gaichas, I. Ortiz, D. Kinzey and N. Friday. 2007. A Comparison of the Bering Sea,

667 Gulf of Alaska, and Aleutian Islands Large Marine Ecosystems Through Food Web

668 Modeling. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-178, 298 p.

669 Barbeaux, S., K. Aydin, B. Fissel, K. Holsman, B. Laurel, W. Palsson, K. Shotwell, Q. Yang,

670 and S. Zador. 2018. Assessment of the Pacific cod stock in the Gulf of Alaska. Ch. 2 in

671 Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the

672 Gulf of Alaska, North Pacific Fishery Management Council, 605 W 4th Avenue, Suite

673 306, Anchorage, AK 99501.

674 Beamer, J. P., D.F Hill, A. Arendt, and G.E. Liston. 2016. High-resolution modeling of the

675 coastal freshwater discharge and glacier mass balance in the Gulf of Alaska watershed.

676 Water Resource Res. 52, 3888-3909.

677 Berntsen, J., E. Svendsen, E., and M. Ostrowski. 1996. Validation and sensitivity study of a

678 sigma-coordinate ocean model using SKAGEX dataset. ICES CM 1996/C:5.

679 Bond, N. A. and D. E. Harrison. 2000. The Pacific Decadal Oscillation, air-sea interaction and

680 central north Pacific winter atmospheric regimes. Geophys. Res. Lett. 27, 731-734.

681 Brodeur, R. D. and W. C. Rugen. 1994. Diel vertical distribution of ichthyoplankton in the

682   northern Gulf of Alaska. Fish. Bull. 9, 223–235.

683 Combes, V. and E. Di Lorenzo. 2007. Intrinsic and forced interannual variability of the Gulf of

684   Alaska mesoscale circulation. Prog. Oceanogr. 75(2), 266-286.

685   doi:10.1016/j.pocean.2007.08.011

686 Cooney, R. T. 1986. The seasonal occurrence of *Neocalanus cristatus*, *Neocalanus plumchrus*,

687   and *Eucalanus bungii* over the shelf of the northern Gulf of Alaska. Continental Shelf

688   Res. 5, 541-553.

689 Cooper, D. W., J. T. Duffy-Anderson, W. T. Stockhausen and W. Cheng. 2013. Modeled

690   connectivity between northern rock sole (*Lepidopsetta polyxystra*) spawning and nursery

691   areas in the eastern Bering Sea. J. Sea Res.84, 2-12.

692 Cowen, R. K., C. B. Paris, A. Srinivasan. 2006. Scaling of connectivity in marine populations.

693   Science 311, 522-527.

694 Cowen, R. K., G. Gawarkiewicz, J. Pineda, S. R. Thorrold, F. E. Werner. 2007. Connectivity in

695   Marine Systems: An Overview. Oceanography, 20, 14-21.

696 Coyle, K., W. Cheng, S. Hinckley, E. J. Lessard, T. Whitledge, A.J. Hermann and K. Hedstrom.

697   2012. Model and field observations of effects of circulation on the timing and magnitude

698   of nitrate utilization and production on the northern Gulf of Alaska shelf. Prog. Oceanogr.

699   103, 16-41, doi:10.1016/j.pocean.2012.03.002.

700 Coyle, K. O., A.J. Hermann, and R.R. Hopcroft. *in press (this volume)*. Modeled spatial-temporal

701   distribution of productivity, chlorophyll, iron and nitrate on the northern Gulf of Alaska

702   shelf relative to field observations. Deep Sea Res. II.

703   Coyle, K. O., G. A. Gibson, K. Hedstrom, A. J. Hermann, and R. R. Hopcroft. 2013.

704   Zooplankton biomass, advection and production on the northern Gulf of Alaska shelf

705   from simulations and field observations. J. Mar. Syst. 128, 185-207,

706   doi:10.1016/j.jmarsys.2013.04.018.

707   Cunningham, K. M., M. F. Canino, I. B. Spies, and L. Hauser. 2008. Genetic isolation by

708   distance and localized fjord population structure in Pacific cod (*Gadus macrocephalus*):

709   limited effective dispersal in the northeastern Pacific Ocean. Can. J. Fish. Aquat. Sci. 66,

710   153-166.

711   Dai, A., T. Qian, K. E. Trenberth, and J. D. Milliman. 2009. Changes in continental freshwater

712   discharge from 1948-2004. J. Climate 22, 2773-2791.

713   Danielson, S., E. Curchitser, K. Hedstrom, T. Weingartner, P. Stabeno. 2011. On ocean and sea

714   ice modes of variability in the Bering Sea. J. Geophys. Res. 116, C12034,

715   doi:10.1029/2011JC007389.

716   Dean, T. A., L. Haldorson, D. R. Laur, S. C. Jewett and A. Blanchard. 2000. The distribution of

717   nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska:

718   associations with vegetation and physical habitat characteristics. Environ. Biol. Fishes 57,

719   271-287.

720   Di Lorenzo, E. and N. Mantua. 2016. Multi-year persistence of the 2014/2015 North Pacific

721   marine heatwave. Nature Climate Change 6, 1042-1048.

722   Dobbins, E. L., A. J. Hermann, P. Stabeno, N. A. Bond and R. C. Steed. 2009. Modeled transport

723   of freshwater from a line-source in the coastal Gulf of Alaska. Deep-Sea Res. II 56, 2409.

724   doi:10.1016/j.dsr2.2009.02.004.

725   Doyle, M. J., and K. L. Mier. 2016. Early life history pelagic exposure profiles of selected

726   commercially important fish species in the Gulf of Alaska. Deep-Sea Res. II, 132, 162-

727   193.

728   Dunn, J. R. and A. C. Matarese. 1987. A review of the early life history of northeast Pacific

729   gadoid fishes. Fish. Res. 5, 163-184.

730   Gibson, G. A., W. Stockhausen, K.O. Coyle , S. Hinckley, C. Parada, A. Hermann, M. Doyle, C.

731   Ladd. *In press*. An individual-based model for Sablefish: Exploring the connectivity

732   between potential spawning and nursery grounds in the Gulf of Alaska. Deep-Sea Res. II.

733   Haidvogel, D. B., H. Arango, W. P. Budgell, B. D. Cornuelle, E. Curchitser, E. Di Lorenzo, K.

734   Fennel, W. R. Geyer, A. J. Hermann, L. Lanerolle, J. Levin, J. C. McWilliams, A. J.

735   Miller, A. M. Moore, T. M. Powell, A. F. Shchepetkin, C. R. Sherwood, R. P. Signell, J.

736   C. Warner, J. Wilkin. 2008. Regional Ocean Forecasting in Terrain-following

737   Coordinates: Model Formulation and Skill Assessment. J. Comput. Phys. 227, 3595-

738   3624.

739   Hermann, A. J., E. N. Curchitser, D. B. Haidvogel and E. L. Dobbins. 2009a. A comparison of

740   remote versus local influence of El Nino on the coastal circulation of the Northeast

741   Pacific. Deep-Sea Res. II 56, 2427-2443. doi:10.1016/j.dsr2.2009.02.005.

742   Hermann, A. J., S. Hinckley, E. L. Dobbins, D. B. Haidvogel, N. A. Bond, C. Mordy, N. Kachel

743   and P. J. Stabeno. 2009b. Quantifying cross-shelf and vertical nutrient flux in the Gulf of

744   Alaska with a spatially nested, coupled biophysical model. Deep-Sea Res. II, 56, 2474-

745   2486, doi:10.1016/j.dsr2.2009.02.008.

746   Higgins, R.W., Y. Zhou and H.-K. Kim. 2001. Relationships between El Niño-Southern

747   Oscillation and the Arctic Oscillation: A Climate-Weather Link. NCEP/Climate

748   Prediction Center ATLAS 8.

749   http://www.cpc.ncep.noaa.gov/research_papers/ncep_cpc_atlas/8/index.html

750   Higgins, R.W., A. Leetmaa, and V. E. Kousky. 2002. Relationships between climate variability

751   and winter temperature extremes in the United States. J. Climate 15, 1555-1572.

752   Hill, D. F., N. Bruhis, S.E. Calos, A. Arendt, and J. Beamer, J., 2015. Spatial and temporal

753   variability of freshwater discharge into the Gulf of Alaska. J. Geophys. Res. Oceans. 120,

754   634-646.

755   Hinckley, S., A. J. Hermann and B. A. Megrey. 1996. Development of a spatially-explicit,

756   individual-based model of marine fish early life history. Mar. Ecol. Prog. Ser. 139, 47-68.

757   Hinckley, S., A. J. Hermann, K. L. Mier, and B. A. Megrey. 2001. Importance of spawning

758   location and timing to successful transport to nursery areas: a simulation study of Gulf of

759   Alaska walleye pollock. ICES J. of Mar. Sci. 58, 1042–1052.

760   Hinckley, S., K. O. Coyle, G. Gibson, A. J. Hermann, and E. L. Dobbins. 2009. A biophysical

761   NPZ model with iron for the Gulf of Alaska: Reproducing the differences between an

762   oceanic HNLC ecosystem and a classical northern temperate shelf ecosystem. Deep-Sea

763   Res. II 56, 2520-2536. doi:10.1016/j.dsr2.2009.03.003.

764   Hinckley, S., C. Parada, J. K. Horne, M. Mazur and M. Woillez. 2016. Comparison of

765   individual-based model output to data using a model of walleye pollock early life history

766   in the Gulf of Alaska. Deep-Sea Res. II 132, 240-262.

767   Hinrichsen, H-H., J. O. Schmidt, C. Petereit, C. Mölmann. 2005. Survival probability of Baltic

768   larval cod in relation to spatial overlap patterns with its prey obtained from drift model

769   studies. ICES J. of Mar. Sci., 62, 878-885.

770   Hirschberger, W. A. and G. B. Smith. 1983. Spawning of twelve groundfish species in the

771   Alaska and Pacific Coast regions, 1975-81. U.S. Dep. Commer., NOAA Tech. Memo.

772   NMFS F/NWC-44, 50 pp.

773   Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe, viewed in the light of

774   biological research. Rapports et Proce`sVerbaux des Re´unions du Conseil Permanent

775   International pour l'Exploration de la Mer, 20, 1–228.

776   Houde, D.E. 2009. Recruitment variability. *in* T. Jakobsen, M. J. Fogarty, B. A. Megrey and E.

777   Moksness, *Fish Reproductive Biology*, Chapter 3, Wiley-Blackwell. ISBN 978-1-4051-

778   2126-2.

779   Hurst, T. P., D. W. Cooper, J. S. Scheingross, E. M. Seale, B. J. Laurel and M. L. Spencer. 2009.

780   Effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod

781   (*Gadus macrocephalus*). Fish. Oceanogr. 18, 301-311.

782   Hurst, T. P., B. J. Laurel, L. Cianelli. 2010. Ontogenetic patterns and temperature-dependent

783   growth rates in early life stages of Pacific cod (*Gadus macrocephalus*). Fish. Bull. 108,

784   382–392.

785   Janout, M. A., T. J. Weingartner, S. R. Okkonen, T. E. Whitledge, D. L. Musgrave. 2009. Some

786   characteristics of Yakutat Eddies propagating along the continental slope of the northern

787   Gulf of Alaska. Deep-Sea Res. II 56, 2444-2459.

788   Johnson, S. W., A. D. Neff, J. F. Thedinga, M. R. Lindeberg, and J. M. Maselko. 2012. Atlas of

789   nearshore fishes of Alaska: A synthesis of marine surveys from 1998 to 2011. U.S. Dep.

790   Commer., NOAA Tech. Memo. NMFS-AFSC-239, 261 p.

791   Kim, J. J., W. Stockhausen, S. Kim, Y-K. Cho, G-H. Seo, J-S. Lee. 2015. Understanding

792   interannual variability in the distribution of, and transport processes affecting, the early

793   life stages of *Todarodes pacificus* using behavioral-hydrodynamic modeling approaches.

794   Prog. Oceanogr. 138, 571-583. doi: http://dx.doi.org/10.1016/j.pocean.2015.04.003.

795   Ladd, C. A., and P. J. Stabeno.2009. Freshwater transport from the Pacific to the Bering Sea

796   through Amukta Pass. Geophys. Res. Lett., 36, L14608, doi:10.1029/2009GL039095.

797   Ladd, C. A., N. B. Kachel, C. W. Mordy and P. J. Stabeno. 2005. Observations from a Yakutat

798   eddy in the northern Gulf of Alaska. J. Geophys. Res., 110, C03003, doi:

799   10.1029/2004JC002710.

800   Large, W. G., S. G. Yeager, 2008. The global climatology of an interannually varying air-sea

801   flux data set. Clim. Dyn. 33, 341-364.

802   Large, W. G., J. C. McWilliams, S. C. Doney, 1994. Oceanic vertical mixing: a review and a

803   model with a nonlocal boundary layer parameterization. Rev. Geophys. 32, 363-403.

804   Laur, D. and L. Haldorson. 1996. Coastal habitat studies: the effect of the Exxon Valdez oil spill

805   on shallow subtidal fishes in Prince William Sound. In: Rice, S.D., R.B. Spies, D.A.

806   Wolfe and B.A. Wright (eds) American Fisheries Society Symposium 18: Proceedings of

807   the Exxon Valdez oil spill symposium. American Fisheries Society, Bethesda, Maryland,

808   pp. 659-670.

809   Laurel, B. J., R. S. Gregory and J. A. Brown. 2003. Settlement and distribution of age-0 juvenile

810   cod *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Mar. Ecol.

811   Prog. Ser. 262, 241-252.

812   Laurel, B. J., A. W. Stoner, C. H. Ryer, T. P. Hurst, A. A. Abookire, 2007. Comparative habitat

813   associations in juvenile Pacific cod and other gadids using seines, baited cameras and

814   laboratory techniques. J. Exp. Mar. Biol. Ecol. 351, 42–55.

815   Laurel, B. J., T. P. Hurst, L. A. Copeman and M. W. Davis. 2008. The role of temperature on the

816   growth and survival of early and late hatching Pacific cod larvae (*Gadus macrocephalus*).

817   J. Plankton Res. 30(9), 1051-1060.

818   Laurel, B. J., C. H. Ryer, B. Knoth , and A. W. Stoner. 2009. Temporal and ontogenetic shifts in

819   habitat use of juvenile Pacific cod (*Gadus macrocephalus*). J. Exp. Mar. Biol. Ecol. 377,

820   28–35.

821   Lett, C., P. Verley, C. Mullon, C. Parada, T. Brochier, P. Penven and B. Blake. 2008. A

822   Lagrangian tool for modeling ichthyoplankton dynamics. Environ. Modelling Software

823   23, 1210-1214.

824   Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis.1997. A Pacific

825   interdecadal climate oscillation with impacts on salmon production. Bull. Am. Met. Soc.

826   78, 1069-1079.

827   Marchesiello, P., J. C. McWilliams, and A. F. Shchepetkin. 2001. Open boundary conditions for

828   long-term integration of regional oceanic models. Ocean Modelling 3, 1-20.

829   Matarese, A.C., A. W. Kendall, D. M. Blood, and B. M. Vinter. 1989. Laboratory Guide to Early

830   Life Stages of Northeast Pacific Fishes. NOAA Technical Report NMFS 80. 652 pp.

831   Mecklenburg, C. W., T. A. Mecklenburg, and L. K. Thorsteinson. 2002. Fishes of Alaska.

832   American Fisheries Society, Bethesda, Md., 1037 pp.

833   Megrey, B. A. and S. Hinckley. 2001. The effect of turbulence on feeding of larval fishes: a

834   sensitivity analysis using an individual-based model. ICES J. Mar. Sci. 58(5), 1015-1029.

835   Narimatsu, Y., T. Hattori, Y. Ueda, H. Matsuzaka, M. Shiogaki, 2007. Somatic growth and

836   otolith microstructure of larval and juvenile Pacific cod *Gadus macrocephalus*. Fish. Sci.

837   73(6), 1257-1264.

838   North, E. W., A. Gallego and P. Petitgas. 2009. Manual of recommended practices for modelling

839   physical-biological interactions during fish early life. ICES Coop. Res. Rep. No. 295.

840   Okkonen, S. R. T.J. Weingartner, S.L. Danielson, D.L. Musgrave, and G.M. Schmidt. 2003.

841   Satellite and hydrographic observations of eddy-induced shelf-slope exchange in the

842   northwestern Gulf of Alaska. J. of Geophysical Res. 108 (c2), 3033.

843   doi 10.1029/2002JC001342.

844   Ottmar, M. L. and T. P. Hurst. 2012. Thermal effects on swimming activity and habitat choice in

845   juvenile Pacific cod (*Gadus macrocephalus*). Mar. Biol. 159, 2185-2194. doi

846   10.1007/s00227-012-2004-8.

847   Parada, C., D. A. Armstrong, B. Ernst, S. Hinckley, and J. M. (Lobo) Orensanz. 2010. Spatial

848   dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea—putting together

849   the pieces of the puzzle. Bull. Mar. Sci. 86 (2), 413-437.

850   Parada, C., S. Hinckley, J. Horne, M. Mazur, A. Hermann, E. Curchister. 2016. Modeling

851   connectivity of walleye pollock in the Gulf of Alaska: Are there any linkages to the

852   Bering Sea and Aleutian Islands? Deep-Sea Res. II 132, 227-239.

853   Paris, C. B., K. C. Lindeman, R. Claro, J. L. Fortuna, R. K. Cowen, R K. 2004. Modeling larval

854   transport from snapper (Lutjanidae) spawning aggregations in Cuba. Proc. Gulf and

855   Caribbean Fish. Inst. 55, 570-576.

856   Pelc, R. A., R. R. Warner, S. D. Gaines, C. B. Paris. 2010. Detecting larval export from marine

857   reserves. Proc. Nat. Acad. Sci. USA 107(43), 18266-18271.

858   Reed, R. K., and J. D. Schumacher. 1984. Additional current measurements in the Alaskan

859   Stream near Kodiak Island. J. Phys. Oceanogr. 14(7), 1,239-1,246.

860 Richwine, K. A., K. R. Smith, and R. A. McConnaughey. 2018. Surficial sediments of the

861   eastern Bering Sea continental shelf: EBSSED-2 database documentation. U.S. Dep.

862   Commer., NOAA Tech. Memo. NMFS-AFSC-377, 48 p.

863 Royer, T. C. 1982. Coastal freshwater discharge in the northeast Pacific. J. Geophys. Res.

864   87(C3), 2017-2021.

865 Royer, T. 1998. Coastal Processes in the Northern North Pacific. John Wiley & Sons, Inc., 605

866   Third Ave. New York NY 10158 USA.

867 Rugen, W. C., and A. C. Matarese. 1988. Spatial and temporal distribution and relative

868   abundance of Pacific cod (*Gadus macrocephalus*) larvae in the western Gulf of Alaska.

869   NWAFC Processed Report 88-18, NOAA/NMFS, Seattle, Washington, 53 pp.

870 Saha, S. and coauthors. 2010. The NCEP Climate Forecast System Reanalysis. Bull. Amer.

871   Meteor. Soc. 91, 1015.1057. doi: 10.1175/2010BAMS3001.1

872 Shchepetkin, A. F., J. C. McWilliams. 2005. The regional oceanic modeling system (ROMS): a

873   split-explicit, free-surface, topography-following-coordinate oceanic model, Ocean

874   Modelling 9 (4), 347-404.

875 Smith, G. B., G. E. Walters, P. A. Raymore and W. A. Hirschberger. 1984. Studies of the

876   distribution and abundance of juvenile groundfish in the northwestern Gulf of Alaska,

877   1980-1982: Part I. Three-year comparisons. NOAA Tech. Mem. NMFS-F/NWC-59.

878 Søiland, H., and M. D. Skogen. 2000. Validation of a three-dimensional biophysical model using

879   nutrient observations in the North Sea. ICES J. Mar. Sci. 57, 816–823.

880 Stabeno, P. J., R. K. Reed, and J. D. Schumacher. 1995. The Alaska Coastal Current: Continuity

881   of transport and forcing. J. Geophys. Res. 100 (C2), 2477-2485.

882   Stabeno, P. J., N. A. Bond, A. J. Hermann, N. B. Kachel, C. W. Mordy and J. E. Overland. 2004.

883   Meteorology and oceanography of the northern Gulf of Alaska. Cont. Shelf Res. 24 (7-8),

884   859–897.

885   Stabeno, P.J., S. Bell, W. Cheng, S. Danielson, N.B. Kachel, and C.W. Mordy. 2016.

886   Stachura, M. M., T. E. Essington, N. J. Mantua, A. B. Hollowed, M. A. Haltuch, P. D. Spencer,

887   T. A. Branch and M. J. Doyle. 2014. Linking Northeast Pacific recruitment synchrony to

888   environmental variability. Fish. Oceanogr. 23 (5), 389-408. Long-term observations of

889   Alaska Coastal Current in the northern Gulf of Alaska. Deep-Sea Res. II

890   doi:10.1016/j.dsr2.2015.12.016

891   Stark, J. W. 2007. Geographic and seasonal variations in maturation and growth of female

892   Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and Bering Sea. Fish. Bull.

893   105, 396–407.

894   Stockhausen, W., R. Lipcius and B. Hickey. 2000. Joint effects of larval dispersal, population

895   regulation, marine reserve design and exploitation on production and recruitment in the

896   Caribbean spiny lobster. Bull. Mar. Sci. 66 (3), 957-990.

897   Stockhausen, W. and R. Lipcius. 2001. Single large or several small marine reserves for the

898   Caribbean spiny lobster? Mar. Freshwater Res. 50, 1605-1614.

899   Stockhausen, W. and R. Lipcius. 2003. Simulated effects of seagrass loss and restoration on

900   settlement and recruitment of blue crab postlarvae and juveniles in the York River,

901   Chesapeake Bay. Bull. Mar. Sci. 72, 409-422.

902   Stockhausen, W. and A. Hermann. 2007. Modeling larval dispersion of rockfish: A tool for

903   marine reserve design? In: J. Heifetz, J. DiCosimo, A.J. Gharrett, M.S. Love, T.

904   O'Connell, and R. Stanley (eds.), Biology, assessment, and management of North Pacific

905   rockfishes. Alaska Sea Grant College Program, University of Alaska Fairbanks.

906 Stockhausen, W. T., K. O. Coyle, A. J. Hermann, D. Blood, M. Doyle, G. Gibson, S. Hinckley,

907   C. Ladd, C. Parada. *In press.* Running the Gauntlet: Connectivity between natal and

908   nursery areas for arrowtooth flounder (*Atheresthes stomias*) in the Gulf of Alaska, as

909   inferred from a biophysical Individual-based Model. Deep-Sea Res. II.

910 Stockhausen, W. T., K. O. Coyle, A. J. Hermann, M. Doyle, , G. Gibson, S. Hinckley, C. Ladd,

911   C. Parada. *In press.* Running the Gauntlet: Connectivity between natal and nursery areas

912   for Pacific ocean perch (*Sebastes alutus*) in the Gulf of Alaska, as inferred from a

913   biophysical Individual-based Model. Deep-Sea Res. II.

914 Thomson, J.A. 1963. On the demersal quality of fertilized eggs of Pacific cod, *Gadus*

915   *macrocephalus* Tilesius. J. Fish. Res. Board Can. 20, 1087–1088.

916 Trenberth, K. E. and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific

917   Climate Dynamics 9, 303-319

918 Trenberth, K. E., and J. W. Hurrell, 1995: Decadal climate variations in the Pacific. National

919   Research Council, Natural Climate Variability on Decade-to-Century Time Scales. D. G.

920   Martinson, K. Bryan, M. Ghil, M. M. Hall, T. R. Karl, E. S. Sarachik, S. Sorooshian, and

921   L. D. Talley, Eds., National Academy Press, Washington, D.C. pp. 472-481.

922 Vaz, R. A. N. and J.H. Simpson. 1994. Turbulence closure modeling of estuarine stratification. J.

923   Geophys. Res. Oceans 99, 16143-16160.

924 Werner F. E., J. A. Quinlan, R. G. Lough, D.R. Lynch. 2001. Spatially-explicit individual based

925   modeling of marine populations: a review of the advances in the 1990s. Sarsia 86, 411-

926   421.

927   Wolter, K., and M. S. Timlin. 1993. Monitoring ENSO in COADS with a seasonally adjusted

928   principal component index. Proc. of the 17th Climate Diagnostics Workshop, Norman,

929   OK, NOAA/NMC/CAC, NSSL, Oklahoma Clim. Survey, CIMMS and the School of

930   Meteor., Univ. of Oklahoma. pp. 52-57. http://www.esrl.noaa.gov/psd/enso/mei/WT1.pdf

931   Wolter, K., and M. S. Timlin. 2011. El Niño/Southern Oscillation behaviour since 1871 as

932   diagnosed in an extended multivariate ENSO index (MEI.ext). Intl. J. Climatology 31,

933   1074-1087.

934   Zhang, Y., J. M. Wallace and D. S. Battisti, 1997. ENSO-like interdecadal variability: 1900-93.

935   J. Climate. 10, 1004-1020.

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938   Table 1. Parameter values, equations and algorithms for Pacific cod IBM.

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Param	Description	Value	Equation/Comments	Units	Source
Egg Stage					
g_E	Growth rate		$g_E = 0.104 + 0.024T - 0.00002T^2$ where, T = temperature (°C)	mm d^{-1}	Hurst et al., 2010
z_{minE}	Min spawning depth	20		m	Dunn and Matarese 1987
z_{maxE}	Max spawning depth	200		m	Dunn and Matarese 1987
v_E	Egg ascent rate	0	Attached to bottom	ms^{-1}	Thomson 1963, Alderdice and Forrester, 1971, Dunn and Matarese 1987
d_{minE}	Min stage duration	8		days	
sd_E	Actual Stage duration		$sd_E = 46.597 - 4.079T$ where, T = temperature (°C)	days	B. Laurel, NOAA/AFSC pers. comm.
sr_E	Egg stage ratio		$sr_E = sr_E + \left(\dfrac{1.0}{sd_E}\right) dt$ where, dt=time step		Trigger for transition to

					next stage $(sr_E \geq 1)$
Yolk-sac Larval Stage					
g_Y	Growth rate		$g_Y = 0.0179 + 0.015T - 0.0001T^2$ where, T=temperature (°C)	mm d^{-1}	Hurst et al., 2010
z_{minY}	Min depth	0		m	Brodeur and Rugen, 1994
z_{maxY}	Max depth	40		m	Brodeur and Rugen, 1994
v_Y	Vertical velocity	1x10^{-4}		ms^{-1}	Random up/down
d_{minY}	Min stage duration	2		days	
d_{maxY}	Max stage duration	15		days	
PNR	Point of no return		$PNR = 34.67e^{-0.126T}$ where, T = temperature (°C)	days	Laurel et al., 2008
yd	Days to yolk-sac absorption		$yd = 14.7662e^{-0.235T}$ where, T = temperature (°C)	days	Laurel et al., 2008
sr_Y	Yolk-sac stage ratio		$sr_Y = sr_Y + \left(\dfrac{1.0}{yd}\right)dt$ where, dt=time step		
p	Probability of feeding		$p = p + \left(\dfrac{1.0}{PNR - yd}\right)d$		
Pre-flexion Feeding Larval Stage					
g_F	Growth rate		$g_F = 0.0179 + 0.015T - 0.0001T^2$ Where T = temperature (°C)	mm d^{-1}	Hurst et al. (2010)

z_{minF}	Min. depth	0		m	Brodeur and Rugen, 1994
z_{maxF}	Max depth	40		m	Brodeur and Rugen, 1994
T_F	Standard Length (SL) to Total Length (TL) conversion		$$TL = SL + \frac{0.5169}{0.9315}$$	mm	B. Laurel, NOAA/AFSC pers. comm.
v_F	Vertical velocity		v_F $$= ((0.081221 + 0.043168 * log_{10}T)TL^{1.49652})/1000.0$$ where, T = temperature (°C)	ms^{-1}	T. Hurst, NOAA/AFSC pers. comm.
d_{minF}	Min stage duration	5		days	
f_F	Length at flexion	13.5		mm	Matarese et al., 1989
Tr_F	Stage transition		$Length > f_F$	mm	
Post-flexion Feeding Larval Stage					
g_{PF}	Growth rate		$g_{PF} = 0.034 + 0.043T - 0.0008T^2$ where, T = temperature (°C)	mm d^{-1}	Hurst et al., 2010
$Lmax_{PF}$	Length at transformation	25		mm	Dunn and Matarese, 1987
zd_{minPF}	Min daytime	20			Hurst et al., 2009

	depth					
zd_{maxPF}	Max daytime depth	40			m	Hurst et al., 2009
zn_{minPF}	Min nighttime depth	0			m	Hurst et al., 2009
zn_{maxPF}	Max nighttime depth	20			m	Hurst et al., 2009
T_{PF}	Standard Length (SL) to Total Length (TL) conversion		$$TL = SL + \frac{0.5169}{0.9315}$$		mm	B. Laurel, NOAA/AFSC pers. comm.
v_{PF}	Vertical velocity		$v_{PF} = ((0.081221 + 0.043168 * log_{10}T)TL^{1.49652})/1000.0$ where, T = temperature (°C)		ms⁻¹	T. Hurst, NOAA/AFSC pers. comm.
Tr_{PF}	Stage transition	Tr_Y	$Length > Lmax_{PF}$		mm	
Epipelagic Juvenile Stage						
g_E	Growth rate		$g_E = -0.081 + 0.079T - 0.003T^2$ where, T = temperature (°C)		mm d⁻¹	Hurst et al., 2010
zd_{minE}	Min daytime depth	20			m	Hurst et al., 2009

zd_{maxE}	Max daytime depth	40			m	Hurst et al., 2009
zn_{minE}	Min nighttime depth	0			m	Hurst et al., 2009
zn_{maxE}	Max nighttime depth	20			m	Hurst et al., 2009
v_E	Vertical velocity		$v_E = ((0.081221 + 0.043168 * log_{10}T)TL^{1.49652})/1000.0$ where, T = temperature (°C)		ms^{-1}	T. Hurst, NOAA/AFSC pers. comm.
h_{minE}	Min settlement depth	10			m	Smith et al., 1984
h_{maxE}	Max settlement depth	70			m	Smith et al., 1984
Tr_E	Stage transition	Tr_Y	$Depth \geq h_{min}$ and $Depth \leq h_{max}$		m	
Benthic Juvenile Stage						
g_J	Growth rate		$g_E = -0.081 + 0.079T - 0.003T^2$ where, T = temperature (°C)		mm d^{-1}	Hurst et al., 2010
h_{minJ}	Min depth	10			m	Minimum model depth
h_{maxJ}	Max depth	70				Smith et al., 1984

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Table 2. Results of grid size test.   945

Grid Size (km)	Number of Matching Settlement Zones in Top 10	Number Simulated
1	n/a	5563
2.5	10	906951
5	9	221952
7	9	101953
10	8	64 954

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959   Table 3. Correlations coefficients between the time series (1996-2011) of percent settled in each

960   nursery area and overall percent settled from the Pacific cod IBM, recruitment (Rct: ln-

961   transformed estimated basin-wide age-0 recruitment) and physical indices. ** indicates

962   correlations that are significant at p < 0.05 ; * indicates correlations that are significant at p <

963   0.10 are italicized. P-values are not corrected for multiple comparisons.

Nursery Area	Rct	MEI	PDO	NPI	AO
101	-0.612**	0.021	0.096	-0.389	0.178
102	0.063	-0.121	-0.475*	0.199	0.194
103	-0.275	0.440*	0.205	-0.213	-0.008
104	0.353	0.104	-0.201	0.201	-0.339
105	0.706**	-0.348	-0.491**	0.419*	0.035
106	0.049	-0.462*	-0.302	0.480*	0.227
107	-0.703**	0.092	0.350	-0.310	0.131
108	-0.581**	0.028	0.186	-0.149	0.254
109	-0.146	-0.005	0.387	-0.394	-0.039
110	-0.379	-0.061	0.289	-0.442*	-0.056
111	0.412	-0.308	-0.244	0.317	-0.269
112	0.275	-0.535**	-0.429*	0.531**	-0.023
113	0.180	0.129	0.330	-0.412	-0.111
TotFracSettled	-0.099	-0.438*	-0.122	0.178	0.070

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966   List of Figures

967   Fig. 1. Time series of female spawning stock biomass (SSB) and age-0 recruitment (Barbeaux et

968   al., 2018) for Gulf of Alaska Pacific cod.

969   Fig. 2. The Gulf of Alaska, with connectivity zones used in Pacific cod IBM. Spawning zones

970   are < 70 m (102 – 113) and 70 to 200 m (202 – 213). Nursery areas are < 70 m (numbered 101-

971   113). Offshore zones start at the 200 m isobaths and extends 125-150 km offshore from that

972   isobaths (numbered 1-13). The Deep Ocean zone is number 0. Alongshore zone names are

973   indicated. The box around the plot indicates the extent of the 3-km ROMS grid.

974   Fig. 3. Conceptual model of the early life history of Pacific cod, showing movement across the

975   shelf from spawning to settlement. X-axis represents time; t_0 is the spawning date. The y-axis

976   represents depth. Numbers above 0-depth line represent individual size.

977   Fig. 4. Average connectivity for the Pacific cod IBM simulation years (1997-2013). The y-axis

978   of both panels shows the spawning areas, with 102-113 representing the shallow (<70 m)

979   spawning areas, and 202-213 representing the deep (70–200 m) spawning areas. Sink area 998

980   representing individuals that left the 3-km grid (mostly to the southwest along the Alaska

981   Peninsula) is shown in a separate panel due to a difference in scale. The x-axis of the matrix

982   shows the sink areas: 101–113 are nursery areas (<70 m), 201–213 are regions where the depth is

983   70–200 m, 1–12 are from the 200 m isobaths to approximately 150 km offshore. Area 0 is the

984   GOA deep basin. The shading represents the probability of moving from spawning area to

985   ending area. Heavy lines on the matrix delineate the different depth regions.

986   Fig. 5. Standard deviation of connectivity for the Pacific cod IBM simulation years (1997-2013).

987   The y-axis shows the spawning areas, with 102-113 representing the shallow (<70 m) spawning

988   areas, and 202-213 representing the deep (70–200m) spawning areas. The x-axis of the matrix
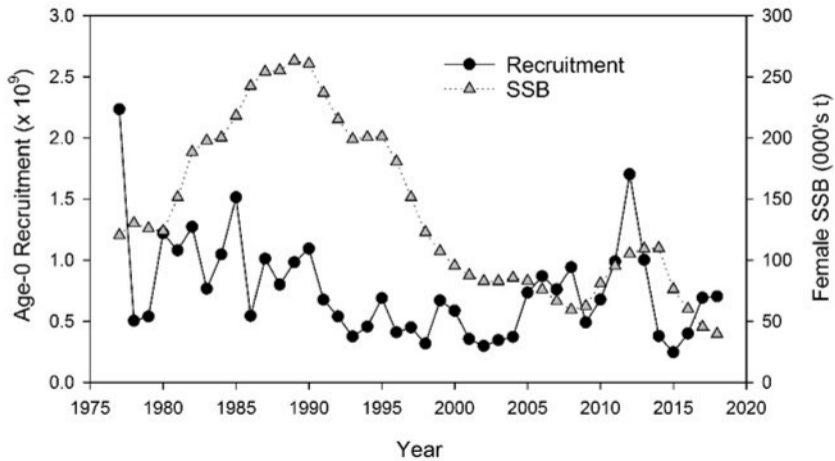
989   shows the sink areas: 101–113 are nursery areas (<70 m), 201–213 are regions where the depth is

990   70–200 m, 1–12 are from the 200 m isobaths to approximately 150 km offshore. Area 0 is the

991   GOA deep basin. Sink area 998 represents individuals that left the 3-km grid, mostly to the

992   southwest along the Alaska Peninsula. The shading represents the standard deviation. Heavy

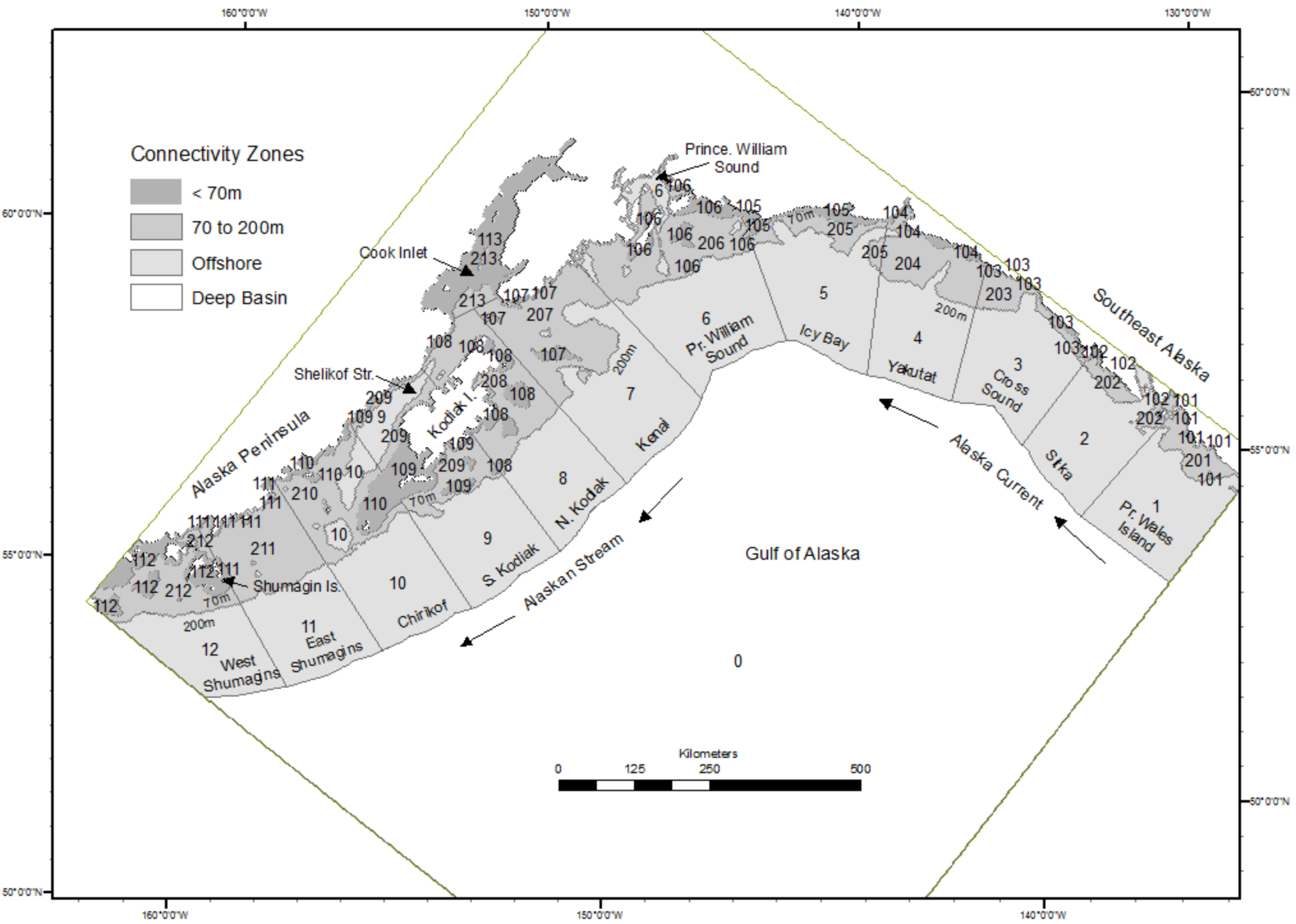993   lines on the matrix delineate the different depth regions.

994   Fig. 6. Spawning areas for selected nursery or ending (Z998) regions. Each panel represents one

995   nursery or ending area. The x-axis shows the spawning areas, with 102-112 being the shallow

996   (<70 m) spawning areas, and 202-212 being the deep (70–200 m) spawning areas. The y-axis

997   represents the probability of transport from each spawning area to the nursery or ending area

998   represented in the panel.

999   Fig. 7. Time series of *NDI* and *OC*, indices calculated from the Pacific cod IBM connectivity
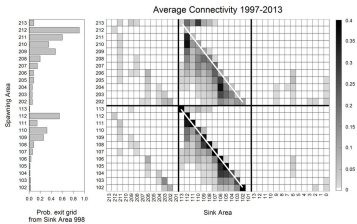
1000   matrices.

1001   Fig. 8. Matrix showing the difference in connectivity probabilities between 1998, the year with

1002   the highest NDI, and the average connectivity matrix from the 1997-2013 time series. The y-axis

1003   shows the spawning areas, with 102-113 representing the shallow (<70 m) spawning areas, and

1004   202-213 representing the deep (70–200 m) spawning areas. The x-axis of the matrix shows the

1005   sink areas. Areas 101–113 are the nursery areas (<70 m), areas 201–213 are regions where the

1006   depth is 70–200 m. Area 998 indicates the probabilities of exiting the 3-km grid from all

1007   spawning areas. Areas 1 – 12 are from the 200 m isobaths to approximately 150 km offshore.

1008   Sink area 0 is the GOA deep basin and sink area 998 represents individuals that left the 3-km

1009   grid. The shading represents the difference in probability of transport from spawning area to

1010   ending area.

1011   Fig. 9. A. Fraction settled (of all individuals simulated) in each nursery area. B. Fraction settled

1012   of individuals from the shallow spawning areas. C. Fraction settled of individuals from the deep

1013   spawning areas. D. Fraction settled (of all individuals simulated) for each year of the simulation.
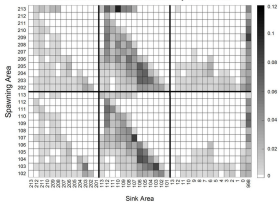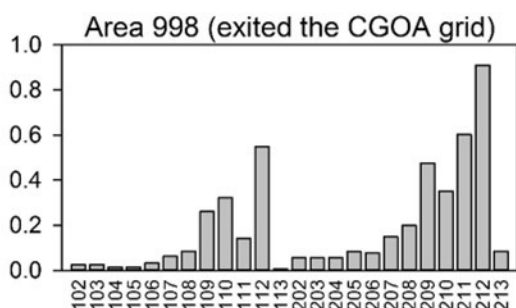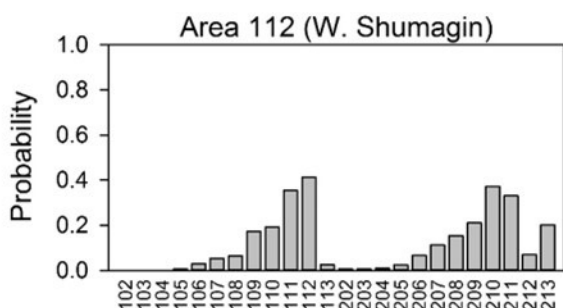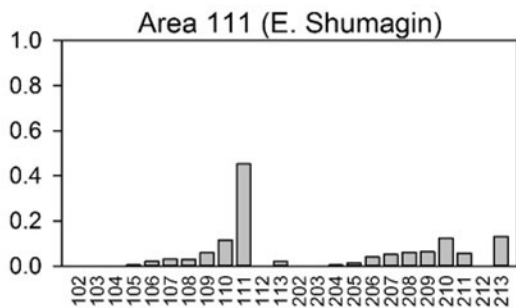
1014

0 m

3-4 mm   4-6 mm   6-10 mm   10-25 mm   25+ mm

YOLK-SAC
LARVAE

1st feeding

FEEDING
LARVAE

flexion

FEEDING
LARVAE

Transformation

EPIPELAGIC
JUVENILES

Settlement

SETTLED
JUVENILES

Depth <70m

Preflexion
larvae, no DVM

Postflexion
Larvae, DVM

MOVE INSHORE

Swim to surface

100m

ADULT
SPAWN

EGGS

On bottom

Hatch:

Continental Shelf

200m

t_0 t_0 + 21-26 days t_0 + 4-6 weeks

Feb-July   July+

Average Connectivity 1997-2013

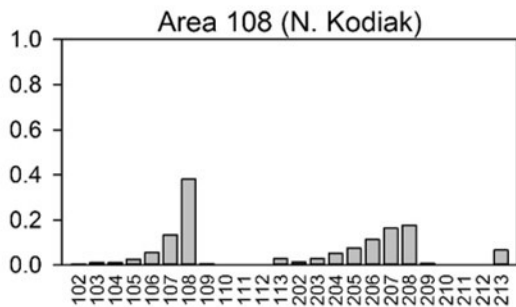Standard Deviation of Connectivity 1997-2013

Area 102 (Sitka) Area 106 (PWS) Area 107 (Kodiak) Area 108 (N. Kodiak) Area 109 (S. Kodiak) Area 111 (E. Shumagin) Area 112 (W. Shumagin) Area 998 (exited the CGOA grid)

Spawning Areas

Difference Between 1998 and Average of Connectivity Matrices