

1 Temporal variability in the reproductive parameters of deepwater rockfishes in the Gulf of
2 Alaska

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21 Abstract

22 Reproductive parameters directly influence estimates of stock biomass and therefore affect the
23 determination of catch levels of many federally managed fish species. Reproductive parameters
24 directly influence stock biomass estimates and therefore affect catch levels of federally
25 managed fish species. These parameters can vary over different temporal scales and a better
26 understanding of how and why reproductive traits change will aid in the management of these
27 species. We examined the reproductive parameters of rougheye rockfish, *Sebastes aleutianus*,
28 and shortraker rockfish, *S. borealis*, captured in December 2015 and compared them with
29 parameters from an earlier published study. Maturity values in the earlier study were derived
30 from samples collected in from 2008 to 2014 with a concentration of fish collected in the winter
31 of 2009 and 2010. Rougheye rockfish had a smaller length and age at maturity during 2015 (447
32 mm, 17.7 years) compared to the earlier sampling period (450 mm, 19.6 years), but neither the
33 interaction of length and time period ($P = 0.507$) nor the interaction of age and time period ($P =$
34 0.270) was significant. Shortraker rockfish also had a smaller length at maturity during 2015
35 (467 mm) compared to the earlier period of time (499 mm) and the interaction of length and
36 time period was not significant ($P = 0.830$). Relative fecundity for rougheye rockfish were not
37 significantly different between the two time periods ($P = 0.444$) and this was also true for
38 shortraker rockfish ($P = 0.341$). Skipped spawning rates were significantly lower in 2015 for both
39 rougheye rockfish (2010 = 37.4%, 2016 = 21.8%, $P < 0.001$) and shortraker rockfish (2010 =
40 60.0%, 2016 = 47.0%, $P < 0.001$). This study was a first step in examining how reproductive
41 parameters for these species may change over time. A comprehensive approach to examining

42 temporal trends in reproductive parameters will aid in the understanding of how changing
43 environmental conditions are affecting the productivity of commercially important species.

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62 Keywords: reproductive biology, rockfish, fecundity, skipped spawning, reproductive failure,
63 reproductive resilience

64 **1. Introduction**

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66 Rougheye rockfish, *Sebastes aleutianus*, and shortraker rockfish, *S. borealis*, are
67 deepwater rockfishes that occur on the continental shelf edge and slope in the Gulf of Alaska
68 (Allen and Smith, 1988; Orr and Hawkins, 2008). These two species are characterized by large
69 size, late maturity, and relatively high fecundity values characteristic of the equilibrium life
70 strategy defined by Winemiller and Rose (1992) that is common in temperate marine fishes.
71 Large body size enhances survivorship during periods of unfavorable conditions, allowing
72 organisms to store energy for future reproductive events, whereas high fecundity allows for
73 higher recruitment during years with conditions that favor survivorship and growth of larvae
74 (Winemiller and Rose, 1992). The lack of life history data combined with the difficulty in ageing
75 shortraker rockfish make it difficult to study patterns of recruitment for this species. The age
76 structure of rougheye rockfish in this region suggest that they have episodic periods of higher
77 recruitment typical of this life history strategy, and it is likely shortraker rockfish have similar
78 recruitment patterns (Echave and Hulson, 2019; Shotwell and Hanselman, 2019). Rockfish of
79 the genus *Sebastes* are live bearers with internal fertilization (Kendall and Lenarz, 1986).
80 Although fecundity tends to be lower than other similar teleost species that occur in the same
81 environment, fecundity of rockfish species within the Alaska region still ranges in the tens to
82 hundreds of thousands (TenBrink and Spencer, 2013; Conrath, 2019).

83 In addition to internal fertilization, rockfish of this genus have other unique reproductive
84 characteristics that contribute to this equilibrium life history strategy. The reproductive mode
85 of members of the *Sebastes* genus is true viviparity, with embryos receiving additional maternal

86 nutrition beyond what is provided from the yolk sac during gestation (Boehlert et al., 1986).
87 Many rockfish species have immature individuals that undergo abortive maturation, where
88 reproductive development is initiated but oocytes are later resorbed (Nichol and Pikitch, 1994;
89 Hannah and Parker, 2007; Conrath and Knoth, 2013). This process is distinguished from skipped
90 spawning, where mature adults skip a spawning season. Skipped spawning has also been
91 documented for these species as well as other members of this genus in the Alaska region
92 (Conrath, 2017; Conrath, 2019). In addition, maternal effects appear to be important for this
93 genus with documented increases in relative fecundity (Beyer et al., 2015), increased larval
94 quality (Berkeley et al., 2004), decreased occurrence of skipped spawning (Conrath, 2017), and
95 earlier parturition (Sogard et al., 2008; Rodgveller et al., 2011) observed with increasing size or
96 age of the fish. All these characteristics increase the likelihood of these species to take
97 advantage of years with favorable conditions and survive years with unfavorable conditions.

98 Both of these species are managed in the Alaska Region by the North Pacific Fishery
99 Management Council. Age at maturity estimates are important components of stock
100 assessments. Rougheye rockfish are managed as a complex with blackspotted rockfish,
101 *Sebastes melanostictus*. In the Gulf of Alaska these two species are modeled together and have
102 combined catch limits but this may be problematic due to differences in growth and
103 reproductive parameters (Shotwell et al., 2014; Conrath 2017). An age-structured population
104 model is used as the primary assessment tool for this complex (Shotwell et al., 2014). Maturity
105 at age estimates are used in this model and influence the estimation of mature female stock
106 biomass. Due to difficulties in aging shortraker rockfish an age-structured model is not used in

107 the assessment of this species. Shortraker rockfish are managed as a Tier 5 species and catch
108 limits are derived from estimates of biomass and natural mortality.

109 Fecundity and skipped spawning information is not currently incorporated into stock
110 assessment for these species, but changes in these parameters provide important insight into
111 how reproductive success may be changing through time in response to environmental
112 conditions. Fecundity has been correlated with prespawning energy reserves and some species
113 downregulate fecundity in response to energy reserves during development (Rijnsdorp, 1991;
114 Skjaeraasen et al., 2006; Kennedy et al., 2009). Skipped spawning is also frequently associated
115 with food availability, fish condition, and energy reserves (Rideout and Rose, 2006; Skjaeraasen
116 et al., 2012; McBride et al.; 2015). Determining how fecundity data and rates of skipped
117 spawning should inform stock assessment for rougheye rockfish and shortraker rockfish is
118 complicated by both a lack of historical data and information on temporal or spatial changes in
119 these parameters.

120 A better understanding of if and how age at maturity, fecundity, and skipped spawning
121 rates vary with time will inform how these parameter estimates should be incorporated into
122 stock assessment efforts. A comprehensive approach examining all of these parameters will
123 provide information on both the success and failure of reproductive efforts. A recent study of
124 the reproductive biology of rougheye and shortraker rockfishes in the Gulf of Alaska collected
125 from 2008 to 2014 found that these species have an age at 50% maturity of 19.6 years and a
126 length at 50% maturity of 45.0 cm for rougheye rockfish and length at 50% maturity of 49.9 cm
127 for shortraker rockfish. Age data was not available for shortraker rockfish. Skipped spawning
128 rates were 37.4% for rougheye rockfish and 60.0% for shortraker rockfish and were related to

129 the total length of the fish with larger fish being less likely to skip a spawning event (Conrath
130 2017). It is unknown how size at maturity, fecundity, and rates of skipped spawning vary in time
131 and therefore it is difficult to determine if these high rates of reproductive failure are a cause
132 for concern. The objective of this study was to examine the reproductive parameters of these
133 species in a different time period to better understand how consistent these parameters
134 remain through time and how they may change in response to changing environmental
135 conditions. During this study, rougheye and shortraker rockfish specimens were collected from
136 the same geographic area as this earlier study in order to examine maturity, fecundity, and
137 skipped spawning rates. In addition, the fecundity of specimens collected for the prior study
138 were examined. These data will be used to comprehensively examine the reproductive success
139 and failure of these two species during these two time periods.

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141 **2. Materials and methods**

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143 Shortraker and rougheye rockfish samples were collected offshore of Kodiak Island using
144 a commercial bottom trawl net, during a scientific charter on the FV *Gold Rush* in December
145 2015. Each fish was weighed (g), measured for length (mm), and the ovary was removed and
146 preserved in 10% neutral buffered formalin. The sagittal otoliths were extracted and placed in a
147 glycerol-thymol solution. A formalin-fixed ovary weight was taken once the samples were
148 returned to the laboratory, and a section of ovary was removed for histological analysis.
149 Rougheye rockfish otoliths were aged by the National Marine Fisheries Service, Alaska Fisheries
150 Science Center's, Age and Growth Laboratory using standard break-and-burn procedures

151 (Chilton and Beamish, 1982). A subsample of 20% of the otoliths were aged by a second reader,
152 and the percent agreement and coefficient of variation were determined. This subsample was
153 also used to assess whether reader bias was present, and, if needed, a second subsample was
154 read to come to an agreed upon age.

155 A cross section of one lobe of the ovary was removed, embedded in paraffin, and
156 sectioned and stained with hematoxylin and eosin using standard histological techniques
157 (Sheehan and Hrapchak, 1980). These sections were examined using a compound microscope in
158 order to assess the type of developmental and regressive structures present within the ovary.
159 Developmental stages were defined based on the terminology of Bowers (1992) with
160 modifications for these deepwater species (Table 1). The section was also examined for
161 regressing or atretic oocytes. Oocyte regression was examined by determining the mean
162 proportion of alpha (degradation of the nucleus, yolk, and the zona radiate), beta (compact
163 with disorganized granulosa cells), and delta (containing yellow-brown pigment) atretic oocytes
164 within three microscope field of views (Hunter and Macewicz, 1985). These sections were also
165 scanned for post ovulatory follicles, muscle fibers, and blood vessels within the ovary.

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167 *2.1 Age and length at 50% Maturity*

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169 Fish were determined to be mature if there was evidence that they would have
170 successfully spawned in 2016 or evidence of a previous spawning (Table 2). Fish were
171 determined to be immature if lacking development beyond the early yolk stage and no
172 evidence of a prior spawning (POFs or widespread late stage atresia). If there was widespread

173 early or alpha atresia and no evidence of a prior spawning event, they were determined to be
174 undergoing abortive maturation and were considered immature. For the maturity analyses,
175 mature fish included both developing mature fish and fish that were skipped spawners.

176 Female age and length at maturity were estimated with a two parameter logistic
177 function given by:

$$178 \quad (1) \hat{p}_x = 1 / (1 + e^{-\delta(x-x_{50\%})}),$$

179 where \hat{p}_x is the estimate of the proportion mature at age or length- x , δ is the slope parameter
180 (the speed at which maturity approaches 100%), and $x_{50\%}$ is the age or length at which 50% of
181 the fish are mature. The observed proportion mature at age or length was calculated as:

$$182 \quad (2) p_x = \frac{m_x}{n_x},$$

183 where m_x was the number of mature fish observed at age or length- x , and n_x was the total
184 number of fish observed at age or length- x . The model was fit to the raw, binomial data. The
185 negative log-likelihood was minimized using the binomial distribution to fit the observed
186 proportion mature at age or length and estimate the parameters used in the logistic function. A
187 penalty term was included that accounted for maturity at age-0 being 0%; the negative log-
188 likelihood of the estimated proportion at age-0 was penalized by the negative-log likelihood at
189 age-0 for a maturity of 0% (after adding a constant term to avoid taking the log of 0) and
190 weighted by 850 – 1000, weighting values that, after sensitivity analysis, brought the estimated
191 maturity of age-0 close to 0% and did not substantially degrade the fit to other observed
192 maturity proportions at age (James et al., 2014). Uncertainty in the logistic function parameter
193 estimates, and the skipped spawning rates were estimated with a bootstrap procedure that
194 sampled with replacement the observed maturity data (Efron and Tibshirani, 1993).

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196 2.2 Fecundity

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198 Fecundity was estimated for both species using all individuals caught in December 2015

199 and for samples collected in November 2009 through January 2010 from the earlier study

200 (Conrath, 2017). Fish were chosen for fecundity analyses if they were mature, had developing

201 oocytes (stage 3 or higher) and had a complete intact ovary. Specimens with a high proportion

202 of alpha atresia (>25%) in the histological slide were excluded from the analysis. Individual

203 potential annual fecundity was estimated by using a gravimetric approach in which the weight

204 of a subsample of oocytes or embryos present was extrapolated to estimate the total ovary

205 weight. Two subsamples were collected from randomly chosen quadrants of one lobe of the

206 ovary. If the coefficient of variation from the initial samples was greater than 5%, two

207 additional subsamples were collected. The individual potential annual fecundity was

208 determined by averaging the fecundity estimates taken for each sample and multiplying by the

209 total ovary weight. In addition, relative fecundity was determined by dividing potential annual

210 fecundity by the somatic weight of the fish. Total annual potential fecundity data was fit to a

211 power function of fork length using the following equation:

$$212 (3) \text{ Fecundity} = a * (\text{fork length})^{b},$$

213 where a is the intercept parameter and b is the slope parameter. In order to examine maternal

214 effect we similarly fit somatic weight to a power function of fork length:

$$215 (4) \text{ Somatic weight} = c * (\text{fork length})^{d},$$

216 where c is the intercept parameter and d is the slope parameter. Then we compared the values

217 of the slope parameters b and d of each species to determine if larger females are
218 disproportionately contributing to the spawning output of the population following Dick et al.
219 (2017).

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221 *2.3 Skipped spawning*

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223 Skipped spawning fish were identified as those specimens with no development beyond
224 early yolk stages that had evidence of a prior spawning. Rates of skipped spawning or
225 reproductive failure do not include individual fish that are immature, including fish undergoing
226 abortive maturity. Histological evidence of a prior spawning included the presence of
227 postovulatory follicles or degrading advanced oocytes (stage 3 or higher), or embryos. Due to
228 the difficulty in distinguishing advanced postovulatory follicles and degrading oocytes from late
229 stage atresia, a 15% or greater percentage of beta and delta atretic oocytes within the ovarian
230 section was also considered evidence of a prior spawning. Two types of skipped spawners were
231 identified based on the definitions in Rideout et al. (2005). Resting skipped spawners were in
232 stage 1 or 2 developmentally with no indication of development within the current
233 reproductive year. Resorbing skip spawners also had no developing oocytes beyond the early
234 vitellogenesis stage (stage 2) and both types of skipped spawners contained either late-stage
235 atresia or postovulatory follicles, evidence of a prior spawning. Resorbing skip spawners were
236 distinguished from resting skipped spawners by the presence of widespread early stage or
237 alpha atresia, evidence that a current brood was initiated but failed to develop. All samples for
238 this study were collected in December and both of these species have seasonally synchronous

239 development, therefore, we expect normally developing fish in this collection to contain
240 oocytes in the ovary that are in the late vitellogenesis or migratory nucleus stage (Conrath,
241 2017). The amount and types of skipped spawners were examined for each species and the
242 relationship between the maternal length and the proportion of skipped spawning was
243 examined using simple linear regressions.

244

245 *2.4 Temporal comparisons*

246

247 Conrath (2017) examined the reproductive biology of rougheye and shortraker
248 rockfishes collected in the years of 2008 to 2014. Samples collected throughout this time period
249 were used in maturity analyses but only samples from the winter of 2009-2010 were used to
250 examine skipped spawning in that study. In addition, samples from this study collected in the
251 winter of 2009-2010 were used in the current study for fecundity analyses. The use of all the
252 samples from multiple years for the maturity analyses provided a more robust estimate of
253 maturity values that included more immature fish over a broader geographic range in the Gulf
254 of Alaska. Concentrating on samples from the winter of 2009 – 2010 for the fecundity and
255 skipped spawning analyses allowed for a focused analysis of differences in these parameters
256 during a time of year that aided the successful discrimination of developing oocytes and atretic
257 structures.

258 Age and length maturity ogives were derived for the 2015 samples and compared to
259 ogives that were published for the earlier time period. A generalized linear model (GLM) with a
260 binomial distribution was used to examine the effect of the interaction of reproductive time

261 period and fork length on maturity status for both species. A second GLM was used to examine
262 the effect of the interaction of reproductive time period and age on maturity status for
263 rougheye rockfish. Each binomial model was repeated using a quasi-binomial distribution to
264 test for over dispersion and the dispersion parameter was examined.

265 Potential total annual fecundity and relative fecundity values for the samples collected
266 in 2015 and for the samples collected in the 2009 and 2010 were compared. Generalized linear
267 models, with Gaussian distribution for response values were used to examine effects of
268 maternal size (somatic weight) and collection time period on total annual potential fecundity.
269 This type of model was also used to examine the effect of the time period of collection on
270 relative fecundity. Diagnostic plots of residual trends verses fitted values and standardized
271 residuals verses theoretical quantiles (Q-Q plots) were examined visually for trends in each
272 model.

273 Skipped spawning rates for samples collected in 2015 compared to the published values
274 for the earlier time period. The collection for the earlier time period occurred from November
275 2009 to January 2010 directly offshore of Kodiak Island. Therefore, all the samples for this
276 analysis were collected in the winter months within the same geographic area. A GLM with a
277 binomial distribution was used to examine the effect of sampling period and maternal length on
278 skipped spawning rates. Each binomial model was repeated using a quasi-binomial distribution
279 to test for over dispersion and the dispersion parameter was examined. The generalized linear
280 models were completed using the packages stats4 (vers. 3.2.0) and multcomp (vers. 3.2.5;
281 Hothorn et al. 2008) in statistical software R, vers. 3.2.0 (R Core Team 2015).

282

283 3. Results

284

285 3.1 Size and age at maturity

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287 During the December 2015 research cruise all rougheye and shortraker rockfish
288 captured were sampled. Length at 50% maturity of rougheye rockfish was calculated to be 447
289 mm (C.I. = 440 – 452 mm) and the age at 50% maturity of rougheye rockfish was calculated to
290 be 17.7 years old (C.I. = 16.4 – 19.4 years old). The age data was more variable than the length
291 data and there were some old immature individuals but they tended to be smaller fish (Fig. 1,
292 Table 3). Deep water rockfish otoliths are difficult to age, and the agreement between otolith
293 reader and tester was low (9.8% for ± 0 and 29.4% CV) due to difficulties interpreting vague
294 growth patterns. All age discrepancies were resolved in the determination of a final age.

295 The majority of developmentally mature fish had ovaries in the migratory nucleus stage
296 that was similar to samples captured in the winter months in the earlier study (Table 3). There
297 were a larger number of fish undergoing abortive maturity (N = 47) than the earlier time period
298 (N = 28). Length and age at 50% maturity were smaller and younger than published values for
299 the earlier time period of 450 mm and 19.6 years (Conrath, 2017) but these differences were
300 not significant. The comparison with the maturity data from the earlier period of time indicate
301 that only length had a significant effect on maturity status ($P < 0.001$), but time period, and the
302 interaction between length and time period were not significant ($P = 0.536$, $P = 0.507$). The
303 quasi-binomial model had a dispersion value less than 1 (0.866), indicating no over dispersion in
304 the model. Similarly, age had a significant effect on maturity status ($P < 0.001$), but time period,

305 and the interaction between age and time period were not significant ($P = 0.090$, $P = 0.270$).
306 The quasi-binomial model had a dispersion value close to 1 (1.49) indicating little over
307 dispersion in the model.

308 The length at 50% maturity of shortraker rockfish was calculated to be 467 mm (C.I. =
309 442 - 491 mm, Fig. 2). This value was smaller than the 2010 length at 50% maturity value of 499
310 mm (Conrath, 2017) but this difference was not significant. All developmentally mature fish had
311 oocytes in either the late vitellogenesis or migratory nucleus stage that was similar to samples
312 captured in the winter months in the earlier study (Table 3). There were also a larger number
313 of shortraker rockfish undergoing abortive maturity ($N = 19$) than the earlier time period ($N =$
314 7). The comparison with maturity data from the earlier time period indicate only length had a
315 significant effect on maturity status ($P < 0.001$), whereas time period and the time period and
316 length interaction were not significant ($P = 0.999$, $P = 0.830$). The quasi-binomial model had a
317 dispersion value close to 1 (1.07), indicating the model was not over dispersed.

318

319 *3.2 Fecundity*

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321 The range and mean of fecundity values of rougheye rockfish for both time periods was
322 similar and the effect of time period on both total annual potential and relative fecundity in the
323 GLM was not significant ($P = 0.99$, 0.30). Somatic weight however, was significantly related to
324 total annual fecundity ($P < 0.001$). There were no obvious trends in residuals in the model
325 diagnostic plots for rougheye rockfish fecundity. Since the effect of time period was not
326 significant, the data from the two time periods was combined for the power regressions of

327 length and weight and length and fecundity. There was a large discrepancy between the slope
328 parameter of the length and weight relationship ($b = 3.11$) and the slope parameter of the
329 length and fecundity relationship ($d = 5.04$) indicating that larger rougheye have a
330 disproportionately large contribution to the spawning productivity of the population (Table 3).

331 The mean fecundity values for shortraker rockfish were also similar for the two time
332 periods and the effect of time period on both total annual potential fecundity and relative
333 fecundity in the GLM was not significant ($P = 0.23, 0.35$). Somatic weight, however, was
334 significantly related to total annual fecundity ($P < 0.001$). There were a few large outliers for
335 this species, which in general had much lower relative fecundity values than rougheye rockfish
336 (Figure 3). Three highly fecund outliers are notable within the model diagnostic plots for the
337 shortraker fecundity models but there were no other obvious trends in the residuals. The
338 fecundity of these outliers was confirmed by reexamining the tissue, oocyte size, and ovary
339 weight and they were left in the model. Since the effect of time period was not significant, the
340 data from the two time periods was combined for the power regressions of length and weight
341 and length and fecundity. There was a slight discrepancy between the slope parameter of the
342 length and weight relationship ($b = 2.85$) and the slope parameter of the length and fecundity
343 relationship ($d = 2.99$) indicating that larger shortraker rockfish are contributing slightly less
344 than would be expected to the spawning productivity of the population (Table 3).

345

346 *3.3 Skipped spawning*

347

348 Rougheye rockfish failure rates for samples collected in 2015 were 21.8% (CI = 15.7 –
349 28.0%) with most skipped spawning of the resorbing type (75.6%, Fig. 4). Skipped spawning
350 rates for this species were significantly related to both time period and fork length ($P < 0.001$, P
351 < 0.001 , Fig. 5). Shortraker rockfish failure rates for samples collected in 2015 were 47.0% (CI =
352 40.1 – 53.8%) with most skipped spawning of the resorbing type (65.7%, Fig. 4). Skipped
353 spawning rates for this species were also significantly related to both time period and fork
354 length ($P < 0.001$, $P < 0.001$, Fig. 5). Skipped spawning rates for both species were lower in 2015
355 than 2009 and 2010 and for shortraker rockfish the primary type of skipped spawning shifted to
356 resorbing skipped spawning in 2015. The quasi-binomial models had dispersion values close to
357 1 (1.02, 0.97), indicating the models were not overdispersed.

358

359 **4. Discussion**

360

361 The reproductive output of a large number of teleost species varies temporally due to
362 changes in a number of reproductive processes. Temporal changes in the age or size at maturity
363 have been documented for a variety of species in a diverse array of locations (Harris and
364 McGovern, 1997; Mangeni-Sande et al., 2018; Hunter et al., 2019). Interannual differences in
365 fecundity (McElroy et al., 2015) and skipped spawning (Rideout et al., 2006; Skjaerrasen et al.,
366 2015) have also been documented in teleost species. This study found the reproductive
367 parameters examined followed the same general patterns for both rougheye and shortraker
368 rockfishes between the two time periods examined. In both species there was a decrease in the
369 length at 50% maturity for 2015 but this change was not significant. This pattern was also

370 reflected in the age at 50% maturity for roughey rockfish. The size and age range was similar
371 between studies for both species but there were a smaller number of small, immature
372 shortraker rockfish in the 2015 sample collection, which may have affected the determination
373 of maturity. There was no significant difference in relative fecundity parameters for both
374 species between the two time periods. In both species, there was a decrease of similar
375 magnitude in the proportion of skip spawners observed between the two time periods. Samples
376 from the earlier study were collected over a broader geographical region, but only samples
377 collected directly offshore of Kodiak Island in the winter of 2009 and 2010 were included in the
378 analyses of fecundity and skipped spawning. It is possible this larger geographic range may also
379 have contributed to differences in maturity values.

380 A more complete understanding of how reproductive processes change through time in
381 response to environmental and fishing changes is important for future assessment of these
382 species. Reproductive processes like maturation and oocyte development are complex and can
383 vary temporally due to demography, phenotypic plasticity, and evolutionary responses of the
384 population (Marty et al., 2014). An evolutionary shift in the length or age at maturity has been
385 documented in many heavily exploited populations with a general trend of the size and age of
386 maturity becoming smaller and younger after a period of exploitation, particularly exploitation
387 that preferentially removes larger, faster growing fish from the population (Harris and
388 McGovern, 1997; Mangeni-Sande, 2019). A smaller size at maturity is generally associated with
389 a smaller potential fecundity and younger fish have been shown to contribute less to the egg
390 production of a population (Kulaw et al., 2017; Mion et al., 2018). Fecundity can also be
391 reduced during the reproductive season through the resorption of developing oocytes

392 (Kennedy et al., 2008). Temporal changes in fecundity and skipped spawning are more
393 commonly related to phenotypic energetic responses to environmental variability and
394 prespawning energy reserves (Rijndsdorp, 1991; Skjaeraasen et al., 2013). In addition, skipped
395 spawning has been proposed as a life history trade off where delaying reproduction may
396 increase fecundity in later years (Rideout et al., 2006; Folkvord et al., 2014; Skjaeraasen et al.,
397 2015).

398 Rougheye and shortraker rockfishes are not targets of directed fisheries and landings
399 are frequently less than established catch limits. Since 2005 total catch of the rougheye and
400 blackspotted rockfish complex ranged from 20 – 60% of the Total Allowable Catch (Shotwell
401 and Hanselman, 2019). Shortraker rockfish catches have been variable, but in general have
402 remained low during the same period though catches in nonpelagic trawl fisheries have had
403 some years with higher exploitation rates (Echave and Hulson, 2019). It is, therefore, unlikely
404 that changes in fishing pressure have had a causal relationship with the observed changes in
405 the reproductive parameters of these two species. Changes in the energy available to fish due
406 to environmental factors are a more likely driver for this change. Buoy data from the Gulf of
407 Alaska indicates that surface ocean temperatures were consistently colder throughout 2009
408 than in 2015 (<https://www.ndbc.noaa.gov/>). A change in water temperatures has the potential
409 to shift the phenology of the reproductive cycle, but there is no evidence that this occurred as
410 mature fish were in similar reproductive stages in both periods. It is not possible to determine if
411 a decrease in skipped spawning rates is related to this environmental change but it is possible
412 more favorable conditions for both species occurred prior to and during the period of
413 reproductive development in 2015.

414 The ability of a species to respond to environmental changes by altering reproductive
415 parameters is dependent on its evolutionary history. Due to underlying differences in the
416 mechanisms of how reproductive parameters change, the time scale of these changes will also
417 be unique to the parameter. Changes in the length or size at maturity that occur due to fishery
418 induced selection for slower growth and smaller age at maturity will likely occur over a much
419 longer time scale than changes in reproductive traits that occur due to energetic or
420 environmental stressors. The latter will likely occur within a year of the reproductive season
421 whereas the former may take a period of years.

422 Many rockfish of the *Sebastes* genus have immature individuals that abort reproductive
423 development (Nichol and Pikitch, 1994; Hannah and Parker, 2007; Conrath and Knoth, 2013),
424 and there is evidence that this may be related to environmental conditions in some species
425 (Hannah and Parker, 2007). A distinction is made here between abortive mature fish and
426 skipped spawners with the former referring to fish that have not spawned before. This
427 distinction is important because the standard practice is to consider abortive mature fish
428 functionally immature and this directly influences maturity ogives developed for these species
429 (Nichol and Pikitch, 1994; Conrath and Knoth, 2013). The proportion of young maturing fish
430 that are able to successfully reproduce has a fairly simple and direct impact on estimates of age
431 and length at maturity with more successful reproduction lowering both the size and age at
432 maturity. It is difficult to know if these abortive mature fish are physiologically mature and
433 environmental factors are the drivers that lead to an unsuccessful reproductive event or if they
434 are not yet physiologically mature.

435 In contrast, skipped spawners are fish that are known to be physiologically mature.
436 Maturity is a physiological event that occurs once during the life of a fish, whether or not they
437 successfully spawn in any given year. It is therefore, most appropriate to include skipped
438 spawners as mature fish within a maturity analysis. However, the inclusion of non spawning fish
439 within a maturity ogive may be problematic for stock assessment efforts and developing a
440 spawning ogive may be more appropriate. Alternative methods to define and model maturity
441 have been developed for some rockfish species (Head et al. 2020). It is difficult to assess the
442 cause of the changes in skipped spawning in this study without additional data from more
443 years. Skipped spawning is similarly thought to occur as a response to limited food resources,
444 poor body condition, or inadequate energy reserves (Skjaeraasen et al., 2012; McBride et al.,
445 2015; Skjaeraasen et al., 2015) and may occur prior to reproductive development (resting skip
446 spawner) or during reproductive development (resorbing skip spawner). Roughey rockfish in
447 the current study that were skipped spawners were predominately of the resorbing type, and
448 shortraker rockfish were comprised primarily of resting skipped spawners in the earlier period
449 and resorbing skipped spawners in the later period. Both are therefore mechanisms for
450 changing reproductive output prior to and during spawning for individual fish, as well as larger
451 potential population level changes that may occur over longer time periods. In addition, the
452 downregulation of fecundity is often thought to occur as a response to available energy
453 reserves, occurring between the onset of reproductive development and spawning and this will
454 also reduce the reproductive output of a fish. Being able to respond to environmental
455 conditions and energetic levels at different time scales may allow fish to optimize tradeoffs
456 between survival, growth, and reproductive output.

457 A better understanding of how meaningful and prevalent changes are in the
458 reproductive productivity for deepwater rockfish and other species will require study of
459 additional years. Changes in reproductive traits over time are a reflection of the ability of a
460 population to be resilient to varying environmental parameters and fishing pressure. Lowerre-
461 Barbieri et al. (2016) define reproductive resilience as, “reproductive capacity of a population to
462 maintain the level of reproductive success needed to result in long-term population stability
463 despite disturbances such as environmental perturbations and fishing.” Factors that may
464 impact reproductive resilience include spatial distribution and heterogeneity and age
465 truncation (Berkeley et al., 2004; Hsieh et al., 2008). Female fish with larger bodies have greater
466 stores of energy that may be able to consistently energetically support spawning during periods
467 of lower food availability or less favorable environmental conditions, thereby increasing the
468 reproductive resilience of the population. The maternal size dependent effect on fecundity has
469 been shown to vary among rockfish species (Beyer et al., 2015; Dick et al., 2017) and our results
470 indicate this effect is stronger in rougheye rockfish than shortraker rockfish. The proportion of
471 rougheye and shortraker rockfishes examined in this study that were exhibiting skipped
472 spawning decreased with increasing size and age. There appears to be a size at which skipped
473 spawning rates become negligible. The truncation of size or age structure is a potential concern
474 in the management of fish species, particularly populations with an equilibrium life history
475 strategy that are characterized by variable reproductive success (Leaman and Beamish, 1984;
476 Vallin and Nissling, 2000; Beldade et al., 2012; Hixon et al., 2014). For these deepwater rockfish
477 species, the increased reproductive success of larger and older females emphasizes the
478 importance of understanding, monitoring, and conserving the age structure of these

479 populations. In addition, fishes that have fixed geographic spawning areas may be less able to
480 withstand the effects of a changing climate (Asch et al., 2019). A better understanding of
481 reproductive resilience of these species will aid in the management of these deepwater rockfish
482 species.

483

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485

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493

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691 **Table 1**
 692 Stages of oocyte and embryo development in ovaries of rougheye (*Sebastes aleutianus*) and
 693 shortraker (*S. borealis*) rockfish. These stages, based on terminology of Bowers (1992), were
 694 used to identify the most advanced development stage present in samples from fish collected
 695 during December 2015 in the Gulf of Alaska.
 696

| Stage | Physical description |
|----------------------------|--|
| 1. Primary growth | Oogonia, early perinuclear and late perinuclear oocytes |
| 2. Early yolk | Oocytes contain the earliest signs of yolk accumulation, small spherical globules of yolk in the periphery of the oocyte |
| 3. Advanced yolk | Oocyte content is at least 50% yolk droplets, nucleus still well defined |
| 4. Migratory nucleus | Nucleus migrates to the periphery of the oocyte, nuclear membrane becomes irregular, nucleoli disappear |
| 5. Ovulation | Yolk material begins to merge and form a single united mass |
| 6. Early embryo | Blastoderm cap present with a large yolk mass |
| 7. Embryo body | Embryo body appears, blastoderm cap of cells develops into recognizable tissue |
| 8. Eyed embryo | Retinal pigmentation becomes apparent and is well defined |
| 9. Postovulatory follicles | The follicles that remain after parturition |

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700 **Table 2**
 701 Classifications used to determine maturity of rougheye rockfish (*Sebastes aleutianus*) and
 702 shortraker rockfish (*S. borealis*) collected in December 2015 in the Gulf of Alaska. POF=
 703 postovulatory follicles. For stages of oocyte and embryo development, see Table 1.
 704

| Class | Oocyte or embryo development | Description |
|----------|-----------------------------------|---|
| Immature | Primary growth | No oocyte development beyond stage 2. |
| | Abortive maturity | Oocyte development is initiated, then oocytes are resorbed. No evidence of prior spawning. Identified histologically by presence of widespread alpha atresia, but no POFs and no widespread beta or delta atresia. |
| Mature | Development | Oocyte or embryo development at stage 3 or at a more advanced stage of development. |
| | No development (skipped spawning) | |
| | Resting | No initiation of oocyte development. Identified histologically by development in stage 1 or 2 with evidence of a prior spawning (beta or delta atresia or POFs). |
| | Resorbing | Oocyte development is initiated, but oocytes are later resorbed. Evidence of a prior spawning present. Identified histologically by widespread alpha atresia and evidence of a prior spawning (POFs or widespread beta or delta atresia). |

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715 **Table 3**
 716 Reproductive parameter estimates of rougheye rockfish and shortraker rockfish collected in
 717 2015 and reproductive parameter estimates from the earlier study (Conrath, 2017). Maturity
 718 stages are presented for mature fish that were developing in the months of November through
 719 January for both studies. N = number of samples, TPAF = total annual potential fecundity, L50 =
 720 length at 50% maturity, A50 = age at 50% maturity, and CI = 95% confidence interval.
 721

| | Parameter | Rougheye | Rougheye, prior study | Shortraker | Shortraker, prior study |
|------------------|------------------------------------|---|--------------------------------------|-------------------------------------|--------------------------------------|
| Maturity | N | 285 | 492 | 270 | 352 |
| | Length range | 366 - 625 mm (mean = 461 mm) | 250 – 740 mm (mean = 470 mm) | 425 - 927 mm (mean = 611 mm) | 380 – 950 mm (mean = 602 mm) |
| | Age range | 9 – 82 years | 4 – 98 years | | |
| | Maturity stages (winter months) | Stage 3, 17.6% Stage 4, 77.8% Stage 5, 4.6% | 13.8% 78.0% 8.3% | 33.9% 66.1% | 32.5% 53.5% 14.0% |
| | L50 | 447 mm (CI 440- 452 mm) | 450 mm (CI 445 – 456 mm) | 467 mm (CI 442 – 491 mm) | 494 mm (CI 479 – 508 mm) |
| | A50 | 17.7 years (CI 16.4 – 19.4 years) | 19.6 years (CI 18.2 – 20.8 years) | | |
| Fecundity | N | 127 | 102 | 112 | 39 |
| | Length range | 418 – 625 mm (mean = 505 mm) | 430 – 630 mm (mean = 488 mm) | 450 – 900 mm (mean = 650 mm) | 500 – 950 mm (mean = 760 mm) |
| | Weight range | 1,204 – 4,210 g (mean = 1,977 g) | 1,152 – 4,694 g (mean = 2,130 g) | 1,628 – 12,150g (mean = 5,100 g) | 2,212 – 13,660 g (mean = 8,218 g) |
| | Mean TPAF range | 133,000 – 1,830,000 oocytes | 79,200 – 1,720,000 oocytes | 39,700 – 1,430,000 oocytes | 124,000 – 1,410,000 oocytes |
| | Relative fecundity range | 87.1 – 436 oocytes/g | 37.9 – 386 oocytes/g | 8.03 – 406 oocytes/g | 16.0 – 361 oocytes/g |
| Skipped spawning | N | 188 | 175 | 230 | 80 |
| | Length range | 415 - 625 mm (mean = 493 mm) | 415 – 626 mm (mean = 486 mm) | 400 – 927 mm (mean = 680 mm) | 450 – 950 mm (mean = 620 mm) |
| | Skipped spawning rate | 21.8% (CI 15.7 – 28.0%) | 37.4% (CI 29.9 – 44.9%) | 47.0% (CI 40.1 – 53.8%) | 60.0% (CI 49.2 – 70.8) |

722

723 Figure Captions.

724

725 **Fig. 1.** Logistic maturity curves for a) length of rougheye rockfish (*Sebastes aleutianus*) and b)
726 age of rougheye rockfish during each time period (observed = observed proportion mature at
727 each size or age; estimated = logistic curve fit to the data; dashed lines = 95% confidence limits,
728 UCL = upper confidence limit, LCL = lower confidence limit, EP = earlier time period (2009 –
729 2014). LP = later time period (2015)). Bars at the top and bottom of the chart represent the
730 number of fish in each 1 cm length or 1 year age bin that are mature (top) or immature
731 (bottom).

732

733 **Fig. 2.** Logistic maturity curve for length of shortraker rockfish (*Sebastes borealis*, observed =
734 observed proportion mature at each size or age; estimated = logistic curve fit to the data;
735 dashed lines = 95% confidence limits, UCL = upper confidence limit, LCL = lower confidence
736 limit, EP = earlier time period (2009 – 2014), LP = later time period (2015)). Bars at the top and
737 bottom of the chart represent the number of fish in each 1 cm length bin that are mature (top)
738 or immature (bottom).

739

740 **Fig. 3.** Relationships of the a) potential annual fecundity (number of developing oocytes) with
741 the power regression curves for both species (data combined for both time periods) and b)
742 relative fecundity, calculated as potential annual fecundity divided by somatic weight, to fork
743 length for rougheye rockfish (*Sebastes aleutianus*) and shortraker rockfish (*S. borealis*). EP =

744 earlier time period (2009 and 2010), LP = later time period (2015), RE = rougheye rockfish, SR =
745 shortraker rockfish.

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747 **Fig. 4.** Proportion of a) rougheye rockfish (*Sebastes aleutianus*) and b) shortraker rockfish (*S.*
748 *borealis*) that experienced skipped spawning caused by resting and resorbing types of skipped
749 spawning, SS = skipped spawners, EP = earlier time period (2009 – 2010), LP = later time period
750 (2015), RE = rougheye rockfish, and SR = shortraker rockfish.

751

752 **Fig. 5.** Proportion of a) rougheye rockfish (*Sebastes aleutianus*) and b) shortraker rockfish (*S.*
753 *borealis*) that experienced skipped spawning by fork length, EP = earlier time period (2009 –
754 2010), LP = later time period (2015). Bars at the top and bottom of the chart represent the
755 number of fish in each 10 mm length bin that are skipped spawners (top) or non-skipped
756 spawners (bottom).









