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Loss of spawning habitat and pre-recruits of Pacific cod during a Gulf of Alaska heatwave

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3 **Loss of spawning habitat and pre-recruits of Pacific cod during a Gulf of**
4 **Alaska heatwave**

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11

12 **Abstract**

13

14 Pacific cod (*Gadus macrocephalus*) stocks in the Gulf of Alaska experienced steep, unexpected declines
15 following an unprecedented 3 yr marine heatwave (i.e., ‘warm blob’) from 2014 to 2016. We contend
16 that stock reproductive potential was reduced during this period, evidenced by a combination of new
17 laboratory data demonstrating narrow thermal hatch success (3 – 6 °C), mechanistic-based models of
18 spawning habitat and correlations with pre-recruit time series. With the exception of single year El Niño
19 events (1998, 2003), the recent 3 yr heatwave (2014-16) and return to similar conditions in 2019 were
20 potentially the most significant impacts on spawning habitat for Pacific cod in the available time series
21 (1994-2019). Continued warming will likely reduce the duration and spatial extent of Pacific cod
22 spawning in the Gulf of Alaska.

23

24

25

26 KEYWORDS: phenology, climate change, match-mismatch, ichthyoplankton, nursery habitat, hatch
27 success, reproductive output

Draft

28 Introduction

29 From late 2013 to 2016, the Gulf of Alaska (GOA) experienced 3–4 °C above average sea surface
30 temperature anomalies (relative to 1980-2010) associated with a reduction in winter heat flux (i.e., ‘warm
31 blob’ Bond et al. 2015) and the second strongest El Niño event on record between 2015 and 2016 (NOAA
32 2016). The 2014 to 2016 marine heatwave is currently considered the largest warm anomaly ever
33 recorded in the North Pacific from 1880 to present (Di Lorenzo and Mantua 2016), and the broad-scale
34 ecosystem response to this event is still being evaluated (Walsh et al. 2018). For the Pacific cod fishery,
35 these impacts have already led to significant economic loss by way of reduced biomass in the GOA
36 (estimated 58% reduction in survey biomass from 2015 to 2017) and an 80% reduction in the
37 recommended acceptable biological catch for 2018 (Barbeaux et al. 2017). Continued declines in 2019 led
38 to the closure of the federal directed fishery for Pacific cod in the Gulf of Alaska for 2020. Such a
39 dramatic change in the fishery has prompted fisheries managers to better examine the links between
40 climate anomalies and reduced recruitment for Pacific cod in an effort to improve advice for timely
41 management actions.

42 Temperature impacts every life history process in marine fish, but early life stages are generally
43 considered more sensitive to environmental conditions than older, larger life stages (Houde 1987).
44 Within the first year of life, the embryonic egg phase generally has the narrowest thermal range for
45 survival, likely due to a finite supply of maternally-provisioned heat shock proteins for cellular repair
46 after thermal stress (Motani and Wainwright 2015). Eggs also lack the ability to behaviorally
47 thermoregulate, unlike juveniles and adults (Kelsch and Neill 1990). As such, these early life stages may
48 set biogeographic boundaries and limit productive capacity for fisheries impacted by climate change
49 (Rijnsdorp et al. 2009), although comparatively few data are available to test these hypotheses.

50 Optimal thermal conditions for Pacific cod eggs in the GOA have been previously unknown,
51 although eggs have been successfully incubated across a broad temperature range (0-8° C; Laurel et al.
52 2008). In the Western Pacific, temperature-dependent hatch rates have been quantified and indicate

53 Pacific cod are highly temperature-sensitive, with highest hatch success occurring between 4° and 6° C
54 (Bian et al. 2016). Pacific cod are also rather atypical among gadids in that they are single-batch
55 spawners and have demersal eggs that adhere to the bottom (Alderdice and Forrester 1971; Laurel et al.
56 2008). Pacific cod females can therefore place eggs in thermal habitats that optimize hatch success,
57 unlike the pelagic eggs of Atlantic cod *Gadus morhua* that disperse in the water column and risk
58 advection to sub-optimal habitats during incubation (Bradbury et al. 2008). Spawning locations in the
59 Gulf of Alaska have not been mapped, but spawning is generally thought to occur from January to June
60 (with peak spawning between Feb - April), at depths of 100 – 200 m in Alaska (Stark 2007; Neidetcher et
61 al. 2014).

62 Pacific cod undertake a variety of regional seasonal migrations between summer feeding and
63 winter spawning grounds. In higher latitudes around Alaska and Canada, maturing individuals move to
64 warmer, deeper water in the fall as inshore waters cool, before returning to warmer, shallower waters in
65 the spring and summer to feed (Bakkala 1984; Ketchen 1961; Palsson 1990; Shimada and Kimura 1994).
66 However, these migratory patterns are reversed (moving inshore in winter and offshore in summer) at the
67 southern extent of their range where seasonal conditions are warmer (Karp 1983; Mishima 1984;
68 Westrheim 1984; Zhang 1984), suggesting Pacific cod distributions may be more strongly linked to
69 temperature than depth. There also appears to be some degree of spatial-temporal plasticity in spawning
70 dynamics. Bering Sea populations appear to adjust spawning earlier in warmer years, and spawn timing
71 tends to occur earlier at lower latitudes on both sides of the Pacific (Neidetcher et al. 2014). For example,
72 spawning for Pacific cod starts in December along the west coast of the continental United States and
73 shifts to February for Canadian stocks further north (Foucher and Westrheim 1990). In the GOA and
74 eastern Bering Sea, Pacific cod spawn later in March and April (Neidetcher et al. 2014; Stark 2007).
75 These observation in migration and phenology are consistent with idea that thermal habitats play an
76 important role in Pacific cod behavior and support the widely accepted view that marine fish place eggs
77 and larvae in environments most optimal for successful hatch and early larval survival.

78 In this study, we conducted new experimental work to parameterize the temperature-dependent
79 hatch success of GOA Pacific cod, and combine this relationship with seasonal water column temperature
80 data to derive indices of spawning habitat suitability for Pacific cod over 26 years and spanning the recent
81 marine heatwave. We then compared spawning habitat suitability with time series data on pre-recruit
82 abundance and adult recruitment over the same time range. Using this approach, we tested the following
83 hypotheses: H₁ Pacific cod have experienced significant shifts in the timing, depth and extent of suitable
84 spawning habitat in warm years; H₂ Pacific cod spawning habitat suitability was lower overall during
85 extreme warm water events (e.g., 1998, 2003 El Niño, 2014-16 'warm blob'); H₃ Pacific cod spawning
86 habitat suitability is a predictor of pre-recruitment abundance and adult recruitment at age-3. These
87 results are discussed in the context of spawning phenology and early warning management for Pacific cod
88 fisheries facing future warming events in the Gulf of Alaska.

89

90 **Methods**

91 **Laboratory experiment**

92 An experiment testing the effects of temperature on Pacific cod eggs was conducted at the AFSC
93 laboratory in Newport, Oregon. The AFSC laboratory has captive adult broodstock collected from the
94 Gulf of Alaska (Kodiak, AK 57.882°N -152.626°W) as age-0 juveniles in 2012 and 2013, as well as
95 temperature-controlled laboratory space for incubation experiments. Environmental conditions for the
96 mature broodstock were maintained at 7–9 °C during the summer and 2–6 °C during the spawning season.

97 Spawning of males (n=3) and female (n=1) broodstock were conducted in early March of 2016 at
98 4 °C to produce a fertilized egg batch following protocols described by Laurel et al. (2008). Eggs were
99 then subdivided into incubation trays and acclimated to each temperature treatment (-1.1, 0.3, 1.9, 4.9,
100 9.0, 11.9 and 16.0 °C) at a rate of 1 °C per hour. After 24 hrs, the egg batch was divided across 21
101 replicate 1-L containers with 220 µm mesh-bottom to track hatch success in an extended temperature
102 incubation experiment. Eggs were volumetrically spread evenly across containers (0.5 ml/container at

103 ~300 eggs). Estimated egg stocking densities for each beaker were adjusted to actual counts based on
104 daily mortality and hatch counts at the end of the experiment. The mesh-bottom containers were
105 suspended in a series of temperature-controlled, flow-through water baths (66×46×38 cm) maintained at
106 each treatment temperature. Temperatures were maintained within 0.2 degrees of their nominal treatment
107 during the course of the experiment. Three replicate containers were used for each temperature treatment
108 (n=7) for a total of 21 separate containers for egg incubation. Temperature-controlled seawater was
109 supplied to each of the seawater baths at a rate of 2-3 L min⁻¹. Water was exchanged daily by gently
110 lifting and lowering containers in each seawater bath. Eggs from each replicate beaker were monitored
111 daily thereafter to measure mortality and hatch. Eggs were considered dead when they were opaque in
112 color. Dead eggs were counted and removed by pipette. As larvae hatched, individuals were transferred
113 by pipette to a separate corresponding 1-L meshed beaker held at the same temperature in the same water
114 bath. Replicate beakers of eggs continued to be checked daily until all embryos either hatched or died.

115 A nonlinear function was used to describe the relationship between hatch success (i.e. the
116 proportion of eggs that successfully hatched) and incubation temperature. We considered two models with
117 the desired properties of being dome-shaped and requiring relatively few parameters (only 3): the curve
118 described by the Cauchy (Lorentzian) distribution, as well as a Gaussian curve (see Tsoukali et al. 2016
119 for a discussion of functional response). Each model was fit to observed hatch proportions within each
120 replicate beaker, weighted by the total number of eggs in each beaker.

121

122 **Spawning habitat index**

123 The longest and most complete seasonal temperature record for the GOA exists at GAK1 (the
124 innermost station on the Seward Line; Fig. S1) which has been maintained by the University of Alaska
125 since 1970. Temperature measurements are taken from the surface to 200 m or 250 m depth
126 approximately monthly throughout the year and reported at discrete depths (0, 10, 20, 30, 50, 75, 100,
127 150, 200, 250 m). Comparison with available spring data from CTD casts at Cape Kekurnoi in the
128 Shelikof region (1986 - 1999) indicates the GAK1 measurements are similar to temperatures where pre-

129 recruit surveys were conducted (Stabeno et al. 2004). A further comparison with temperature profile data
130 from March surveys in Shelikof Strait (2003 - 2019) confirms that GAK1 is capturing thermal conditions
131 representative of a broader part of the GOA shelf (Figure S2). For this study, we use temperature data
132 from GAK1 beginning in 1994 as measurements in January and February were uncommon prior to then.
133 To account for variation in seasonal timing and frequency of measurements, temperature measurements
134 were interpolated to a 1 m × 1 day grid using bivariate linear interpolation across depths and days,
135 implemented using the Akima package in R (Akima and Gebhardt 2015).

136 Seasonal and depth-specific estimates of spawning habitat suitability were calculated using the
137 interpolated temperature profiles at depth combined with experimentally-derived temperature-dependent
138 hatch success of Pacific cod eggs. An annual index was developed by taking the average of hatch success
139 probability across depths of 100 - 250 m from January – April based on known spawning dynamics for
140 Pacific cod in Alaska (Neidetcher et al 2014; Stark 2007). While water column and near-bottom
141 temperatures at GAK1 may not precisely capture bottom temperatures for a given depth or area, this
142 index integrates across depths and time to capture interannual variability in overall spawning habitat
143 suitability. This index of spawning habitat suitability was then compared with subsequent measures of
144 year-class abundance at larval, age-0, and age-3 stages, lagged as appropriate to correspond to year of
145 hatching, as described below, using Pearson's correlation coefficients. Time series were inspected for
146 autocorrelation prior to analyses.

147

148 **Pre-recruit/recruitment time series**

149 *Ichthyoplankton*

150 The AFSC conducted ichthyoplankton surveys in the Gulf of Alaska, with annual surveys from
151 1981 – 2011, and biennial surveys thereafter. Larvae were sampled primarily using paired 60 cm bongo
152 nets with 505-µm mesh. Oblique tows were carried out from 100 m depth to the surface or from 10 m off
153 bottom in shallower water (Matarese et al. 2003; Ichthyoplankton Information System
154 <https://access.afsc.noaa.gov/ichthyo/>). Flowmeters were mounted in the frame of each net to determine

155 the amount of water filtered for each tow. The contents of one net were preserved in 5% formalin for later
156 sorting and quantitative enumeration at the Polish Plankton Sorting Center in Szczecin, Poland. Historical
157 sampling has been most intense in the vicinity of Shelikof Strait and the shelf southwest of Kodiak Island
158 during mid-May through early June (Fig. S1), a time-frame when Pacific cod larvae are abundant in the
159 water column (Doyle et al. 2009). From this area and time, a subset of data has been developed into a
160 time-series of larval Pacific cod abundance by calculating the area-weighted mean catch per 10 m² (after
161 Doyle et al. 2009).

162 *Age-0 juveniles*

163 Newly settled age-0 juvenile cod were surveyed by a 36-m demersal beach seine along the
164 Kodiak Island coast from 2006-present (See Laurel et al. 2017 for details). The survey targets juvenile
165 cod over a relatively small spatial extent, but represents the only age-0 time series spanning the pre- and
166 post-‘warm blob’ years in the GOA. Seine effort is restricted to 16 fixed-site locations spread equally
167 across two embayments on the northeast portion of the island (Fig. S1). Site locations are dominated by
168 a mix of eelgrass *Zostera marina*, *Laminaria saccharina* or ‘bare’ mineral substrates (sand-small cobble)
169 at an average depth of 2–4m. Seine sites were surveyed twice on successive days during two summer
170 sampling periods, July 14–21 and August 21–28, in each year. A total of 14 years (2006-19) of survey
171 data were available for this study (n=896 seine hauls). From these data, a time-series of annual Pacific
172 cod abundance was calculated based on the average catch of age-0 cod per haul across all sites.

173

174 *Age-3 recruitment*

175 Estimates of abundance at age 3 were taken from the stock assessment model for Gulf of Alaska
176 Pacific cod, which is an age-structured model fit to survey and fishery data (Barbeaux et al. 2018).
177 Recruitment to the fishery occurs at age 3-4, and estimates of year-class strength in the assessment model
178 are increasingly reliable from age 3.

179

180

181 **Results**

182 *Experimental results*

183 Hatch success in Pacific cod was highly temperature-sensitive, indicated by the narrow thermal range of
184 proportionately higher hatch success at 5 °C and steep decline in the proportion of eggs that hatched at
185 temperatures below 3°C and above 7 °C (Fig. 1). Temperature (T) significantly impacted percent hatch
186 success (H) in the statistical model (ANOVA; $F_{6,14} = 41.35$, $P < 0.001$), and described 96% of the
187 variation in hatch success as a continuous variable in the following Cauchy model:

$$188 \quad H = \frac{0.453}{1 + \left(\frac{T - 4.192}{2.125}\right)^2}$$

189 A Gaussian model fit to the same data (Fig. 1) explained 95% of the variance in hatch success and had a
190 greater residual standard error (0.74 compared to 0.67 for the Cauchy model). We used the Cauchy model
191 to derive a spawning habitat suitability index, and the Gaussian model is presented for comparison.

192 *Spawning habitat suitability*

193 Thermal habitat for successful hatching of Pacific cod eggs has been plentiful in most years
194 during the months of January to April in the Gulf of Alaska (Fig. 2). On average, in January, the most
195 suitable habitat is in shallower waters down to 50m, while deeper regions remain warmer than optimal for
196 successful hatching. From February to April, suitable habitat extends through the water column down to
197 250m. By May, the surface begins to warm and suitable habitat is restricted to only deeper waters (Figs. 2
198 and S3).

199 In 2015, 2016 and 2019, suitable habitat was substantially reduced within the time series (1994-
200 present) due to warm temperatures throughout the water column (Fig. 2). Based on temperatures from
201 January to April in waters >100 m, the probability of successful hatch in these recent warm years was
202 57% - 59% that of an average non-heatwave year, and less than half that observed in 2012, the year with
203 the highest habitat index (Fig. 3a). The years 1998 and 2003 also showed reductions in habitat due to
204 warm events, but these events were more limited in their depth (1998) or temporal extent (2003) (Fig. 2

205 and 3a). In most years, the limiting factor for hatch success was the presence of warmer-than-optimal
206 waters, but in a few years (e.g. 2007, 2009, 2012), shallower waters in late winter were colder than the
207 optimum for hatch success. In 2019, a return of warm conditions again reduced suitable habitat for Pacific
208 cod eggs in the GOA. Spawning habitat suitability based on a Gaussian model fit was highly correlated (ρ
209 = 0.98) with suitability based on the Cauchy model.

210 *Pre-recruitment abundance*

211 Interannual variation in ln-transformed abundance of Pacific cod larvae was significantly
212 correlated with the index of spawning habitat suitability ($\rho = 0.76$, $p < 0.001$), with fewer larvae in years
213 when the thermal habitat was less suitable for successful hatching of eggs (Fig. 3b). This relationship
214 continued to hold for subsequent life stages, including the abundance of age-0 cod measured in nearshore
215 nursery habitats during their first summer ($\rho = 0.50$, $p < 0.05$; Fig. 3c) and subsequent estimated numbers
216 of age-3 recruits to the population ($\rho = 0.57$, $p < 0.01$; Fig. 3d). The habitat suitability, larval, and age-0
217 time series did not have significant autocorrelation, however the age-3 time series was significantly
218 autocorrelated at lag 1 ($p < 0.05$). The years 2015, 2016, and 2019 had the lowest observed abundance of
219 larvae and age-0 juveniles in the time series (Fig. 3b, 3c, S4). Estimated recruitment to age 3 has not yet
220 been observed for the 2016 and 2019 year-classes, but was record low in 2015 (Fig. 3d, S4).

221 **Discussion**

222 Our study suggests that poor hatch success due to a reduction in thermal habitat suitability may
223 have contributed to low recruitment during the recent marine heat wave in the GOA. Experimental results
224 show narrow thermal tolerance of Pacific cod eggs, with an optimum around 4-5 °C and rapid decline at
225 warmer and cooler temperatures. The precipitous drop in hatch success above and below 5 °C is
226 consistent with experimental data from the Strait of Georgia, B.C. (Alderdice and Forrester 1971) and
227 southwest Japan (Bian et al 2016), which collectively suggest Pacific cod have much higher temperature
228 sensitivity than other gadids with pelagic eggs (e.g., Atlantic cod, Geffen et al. 2006; walleye pollock,
229 Laurel et al. 2018; Tsoukali et al. 2016). Such narrow thermal tolerance may reflect the relatively stable

230 thermal conditions encountered by demersal eggs under normal conditions and the ability of females to
231 select spawning habitat to optimize fitness for offspring. A characteristic feature of the recent GOA
232 marine heatwaves was the presence and persistence of warm waters even at depth, which drastically
233 reduced the availability of thermal habitat conducive to offspring survival. Pacific cod appear to have a
234 narrow thermal tolerance at the egg stage that leaves them especially vulnerable to warming.

235 While the GOA heatwave likely imparted bioenergetic stress across the full life history of Pacific
236 cod (Zador and Yasumiishi 2017), this study demonstrates one mechanism by which warm temperatures
237 may limit recruitment to the fishery: stock reproductive potential. A constriction in the duration of
238 suitable hatching temperatures has similarly been hypothesized to be the cause for a decline in Baltic
239 spring-spawning herring *Clupea harengus* (Dodson et al. 2018), another stock with demersal eggs.
240 However, other mechanisms may link warmer temperatures to reduced recruitment. In spring-spawning
241 marine fish, temperature-dependent metabolic demand can impact surplus energy available for
242 reproduction that is already depleted from overwintering (Pankhurst 1997). For example, Atlantic cod
243 will skip spawning when there is insufficient energy (liver stores) to support gonad development (Rideout
244 et al. 2006) and other species may fail to make migrations to spawning grounds (Milton and Chenery
245 2005). Thus, it is possible that warm temperatures may additionally lead to reduced reproductive output
246 through effects on maternal conditions and spawning activity.

247 Our first and second hypotheses were supported by the annual habitat suitability model outputs,
248 indicating that optimal spawning habitat was reduced (H_1) and spatio-temporally restricted (H_2) to
249 shallower regions and earlier times in the year in the warmest years (1998, 2003, 2015, 2016, 2019).
250 However, adapting the timing and location of spawning to match changes in optimal spawning habitat
251 will depend on a number of physiological and behavioral factors. Temporal plasticity in spawn timing
252 (phenology), while potentially favorable for maximizing hatch success, may result in larvae hatching into
253 a poor foraging environment; that is, 'match/mismatch' processes (Durant et al. 2007). Spring spawn
254 timing may also be constrained by bioenergetics, hormone secretion and gametogenesis that are regulated

255 by preceding fall and winter environments (Pankhurst 1997). Warm years are indeed associated with
256 accelerated gonad maturation and early spawning in Pacific cod in the Bering Sea (Neidetcher et al.
257 2014). Behavioral thermoregulation of the spatial and temporal release of eggs would be highly adaptive
258 for a thermally-sensitive, single-batch spawner like Pacific cod, although no spring data are available to
259 confirm earlier shifts in spawning during the marine heatwaves. Spatial heterogeneity in thermal habitats
260 within the GOA may provide opportunities for spawners to select suitable microhabitats even when mean
261 temperatures are above optimal. Indeed, observations of adult Pacific cod shifting to deeper, cooler
262 regions during the summer in response to warming suggests this species can cue to preferred thermal
263 feeding habitats when they are available (Yang et al. 2019). Improved knowledge of Pacific cod spawning
264 locations and behavior in the Gulf of Alaska could lead to better characterization of spawning habitat
265 suitability and its importance as a limiting factor for recruitment success.

266 The low numbers of larval and age-0 juvenile stages observed during the marine heatwave may
267 suggest spawning output was lower (supporting H₃), but may also be the result of increased post-hatch
268 mortality. Although larvae and juvenile Pacific cod can grow and survive over a broad range of
269 temperatures (2 – 11 °C; Hurst et al. 2012), the thermal conditions during the 2014-16 period would be
270 metabolically demanding for larvae if prey densities were low (Laurel et al. 2011) and potentially
271 impactful on growth following settlement into shallow nursery areas (Laurel et al. 2017). Temperature
272 can also impact larval survival indirectly through trophic links, for instance through changes in prey
273 quality or by altering the timing and magnitude of zooplankton prey production (Durant et al. 2007).
274 Disentangling these indirect effects of temperature are challenging. However, even given considerable
275 uncertainty in abundance indices, including stock assessment estimates of abundance at age-3, we were
276 able to detect a clear relationship between thermal conditions during spawning and eventual year-class
277 size, pointing to the importance of processes occurring during this life stage.

278 Pacific cod recruitment is characterized by occasional strong year-classes, and multiple
279 consecutive years of low recruitment are not unprecedented (Barbeaux et al. 2018). Early indications
280 based on age-0 abundance estimates suggest that the 2017 and 2018 year classes may be strong (B. Laurel

281 unpub. data). However, long-term warming in the GOA and predicted increased frequency of heatwaves
282 means thermal conditions will become increasingly unfavorable for Pacific cod. Projections under
283 Representative Concentration Pathway 8.5 (“business as usual”) indicate mean winter SST in the Gulf of
284 Alaska increasing at least 3°C in the next century (Scott et al. 2016). Indeed, heatwave conditions have
285 returned to the Western Gulf of Alaska in 2019 after only a two-year hiatus, and sea surface temperatures
286 are forecasted to remain 0.5 to 2 °C above average into 2020
287 (<http://www.cpc.ncep.noaa.gov/products/NMME/seasanom.shtml>). Complex bathymetry and its
288 interaction with currents and on-shelf flow may provide some local thermal refugia for spawning Pacific
289 cod even in warm years, but large-scale population-level shifts in spawning area are unlikely. Regions in
290 the far Western Gulf of Alaska are typically cooler than Central and Eastern GOA, but these regions are
291 downstream of important coastal nursery areas identified for juveniles in the Central GOA (Fig. S1,
292 Stabeno et al. 2016; Laurel et al. 2017) and at the edge of a narrow shelf where there is high risk of off-
293 shelf larval advection (Doyle et al 2009; Hinckley et al. 2019). Like the extreme Western GOA, nearby
294 spawning areas in the Aleutians (Unimak Pass) and Bering Sea shelf may remain thermally suitable for
295 Pacific cod with continued warming, but these populations are genetically distinct (Spies 2012) and also
296 downstream of ocean currents that could potentially seed the Gulf of Alaska with larvae and juveniles.
297 Tagging studies also suggest very limited movement of Pacific cod between the Aleutian/Bering region
298 and the Central Gulf of Alaska (Rand et al. 2014). Although distinct east-to-west genetic structure and
299 reduced gene flow within the Gulf of Alaska (Drinan et al. 2018) will increase selection pressure on local
300 populations to adapt to changing thermal habitats, the natural adaptation rates in longer-lived species like
301 cod will likely fall behind projected rates of medium- to long-term climate warming (Reed et al. 2011).

302 **Conclusion**

303 Our study suggests that loss of spawning habitat from extreme warming events contributes to
304 poor recruitment for Pacific cod in the Gulf of Alaska. The most recent warming events (2014-16, 2019)
305 corresponded with multiple years of sustained, below average habitat suitability. We also contend that

306 the spatial-temporal extent of suitable spawning habitat for Pacific cod will continue to decline as
307 conditions continue to warm. As single-batch, seasonal spawners, the offspring of Pacific cod have an
308 inherently high exposure risk to environmental conditions for growth and survival (Lowerre-Barbieri et
309 al. 2011). A further narrowing or shift in spawning activity could exacerbate larval mismatch with spring
310 productivity (Durant et al. 2007) or place larvae outside key advective pathways for transport to critical
311 juvenile nearshore nursery areas (Hinckley et al. 2019). While these processes merit further study, the
312 direct impact of temperature on egg survival, coupled with the apparent loss of both adults and pre-
313 recruits in the Gulf of Alaska, is strong evidence that spawning output by Pacific cod will be significantly
314 reduced with continued regional warming.

315

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324 National Marine Fisheries Service, NOAA.

325

327 **Figure Captions**

328

329 Figure 1: The effects of temperature on proportional hatch success of eggs batches from Gulf of
330 Alaska Pacific cod (*Gadus macrocephalus*) incubated in the laboratory. Fitted lines are the
331 results of 3-parameter Cauchy (solid black) and Gaussian (dashed gray) model fits. Data are
332 based on individual replicate 1 L beakers incubated across separate water baths (See Methods).

333

334 Figure 2: Habitat suitability for Pacific cod spawning based on temperature profiles at depth
335 combined with experimentally-derived temperature-dependent hatch success of eggs (Fig. 1).
336 Panels are based on temperature data interpolated to a 1 m \times 1 day grid using bivariate linear
337 interpolation across depths and days. Points indicate the time and depth of actual temperature
338 measurements, although note that temperature measurements from one month prior to and one
339 month beyond the period shown were used for interpolations. Temperatures were measured at
340 the GAK1 oceanographic station near Seward, Alaska. Dashed box in upper left panel indicates
341 the months and depths over which habitat suitability was averaged to create an index of
342 spawning habitat suitability. Habitat suitability for all months of the year is shown in Fig. S3.

343

344 Figure 3: Spawning habitat suitability index (a), calculated as the mean habitat suitability from
345 January to April at depths greater than 100 m. Spawning habitat suitability is based on
346 temperature profiles at depth combined with experimentally-derived temperature-dependent
347 hatch success of eggs. Results using both the Cauchy and Gaussian response curves are shown.
348 Horizontal dotted lines show the time-series averages. Spawning habitat suitability is positively
349 correlated with relative abundance of (b) larvae (\pm 1 SE), (c) age-0 juveniles (\pm 1 SE), and (d)
350 estimates of abundance at age 3 (\pm 1 SD). Larval and juvenile CPUE are based on biannual

351 and annual surveys in the Western Gulf of Alaska (Fig. S1), whereas age-3 estimates are based
352 on an age-structured stock assessment model fit to survey and fishery data (See Fig. S4 for time
353 series). Years are labeled to highlight heatwave (2014-2016, 2019) and El Nino (1998, 2003)
354 years, as well as the year with highest spawning habitat index (2012). Missing labels in
355 individual panels indicate no observation or available estimate for that year.

356

357 Figure S1: Map of Gulf of Alaska indicating the pre-recruit survey area for Pacific cod and
358 locations of available sub-surface temperature data. Pacific cod spawning occurs along the
359 narrow shelf region around Kodiak and the Alaska Peninsula during the late winter/early spring.
360 Eggs are demersal, but larvae are available to ichthyoplankton sampling gear late May – early
361 June as they are advected to the southwest by the Alaska Coastal Current. Age-0 juvenile
362 sampling has been conducted by beach seine in two embayments (Anton Larsen Bay, ALB;
363 Cook’s Bay, CB) on the northeast side of Kodiak Island from 2006 to present.

364

365 Figure S2: Comparison of temperature data from GAK1 (100m and 250m) and from acoustic
366 trawl surveys conducted in Shelikof Strait and Sea Valley (Figure S1). For comparison, all data
367 were subset to include only values from March 11 - 31, which is the period for which consistent
368 measurements in Shelikof exist. Temperature sensors were mounted to the headrope of the trawl
369 net, and temperature was recorded at the maximum haul depth. Only hauls with maximum depths
370 between 100m and 250m were used for this comparison. Note that the depth, location, and exact
371 timing of hauls varied among years. Bottom depth at most haul locations ranged from 200 -
372 300m.

373

374

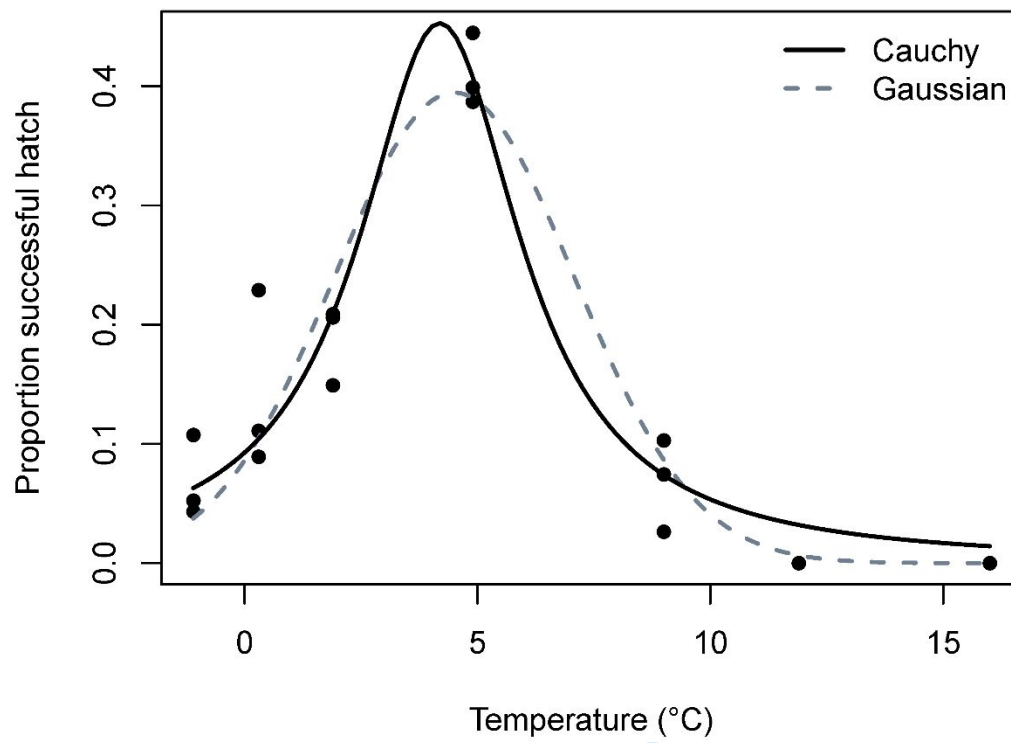
375 Figure S3: Habitat suitability for Pacific cod spawning based on temperature profiles at depth
376 combined with experimentally-derived temperature-dependent hatch success of eggs, as in
377 Figure 2. Habitat suitability for all months of the year is shown.

378

379 Figure S4: Time series of larval and juvenile CPUE (top panels) from biannual and annual
380 surveys in the Western Gulf of Alaska (Fig. S1). Time series of age-3 abundance estimates
381 (bottom panel) are based on an age-structured stock assessment model fit to survey and fishery
382 data, and plotted by year class.

383

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384 **Figure 1:**

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Figure 2:

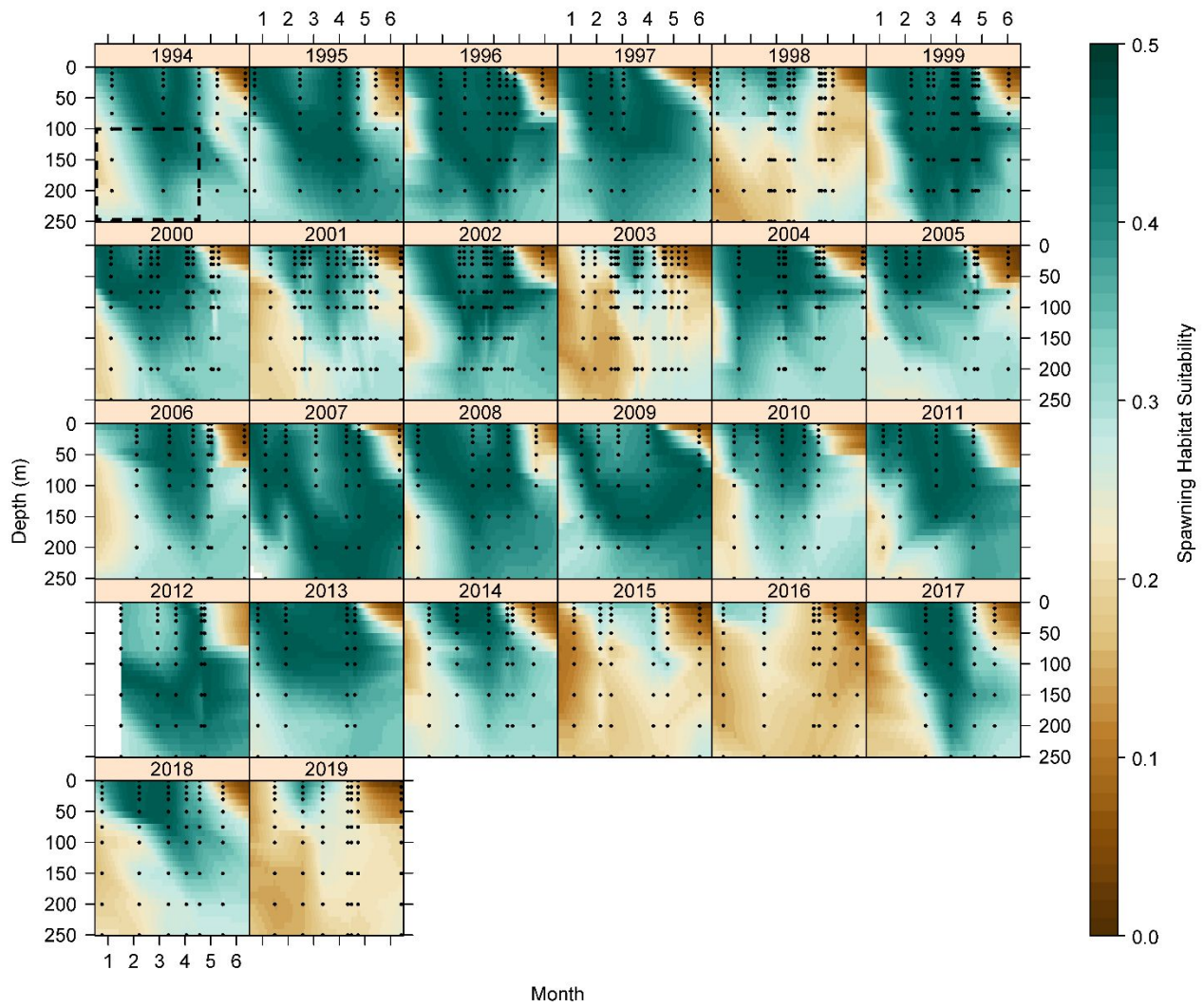
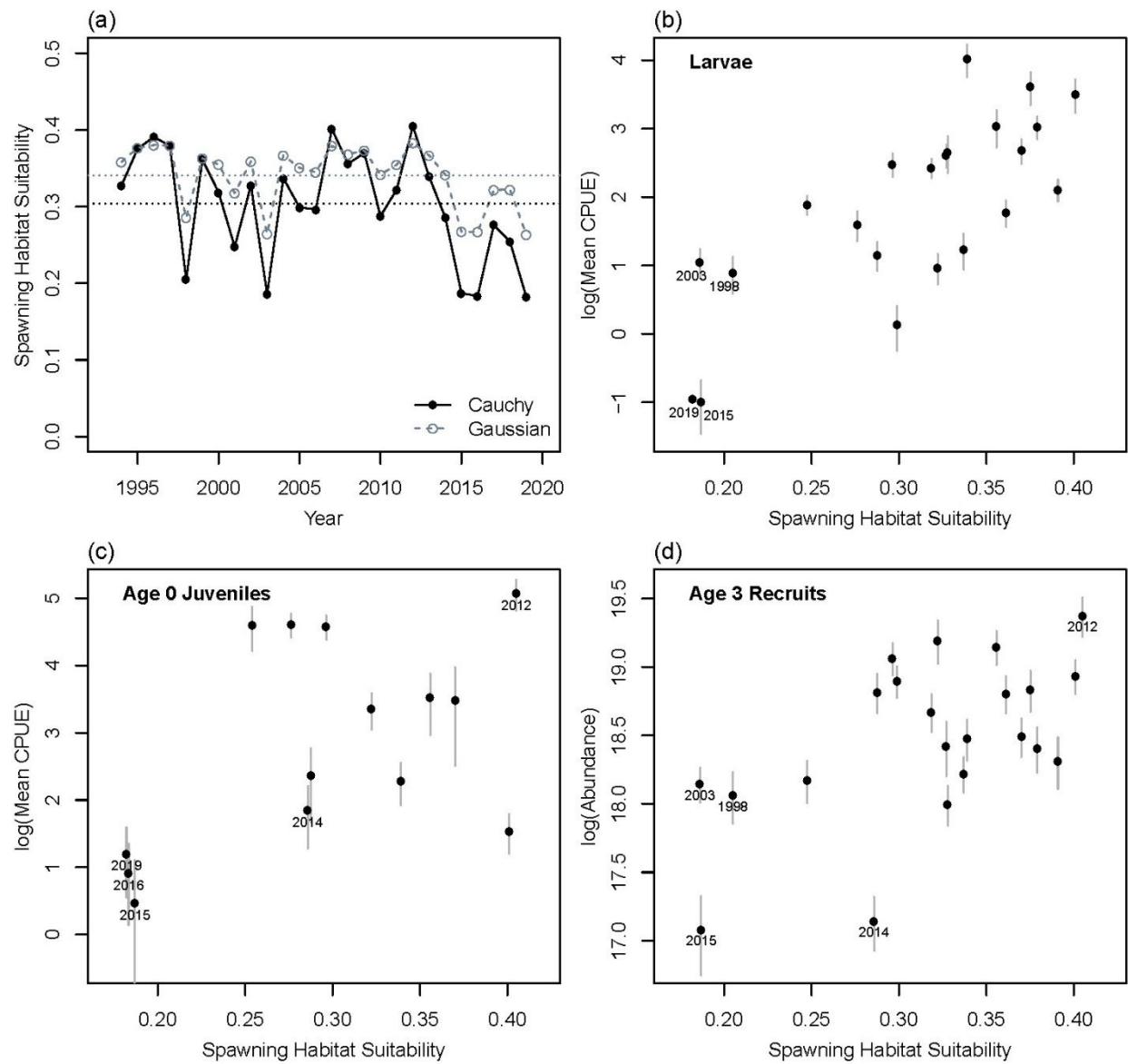


Figure 3:

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