

1                   **The consequences of size-selective fishing mortality for larval production and**  
2                   **sustainable yield in species with obligate male care**

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22 **Abstract**

23           Size-based harvest limits or gear regulations are often used to manage fishing mortality  
24 and ensure the spawning biomass of females is sufficiently protected. Yet, management  
25 interactions with species' mating systems that affect fishery sustainability and yield are rarely  
26 considered. For species with obligate male care of eggs, it is possible that size-specific harvest of  
27 males will decrease larval production. In order to examine how size-based management practices  
28 interact with mating systems, we modeled fisheries of two species with obligate male care,  
29 *Symphodus melops* (corkwing wrasse) and *Ophiodon elongatus* (lingcod) under two management  
30 scenarios, a minimum size limit and a harvest slot limit. We simulated the population dynamics,  
31 larval production, and yield to the fishery under a range of fishing mortalities. We also modeled  
32 size-dependent male care to determine its interaction with management. In both species, the slot  
33 limit decreased yield by less than 12% at low fishing mortalities; at higher mortalities,  
34 individuals rarely survived to outgrow the slot and spawning potential decreased substantially  
35 relative to unfished levels. The spawning potential decreased less when managed with a slot limit  
36 if we included a positive feedback between male size, care, and hatching success, but the benefit  
37 of implementing the slot depended both on the relative proportions of males and females selected  
38 by the fishery and on our assumptions regarding male size and care. This work highlights that the  
39 effects of size- and sex-selective fisheries management can be nuanced and produce counter-  
40 intuitive results.

41

42 **Keywords**

43 Fisheries, slot harvest limit, minimum size limit, population model, male care, sexual selection,  
44 wrasse, lingcod

## 45 **Introduction**

46           The sustainability of a fishery depends on the intensity of fishing pressure, the selectivity  
47 of the fishery for different sizes, ages, or sexes, and natural variation in population age and size  
48 structure arising from the species' biology (Lowerre-Barbieri et al., 2017). Sustainable fisheries  
49 management aims to maximize yield to the fishery, either in numbers or in biomass, over the  
50 long term, by controlling total fishing mortality, the selectivity of the fishery, or both. To  
51 achieve this aim, management must also account for annual changes in population abundance  
52 and age structure due to fishing, natural environmental variation, and biological responses of the  
53 fished species to these processes (Halliday & Pinhorn, 2009; Zhou et al., 2010). A large body of  
54 theoretical and empirical literature has shown that recruitment to the fishery (i.e., larval or  
55 juvenile survival) is related to spawning biomass and contemporary environmental conditions  
56 (Browman, 2014; Munch, Giron-Nava, & Sugihara, 2018; Pritt, Roseman, & O'Brien, 2014),  
57 but that over longer time scales, generation time, body size, and age at maturation are positively  
58 correlated with a stock's risk of overexploitation (Hutchings & Kuparinen, 2017; Hutchings &  
59 Reynolds, 2004; Kindsvater, Mangel, Reynolds, & Dulvy, 2016).

60  
61           The potential effects of fishing on mating system dynamics and recruitment success have  
62 rarely been incorporated into management, despite evidence fishing can affect these processes  
63 (Alonzo & Mangel, 2004; Kendall & Quinn, 2013; Rowe & Hutchings, 2003; Sørvalen et al.,  
64 2018). The effects of fishing on mating systems may be most important when fishing targets a  
65 specific size in sexually dimorphic species (Carroll & Lowerre-Barbieri, 2019; H.K. Kindsvater,  
66 Reynolds, Sadovy de Mitcheson, & Mangel, 2017; Sørvalen et al., 2018). In such cases,  
67 differential mortality between the sexes and altered sex ratios can increase the likelihood of egg

68 or sperm limitation (depending on which sex is larger; Gosselin, Sainte-Marie, & Bernatchez,  
69 2005; Hines et al., 2003). While the importance of large females to egg production and larval  
70 survival is well acknowledged (Arlinghaus, Matsumura, & Dieckmann, 2010; Birkeland &  
71 Dayton, 2005; Hixon, Johnson, & Sogard, 2014), the reproductive role of (large) males is often  
72 ignored. However, males and sperm may also be limited (Alonzo *et al.* 2008; Sato 2012), body  
73 size can have positive paternal effects (Uusi-Heikkilä, Kuparinen, Wolter, Meinelt, &  
74 Arlinghaus, 2012), and theory predicts reduced reproductive rates when females are choosy but  
75 males with preferred phenotypes are scarce (Møller & Legendre, 2001).

76 The interaction between fishing and obligate male care, in which territorial males must  
77 defend eggs laid in nests to ensure eggs successfully hatch, has rarely been studied despite the  
78 fact that several commercially and recreationally important species display this behavior (Table  
79 1; Halvorsen et al. 2017; King and Withler 2005; Sutter et al., 2012). For these species, size-  
80 selective fishing could decrease larval production by limiting the availability of nests or the  
81 quality of male care, by selecting for smaller males. Smaller males may have smaller nests, fewer  
82 nests or provide less effective care (Cargnelli & Neff, 2006; Ingebrigst Uglem & Rosenqvist,  
83 2002; Wiegmann & Baylis, 1995). Moreover, the most effective guarding males could be the  
84 largest, most aggressive males, so that the traits that correlate with the most effective parental  
85 care could also increase vulnerability to fishing (Andersen, Marty, & Arlinghaus, 2018; Sutter et  
86 al., 2012).

87 Despite growing recognition of the importance of maintaining diverse size structure in  
88 fished populations, there is little theory predicting how size-selective fishing will interact with  
89 reproductive behavior and influence population productivity. Conventional wisdom suggests  
90 size-selective management (e.g., minimum size limits), designed to allow individuals to mature

91 and reproduce successfully before being fished, will ensure sustainable yields in the long term (  
92 Birkeland, & Dayton, 2005; Froese, 2004; ). More recently, protection of the largest, oldest  
93 individuals has been recognized as a desirable management outcome if large individuals play  
94 important roles ecologically or contribute high quality larvae to the population (Ahrens, Allen,  
95 Walters, & Arlinghaus, 2020; Hixon, Johnson, & Sogard, 2014). A maximum size limit, in  
96 addition to a minimum size limit, often referred to as a harvest slot, has been suggested to  
97 prevent sex-selective harvest when one sex grows faster than the other (Halvorsen et al., 2016;  
98 Morson, Munroe, Harner, & Marshall, 2017). Slot limits have been increasingly implemented in  
99 recreational fisheries as a means of ensuring that fishing's effects on stock size, age, or sex  
100 structure are balanced, or to maintain a suitable number of large fish available to anglers (Gwinn  
101 et al., 2015). Slot limits have been advocated in fisheries for species in which mating success  
102 and egg survival also depend on body size as in species with obligate paternal care (Halvorsen et  
103 al., 2017). However, when considering the effectiveness of a minimum size limit vs. a slot limit,  
104 it can be unclear how each management action will interact with the species' mating system and  
105 sex-specific growth differences to affect fishery sustainability and yield. For example, in species  
106 with paternal care, it is unclear whether it is more important for management actions to protect  
107 females (typically the gamete-limiting sex) or males to ensure a sustainable larval supply.

108         To explore these alternatives, we use simulations of age-, size- and sex-structured  
109 population dynamics to understand how fishing will interact with natural variation in male and  
110 female size structure. We focus on comparing the effects of different size-selective management  
111 scenarios in species with obligate male care, but different mating systems and different sex-  
112 specific growth patterns. With a model of age-, size- and sex-structured population dynamics, we  
113 compare the effects of a fishery selecting predominantly the large nesting males of a species with

114 multiple male phenotypes (*Symphodus melops*, the corkwing wrasse), with a fishery for a species  
115 where females are the larger sex, and both males and females are caught (*Ophiodon elongatus*,  
116 lingcod). Both of these species have obligate male care of eggs laid in benthic nests. We  
117 specifically evaluate the consequences of alternative management tactics (a minimum size limit  
118 vs. a slot limit) on the production of eggs and recruits by calculating the Spawning Potential  
119 Ratio (SPR) and yield in numbers. By tracking male and female numbers and sizes in the model,  
120 we are able to quantify the effects of management on both egg production and the availability of  
121 paternal care. In comparing these species, we aim to gain general insights into the way that  
122 species biology and fishery selectivity interact.

123         As fishing removes males of a specific size, the average size of a nesting male is  
124 expected to decrease, because fewer males will survive to the largest age and size class. Whether  
125 fishing affects larval production in species with male care depends on the consequences of size-  
126 and sex-selective fishing for the egg density in each nest, and the extent to which egg  
127 survivorship depends on density. In fishes, male care is often regarded as shareable, although  
128 there is some evidence for density-dependent egg survival within a nest (Klug, Lindstrom, & St.  
129 Mary, 2006). In addition, male size has shown to be positively correlated to the intensity of care  
130 and nest survival (Suski & Ridgway, 2007; Wiegmann & Baylis, 1995). Here, we develop a new  
131 metric of the availability of care *per egg* and quantify how that is expected to change with the  
132 impacts of fishing on nest size and number, as well as on egg production. This is the first  
133 theoretical investigation of the interplay between fishing and larval production in species with  
134 alternative mating tactics and obligate male care.

135

136

137           **Study species**

138           We modelled two contrasting fisheries for species with obligate male care: the  
139 commercial fishery for live *S. melops* in southern and western Norway and the recreational  
140 fishery for *O. elongatus* in the northwestern USA. These are among the two best-studied marine  
141 fisheries for species with parental care, and each fishery has a history of management that  
142 includes minimum size limits and slot limits.

143           *Corkwing wrasse*

144           *S. melops*, the corkwing wrasse, has two male mating tactics, with large nesting males  
145 providing care for eggs and sneaker males that steal fertilizations during spawning events (Potts,  
146 1974; I. Uglem, Rosenqvist, & Wasslavik, 2000). Male and female corkwing wrasse have  
147 different growth and maturation rates, as do the two male life-history pathways (territorial  
148 nesting males and sneakers (Halvorsen et al., 2016; Uglem, Rosenqvist, & Wasslavik, 2000).  
149 Sneaker males mature after one year. Nesting males and females mature between two and three  
150 years, and can live for up to nine years.

151           The parameters for growth and maturation rates in our model were estimated from the  
152 data published in Halvorsen et al. (2016), combined with more recent samples collected in 2017..  
153 Growth and maturation rates as a function of age are plotted in Figure 1 (a,c); functions are in  
154 Table 2; Parameter estimates are in Table 3. We assume mass-at-age  $W(a)$  is a cubic function of  
155 length, and we estimate egg production as a function of mass following the estimates in Chalaris  
156 (2011). Like many batch spawners, corkwing wrasse are income breeders, but very little is  
157 known about female re-mating rates (Stiver et al., 2018; Ingebrigt, Uglem & Rosenqvist, 2002)  
158 and the number of times individual females spawn each season is unknown. While we do not  
159 have direct information on natural mortality rates for each life-history type of corkwing wrasse,

160 estimates of total mortality (natural mortality and fishing mortality) can be estimated from the  
161 frequency of each age class by life-history type in the catch data (Halvorsen *unpublished data*).  
162 The commercial fishery for live corkwing wrasse has grown rapidly since 2010 as the wrasse are  
163 used in louse biocontrol in salmon aquaculture ((Blanco Gonzalez et al., 2019; Halvorsen et al.,  
164 2017). The fishery is size-selective, as the largest individuals fare better in salmon pens, and  
165 since nesting males grow faster and mature older than females and sneaker males, their life  
166 history is less protected by the current minimum size regulations. To account for this, a slot  
167 harvest limit - where only fish between 120 and 170 mm can be retained – has been proposed to  
168 protect the largest males in response to scientific concerns about the effects of fishing on the  
169 mating system (Fig 1a; Halvorsen et al., 2017). In England, corkwing wrasse is managed by slot  
170 sizes in two districts (IFCA 2020).

171

## 172 *Lingcod*

173 We compared the effect of fisheries management on the wrasse system with a species  
174 with a contrasting life history (Figure 1, b,d), *O. elongatus*, lingcod. The lingcod is the only  
175 extant member of the family Hexagrammidae and is native to western North America. Lingcod  
176 are large, long-lived fish, although the ages of maturity of the nesting male wrasse and lingcod  
177 are both between two and three years (Cass, Beamish, McFarlane, & Canada. Department of  
178 Fisheries and Oceans., 1990; King & Withler, 2005). Lingcod females are capable of growing to  
179 over two meters long and they live, on average, six years longer than males, with lower natural  
180 mortality. As in the corkwing wrasse, males will defend eggs laid by one or more females in  
181 benthic habitat for a period of 6 to 8 weeks, depending on water temperature.



182           Estimates of growth, maturation, and mortality rates, as well as estimates of mass-  
183 specific egg production by females, and initial size at recruitment, were reported in Jagielo and  
184 Wallace (2005), an international stock assessment that encompassed populations from California  
185 to the Salish Sea. While there is undoubtedly some regional variation in growth and body size,  
186 these growth and maturation values are representative of the species and are useful when  
187 examining the effect of the contrasting life histories and mating systems of lingcod and corkwing  
188 wrasse (Figure 1). There are two notable differences in lingcod growth patterns and mating  
189 system that differ from the corkwing wrasse. First, female lingcod are the larger sex, and spawn  
190 with only one male each season. Second, while smaller males are known to steal fertilizations by  
191 sneaking during spawning events, it is likely that male mating tactics change ontogenetically as  
192 males grow, and are not separate life history pathways (King and Withler 2005).

193           Lingcod have been fished commercially and recreationally for decades and were  
194 considered to be overfished by the late 20th century due to intense fishing in the 1980s and  
195 1990s (Haltuch et al., 2017; Jagielo & Wallace, 2005). Management has varied among Alaska,  
196 British Columbia, Washington, Oregon, and California according to the history of the fishery and  
197 natural latitudinal variation in growth and body size. Current management practices are a mix of  
198 area closures, bag limits, minimum-size limits, and slot limits in different parts of the range. In  
199 Washington State, recreational fishers are regulated by a slot limit of 26-36 inches (Fig 1b). Due  
200 to the implementation of precautionary management measures in recent years, lingcod  
201 populations are rebuilding and appear to be stable throughout much of the range (Haltuch et al.,  
202 2017).

203

204

205           **Methods**

206           We developed a deterministic model of equilibrium population dynamics (Table 2),  
207 which is closely related to the size-and age- structured model commonly used in fisheries stock  
208 assessments (Mangel 2006). However, our model differs in several important ways. First, we  
209 allowed for the sexes to have different growth rates. We also addressed the two growth patterns  
210 of the different male life history strategies (nesting male and sneaker) for the corkwing wrasse  
211 population. Second, we modeled differences in natural mortality and fishery susceptibility for  
212 each life-history type. Third, we considered the relationship between the male size structure,  
213 paternal care, and larval production. Figure 2 shows a general schematic of the model. With this  
214 model, we can evaluate the potential consequences of fishing for population productivity, given  
215 different assumptions regarding how male size structure affects the availability of paternal care  
216 in nests and the resulting consequences for the production of larvae.

217

218           *Male size and paternal care*

219           We assume the effectiveness of paternal care in a nest – which is essential for the  
220 production of viable larvae in both species – increases with the size of nesting males in both  
221 corkwing wrasse and lingcod. In both species, larger males have larger nests and nest multiple  
222 times in a season or defend multiple nests at once (King & Withler, 2005b; Potts, 1985; Ingebrigtsen  
223 Uglem & Rosenqvist, 2002). It is also possible that large males are more effective at nest defense  
224 than small nesting males, as is the case for smallmouth bass (Wiegmann & Baylis, 1995).  
225 However, the exact relationship between egg number and larval numbers as a function of male  
226 size and nest size is unknown for these and most other species. Per-capita survival of eggs in the  
227 nest could be a decreasing function of egg density and nest size (i.e., larval production could be a

228 density-dependent function of egg number due to crowding). Both males and females may be  
229 adapted to avoid spawning under conditions of nest crowding, but if the number of nests is  
230 limited, they might choose to spawn anyway. As there are a range of possibilities, as a starting  
231 point, we chose a simple relationship between male size and available nest care to represent both  
232 male nest size and number of nests. We developed a Male Size Index, which we represent as  $\theta$ ,  
233 representing the probability that a territorial male of a given length is mature, and the average  
234 length of territorial males, weighted by the abundance of each age class (Table 2). We modeled  
235 available nest care as a power function, such that care  $C = \theta^p$ . We varied  $p$  from one (linear) to  
236 1.25 (slightly concave up). We used the nest care function to calculate the per-egg availability of  
237 care in a nest as the ratio of available care  $C$  to total egg production each year. Both care  
238 availability and egg production decreased with fishing, but the selectivity of fishing pressure for  
239 each sex determined whether *care-per-egg* decreased or increased. We characterize this change  
240 as the Care Ratio, which we represent as  $R$ : the care-per-egg in the fished population, relative to  
241 the care-per-egg in the unfished population (Table 2).

242 Using this new metric  $R$ , we evaluated the consequences of a feedback from fishing on  
243 larval production, the total number of eggs that hatch successfully year, due to a change in care-  
244 per-egg. We assumed larval hatching success changed proportionally according to the Care Ratio  
245 in this subset of our analyses. For example, if available care per egg decreased with fishing  
246 mortality relative to the unfished population (i.e.,  $R < 1$ ), we assumed this also decreased larval  
247 hatching success by the same fraction. In this way we estimated the indirect effect of changes in  
248 per-egg availability of care after fishing removed some males and females. Our goal was to  
249 compare the net effect of these changes to male and female demography on yield and larval  
250 production, with and without the potential feedback between care availability and hatching

251 success. In every scenario, we calculated expected yield and larval production, sometimes  
252 referred to as spawning potential. The latter is correlated with a population's capacity to buffer  
253 stochastic environmental variation (Kindsvater et al., 2016; O'Farrell & Botsford, 2005).

254

### 255 *Recruitment and population dynamics of both species*

256 Births and deaths in our simulated population were determined by the demographic  
257 composition of males and females. The maturation rate and mortality rate of each sex of each  
258 species determines the number of mature individuals in each age class ( $a$ ) alive at time  $N(t)$ , if  
259 they are mature  $p_m(a)$ , and the relationship between fecundity and body mass  $W(a)$ . Egg  
260 production  $E(t)$  depends on the number and size of mature females, and the mass-fecundity  
261 relationship for each species (Table 2; parameters are given in Table 3). In scenarios with no  
262 indirect effect of care availability, egg production and larval production  $P(t)$  were perfectly  
263 correlated,  $E(t) = P(t)$ . As illustrated in Figure 2, with a feedback incorporating care  
264 availability, larval production decreased according the care ratio,  $E(t) = RP(t)$ . For all  
265 scenarios, we assumed the population dynamics are regulated by density-dependence in  
266 recruitment to the year one age class. In other words, larval survival from hatching to recruitment  
267 depends on larval density, but adult survival and growth are independent of density. We assumed  
268 the recruitment function followed the Beverton-Holt equation (Mangel, 2006). The Beverton-  
269 Holt relationship specifies the maximum probability that a larva survives to recruitment  $\alpha$  (i.e.,  
270 the productivity of the population at low density) and a metric of the strength of density  
271 dependence  $\beta$ . These parameters arise from specific environmental conditions that are difficult to  
272 measure, so they are often estimated from stock-recruitment relationships that relate recruitment  
273 to spawning stock biomass (Mangel, 2006). In species lacking stock-recruitment relationships,

274 such as the corkwing wrasse, we can characterize the effects of fishing on a population relative  
275 to an arbitrary unfished population. For comparison, we completed the same analysis on lingcod.  
276 Importantly, as long as recruitment overfishing is not occurring, our assumptions regarding  
277 density-dependent recruitment (i.e., the Beverton-Holt stock recruitment curve) do not have a  
278 strong effect on relative yield and relative spawning potential (sometimes called the Spawning  
279 Potential Ratio, SPR). To make sure this assumption is valid for the results presented here, we  
280 used a range of values for  $\alpha$  and  $\beta$  and checked to make sure they did not influence on our  
281 conclusions.

282         After individuals recruit to the population model after 1 year at size  $L_R$  (in cm), they  
283 grow and reproduce each year according to the specific growth, maturation, and mortality rates  
284 reported for each species (Table 3, Figure 2). Individuals live to at most  $A_{max}$  years. Given the  
285 balance of birth and death rates, the population will equilibrate at a steady state population  
286 biomass. We checked that our simulated populations all reached this equilibrium within 100  
287 years, at which time we “fished” our populations and made sure the fished population reached a  
288 new steady state. The selectivity of fishing mortality varied according to the management  
289 scenario we simulated. We evaluated a range of fishing mortality coefficients ( $F$  in Tables 2 and  
290 3) for each scenario. For each species, we compared a minimum size limit with a slot size limit,  
291 based on size limits currently used in management. We also compared scenarios with and  
292 without a feedback between care and larval production. This factorial comparison allowed us to  
293 tease apart the effects of management on the indirect effects of fishing on yield and larval  
294 production. Doing this for both species revealed how the details of each life history interacted  
295 with management decisions.

296

297           **Results**

298           For each factorial combination, we calculated yield to the fishery in numbers of fish,  
299 rather than biomass. To evaluate spawning potential, we compared the lifetime egg production of  
300 individuals in the fished population to those in the unfished, which is a method of calculating the  
301 Spawning Potential Ratio (SPR; e.g. Kindsvater et al., 2016). This reference point is commonly  
302 used to understand the recovery potential of a population, and conversely, its risk of  
303 overexploitation (O'Farrell & Botsford, 2005). Finally, we calculated the Care Ratio  $R$ : the care  
304 per egg available in the fished population, relative to the unfished population (Table 2).

305           *Corkwing wrasse*

306           Figure 3 shows that implementing the harvest slot limit led to a small decrease in yield to  
307 the wrasse fishery. A decrease in yield after the implementation of the slot is expected, because  
308 the largest individuals are protected from fishing. Natural mortality is high enough in corkwing  
309 wrasse that very few individuals in our model survived to grow beyond the maximum size limit,  
310 especially under strong fishing mortality. Therefore, the percent change in yield between the  
311 minimum size limit and the slot was greatest at low fishing mortality (Fig. 3c). This implies that  
312 for species with high natural mortality, the benefits of a slot limit will be countered by any  
313 corresponding change in fishing mortality on size classes within the slot. In other words, if the  
314 harvest rate of size classes within the slot increases as fishers respond to its implementation, it is  
315 possible the benefits of the slot will be undetectable.

316           In our model, yield did not change in the scenarios including the feedback between male  
317 size structure and larval production. While the slot limit increased care capacity by decreasing  
318 the number of large males captured, the minimum size limit was sufficient to protect egg  
319 production enough that recruitment to the adult population (at age one) was not affected. This is

320 a consequence of our use of a deterministic Beverton-Holt recruitment function. Because stock  
321 recruitment relationships vary according to inter-annual environmental fluctuations, the result  
322 that yield is stable under high size-selective fishing mortality is an oversimplification of reality  
323 and could lead to overconfidence in a fishery's sustainability. Therefore, we focus on the  
324 Spawning Potential Ratio (a proxy for larval production) as an indicator of the ability of the  
325 population to buffer environmental stochasticity.

326 The dashed lines in each panel of Figure 4 show the SPR (squares) and the Care Ratio  $R$   
327 (circles), which reflects the care capacity of the population. We plot  $R$  even in the scenarios  
328 where there is no indirect effect of care capacity on egg survival, to better illustrate the  
329 interaction between spawning potential and  $R$ . As expected, spawning potential is lower at all  
330 levels of fishing mortality when egg survival to the larval stage decreases with the availability of  
331 care. In other words, fishing has a stronger negative effect on larval supply when we assume  
332 there is an effect of care capacity on larval production. However, implementing a harvest slot  
333 mitigates this effect (compare SPR in Fig. 4c and 4d). Additionally, the efficacy of the slot in  
334 increasing larval supply (i.e., the difference in squared dashed-lines in 4d to 4b) depends on the  
335 shape parameter  $p$ , which determines nonlinearity of the relationship between male size and care  
336 capacity. At higher values of  $p$  ( $1 < p < 2$ ), protecting the largest males with a slot limit has an  
337 outsized effect on the population's care capacity and increases the SPR in Fig 4d, especially at  
338 low levels of fishing mortality when the slot is most effective (not shown).

339 *Lingcod*

340 As in the wrasse, the yield to the fishery (in number of fish) decreased with the  
341 implementation of a harvest slot limit (Fig. 5), but did not vary with an effect of care capacity on  
342 larval production. Again, we attribute this stability in catch to our choice of the Beverton-Holt

343 stock recruitment function and the fact the minimum size limit is sufficient to prevent  
344 recruitment overfishing in our deterministic model. As in the wrasse, yield differences arising  
345 from the two management scenarios was greatest at low fishing mortality; at high rates of fishing  
346 mortality yield did not differ substantially between the minimum size and slot limit scenarios  
347 (Fig. 5), as few individuals survived to outgrow the maximum size limit.

348         Lingcod females are larger than males, so under a minimum size limit, the main effect of  
349 fishing was to strongly reduce the spawning potential of females (Fig. 6a, dashed line with  
350 squares). Including a feedback with care capacity mitigated this decrease in SPR (Fig. 6c, dashed  
351 line with squares). This pattern held in both management scenarios, but the increase due to care  
352 was more dramatic in the minimum size limit scenario (Fig. 6a and 6c). This is because in  
353 lingcod, the availability of care increased *above* unfished levels after fishing, because egg  
354 production decreased faster than nests. The increase in care-per-egg is reflected in a Care Ratio  
355 greater than one in all fishing scenarios (Fig. 6). This effect was less dramatic with slot limit, as  
356 these only protected the female population; males did not grow beyond the upper size limit (Fig.  
357 1b). For this reason, the shape parameter  $p$ , representing the degree to which the largest males  
358 contributed disproportionately to total care capacity, did not affect the results in Fig. 6.

359

## 360         **Discussion**

361         Our study is part of a growing body of literature evaluating the potential for size-selective  
362 management strategies to balance yield, spawning potential, and long-term fishery sustainability  
363 (Gwinn et al., 2015; Kindsvater et al., 2017, Ahrens et al., 2020). The influence of male size  
364 structure on population productivity in fished species with obligate male care has been  
365 recognized as an important aspect of effective management, but left un-explored (Halvorsen et



366 al., 2016; Stubberud et al., 2019). Here, we modelled fisheries for two such species to investigate  
367 the effects of different size-selective management strategies on yield, spawning potential, and  
368 care. By using a simulation approach, we were able to investigate the possible importance of an  
369 indirect effect (feedback) of fishing on per-egg care, which depends on both male and female  
370 size structure. We found that for both species, without any assumptions about how male care  
371 influences larval production, the slot limit was most effective at protecting larval production  
372 when fishing mortality was low. Under high fishing mortality, in the steady state, very few  
373 individuals survived beyond the maximum size limit. This result might change if fishing  
374 decreases natural mortality, which is possible if the mechanisms of adult mortality are density  
375 dependent. This is a plausible mechanism for compensatory productivity, especially for species  
376 with high natural mortality (Andersen, Jacobsen, Jansen, & Beyer, 2017; Rose, Cowan,  
377 Winemiller, Myers, & Hilborn, 2001). Furthermore, our results indicate that slot limits alone  
378 could be insufficient to prevent overexploitation. In both species, implementing a slot limit led to  
379 a difference in yield of 5% or less once fishing mortality ( $F$ ) exceeded 0.4 (Fig. 3c, Fig. 5c),  
380 while spawning potential was reduced to 60% or less of unfished levels in the wrasse when we  
381 assumed a decrease in care availability due to fishing. Our results suggest the growth patterns  
382 and mating systems of both species may increase their vulnerability to overfishing, for different  
383 reasons, and despite management measures.

384

### 385 *Corkwing wrasse*

386 The benefit of the slot limit to larval production - relative to populations managed with a  
387 minimum size limit - could only be detected in the corkwing wrasse simulations when care was  
388 reduced by fishing in a way that reduced the proportion of surviving larvae by the fraction  $R$ .

389 This is because, under fishing, no females grew large enough to benefit from the maximum size  
390 limit, so the slot did not affect egg production. The details regarding how care affects larval  
391 survival are important. First, we assumed per-capita egg survival decreased linearly with nest  
392 availability, i.e. there were no non-linear effects (such as increased survival at low density). This  
393 assumption may not hold for all species with obligate male care, but in *S. ocellatus*, a congeneric  
394 wrasse species, male care is largely sharable (i.e., we don't expect a decrease in egg survival at  
395 high densities) and at low egg densities, males are more likely to abandon nests (Alonzo 2004).  
396 Second, the more nonlinear the relationship between the Male Size Index and care capacity, the  
397 more effective the slot limit was at increasing larval production. We do not know how much  
398 more effective larger males are in providing care, but in the corkwing wrasse, large males have  
399 larger nests and start nesting earlier, which could allow them to care for more eggs and complete  
400 more nesting cycles in a spawning season, suggesting that they do provide an outsized  
401 contribution to care (Ingebrig, Uglem & Rosenqvist, 2002). Finally, in corkwing wrasse, size-  
402 selective fishing has two impacts: disproportionate removal of nesting males, and decreasing the  
403 amount of care available for eggs. We did not model the effect of male removal on fertilization  
404 success, because this species also has sneaker males capable of fertilizing eggs, so when some  
405 nesting males are present, sperm limitation is unlikely. However, in the long term, any increase  
406 in the mating success of these smaller males may be offset by changes in the inter- and intra-  
407 sexual dynamics of males and females, as the fitness of sneaker males also depends on the  
408 frequency of nesting males and the choosiness of females.

409

410 *Lingcod*

411 By contrast, for lingcod, the slot limit was effective in increasing larval production  
412 (relative to that expected under a minimum size limit), even without a feedback between nest  
413 availability and care capacity. However, the fishery selectively removed a greater proportion of  
414 the female spawning population than the male population. As a result, this species remained  
415 vulnerable to recruitment overfishing, even with a slot limit in place, if total fishing mortality  
416 was not controlled. This result is likely to be the case for any species where females are much  
417 larger than males and fishing is strongly size-selective (regardless of whether they have male  
418 care). For this reason, our assumptions about the potential indirect effects of fishing on male  
419 care were less important than the direct effect of fishing on egg production. For lingcod,  
420 spawning potential was reduced to 40% or less of unfished levels once fishing mortality  
421 exceeded 0.4, unless we assumed there was a “rescue” effect due to the increase in availability of  
422 per-egg care (Fig. 6). Currently we do not know whether increased care availability has any such  
423 compensatory effect, or if it does, whether the magnitude we considered is realistic. However,  
424 our result suggests the use of bag limits, in addition to slot limits, have been important in  
425 allowing lingcod stocks to rebuild.

426

427 In our model, recruitment depended on a deterministic Beverton-Holt relationship  
428 between larval production and survival. Therefore, our model results regarding yield were not  
429 sensitive to our assumptions about feedbacks from male care (Fig. 3; Fig. 5), despite differences  
430 in larval production (SPR) arising under different management and harvest scenarios (Fig 4, Fig.  
431 6). In reality, we expect that the relationship between larval supply and yield will fluctuate  
432 according to environmental conditions, though detecting this relationship is notoriously tricky  
433 (Munch et al., 2018). By using the Beverton-Holt relationship, we assumed there was no

434 compensatory density-dependence (as there would be if we used a Ricker function). We chose  
435 the Beverton-Holt because it is a more conservative model of recruitment dynamics (i.e., fishing  
436 does not increase population productivity as it would under a Ricker model). We also have no  
437 evidence for cannibalism at high population densities, or for interference in egg survival at high  
438 adult population densities, which have been suggested to drive Ricker-like dynamics in some  
439 species. If we had used a Ricker function, the relative increase in larval production expected after  
440 implementing a slot size limit would be offset by the decline in recruitment success at high larval  
441 densities.

442

443       When males of different sizes compete for fertilizations, as in species large fighter males  
444 and smaller sneaker males, it is unclear how adaptation to size-selective fishing will affect the  
445 distribution of male sizes and population productivity (DeFilippo et al., 2019; Kendall et al.,  
446 2014; Kendall & Quinn, 2013). Some theory predicts that sexual selection will reinforce  
447 adaptation to fishing when males are under directional sexual selection, but fishing increases  
448 variance in male reproductive success (Hutchings & Rowe, 2008). There is some evidence from  
449 sockeye salmon, however, that the removal of large males by fishing elevates the relative fitness  
450 of secondary males (in salmon, known as “jacks”), and increases the frequencies of smaller  
451 males in subsequent generations (DeFilippo et al., 2019). In other species with multiple male  
452 mating tactics, this may not be the case. For example, in a wrasse with paternal care, high  
453 sneaking rates have been found to decrease the willingness of nesting males and females to mate  
454 (Alonzo & Heckman, 2010; Alonzo & Warner, 1999). In this case, it is possible that sexual  
455 selection will actually decrease the success of the remaining (unfished) nesting males in the short  
456 term, because the density of small sneaker males at remaining nests will increase. The frequency-

457 dependent selection that is maintaining the stable polymorphism in male mating tactic may be  
458 disrupted, and the potential interactions with fishing-induced selection on maturation and growth  
459 is unknown. One possibility is that by increasing sneaker density at nests, fishing could indirectly  
460 hamper population productivity by decreasing the number of eggs that are spawned, even if  
461 females are not fished directly – an undesirable outcome of size-selective management.

462         In species that do not have secondary males, such as lingcod, it is possible that  
463 fertilization rates could be a limiting factor in fisheries that target large males (Alonzo and  
464 Mangel 2004). Several studies support the assumption of a positive correlation between male  
465 body size and reproductive success in fishes with male care (Bose et al., 2018; Cargnelli & Neff,  
466 2006; Wiegmann & Baylis, 1995). Among fisheries targeting fishes with male care, some are  
467 managed by harvest slots, reflecting that the importance of large males (and females) is  
468 acknowledged (Table 1). Several of these species are also protogynous hermaphrodites. For these  
469 species, management that protects the largest individuals may be necessary to prevent depletion  
470 of terminal males to avoid sperm limitation, and can also help to buffer fisheries-induced  
471 reduction in size- at sex-change (Alonzo et al., 2008; Kindsvater, Reynolds, Sadovy de  
472 Mitcheson, & Mangel, 2017; Sato et al., 2018).

473         Although harvest slots may seem to be an intuitive measure to balance fishing mortality  
474 between sexes, we show that management protecting large individuals of any sex is likely to  
475 have small effects if natural mortality is relatively high. That does not mean that large males  
476 should be ignored, but rather that management strategies are carefully evaluated and effects  
477 monitored. Our results are consistent with three rules of thumb to promote the sustainability of  
478 fisheries for species with paternal care: (i) control fishing mortality (e.g. implement quotas or  
479 bag limits); (ii) allow both males and females to spawn at least once before fished (e.g. enforce

480 minimum size limits or gear modifications) and (iii) reduce or restrict fishing during the nesting  
481 period which can directly affect productivity if guarding males are fished (Froese, 2004;  
482 Overzee & Rijnsdorp, 2015; Suski 2003.). A spawning season closure has been implemented in  
483 the Norwegian wrasse fishery in recent years, but wrasse can be fished during the spawning  
484 season in Sweden (Faust, Halvorsen, Andersen, Knutsen, & André, 2018). Lastly, in order to  
485 better predict the consequences of harvesting fish with male care, dedicated field studies are  
486 needed under realistic conditions. For example, how does disproportional removal of large males  
487 affect competition and social hierarchies among remaining males, and to what extent does  
488 reduced availability of nests affect female mating decisions and offspring survival?

489 In summary, our results highlight the need to exert caution when managing fishes with  
490 obligate male care, and that slot size limits are no silver bullet for ensuring long term viability if  
491 overall fishing mortality is high and not controlled. Furthermore, the evolutionary outcomes of  
492 size-selective fishing for the relative fitness of the alternative reproductive tactics deserves  
493 further scientific investigation. Despite these caveats, our results suggest that the current  
494 management strategies used for both corkwing wrasse in Norway and lingcod in western North  
495 America, have likely benefited the sustainability and rebuilding rates of the respective fisheries.

496

497

#### 498 **Acknowledgements**

499 This work was supported by NSF DEB-1556779 to HKK, funding from Virginia Tech to  
500 HKK, NSF IOS-1655297 to SHA and funding from the University of California Santa Cruz to  
501 SHA.

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774 **Figure captions**

775

776 **Figure 1.** Length-at-age functions and age-specific maturation rates for Corkwing wrasse (left  
777 column) and lingcod (right column). For the wrasse, estimates of growth (panel a) and  
778 maturation rates (panel b) are available for each life-history pathway in the western Norway  
779 stock (females: black line; nesting males: blue line; sneaker males: red line). For lingcod, sex-  
780 specific estimates (females: black; males: blue) are available from stocks in Washington State.  
781 Note female lingcod are the larger sex. Parameters for each function are given in Table 3.

782

783 **Figure 2.** Generic schematic of the population model and where the reproductive behavior  
784 operates. The model assumes that recruitment to the adult population happens at after one year of  
785 age for both species. After that, they experience constant annual mortality, which varies  
786 according to sex and male tactic. Maturation rates for each sex and life history vary according to  
787 age and/or size, depending on how they were estimated empirically (Table 3). Female fecundity  
788 depends on her mass, which is a function of her age in this model. In the scenarios where we  
789 included an effect (feedback) of male care, the probability an egg hatched and becomes a  
790 planktonic larva is proportional to the Care Ratio  $R$ , based on the average size of territorial  
791 mature males, weighted by their frequency in a stable age distribution under fishing, relative to  
792 their frequency in the unfished population (Table 2).

793

794 **Figure 3.** Spawning potential and care capacity for each of the factorial combinations of  
795 corkwing wrasse simulations. We modeled fisheries with a minimum size limit (left column) or a  
796 slot limit (right column), each with (bottom row) and without (top row) a feedback between care

797 and larval production, across a range of fishing mortalities. Blue square-dashed lines represent  
798 the SPR - relative larval production - at each level of fishing mortality. In each plot, red circle-  
799 dashed lines represent the Care Ratio,  $R$ . For corkwing wrasse,  $R$  was bounded between 0 and 1,  
800 so the right y-axis scale represents both dashed lines.

801

802 **Figure 4.** Yield of corkwing wrasse, in numbers of fish, for the minimum size limit (panel a) and  
803 the slot limit (panel b). We calculate the percent difference in yield under the two management  
804 scenarios (panel c). Yield is always greater under the minimum size limit.

805

806 **Figure 5.** Spawning potential and care capacity for each of the factorial combinations of lingcod  
807 simulations. Again, we modeled fisheries with a minimum size limit (left column) or a slot limit  
808 (right column), each with (bottom row) and without (top row) a feedback between care and larval  
809 production, across a range of fishing mortalities. Blue square-dashed lines represent the SPR -  
810 relative larval production - at each level of fishing mortality. In each plot, red circle-dashed lines  
811 represent the Care Ratio  $R$ . For lingcod,  $R$  increased above 1 (with no fishing), ranging from 3-  
812 20 under the highest level of fishing mortality  $F$ . The right y-axis scale (red) indicates this  
813 change, which was greatest under a minimum size limit (panel a), as egg production was  
814 severely depleted in this scenario.

815

816 **Figure 6.** Yield of lingcod, in numbers of fish, for the minimum size limit (panel a) and the slot  
817 limit (panel b). We calculate the percent difference in yield under the two management scenarios  
818 (panel c). Yield is always greater under the minimum size limit, but that difference narrows as  
819 the population becomes overfished.

**Table 1. Fished species with male care.**

Species	Larger sex	Alternative male tactic	Hermaphroditism	Habitat	Fishery	Management includes slot limit (some populations)
Ballan wrasse ( <i>Labrus bergylta</i> )	Male	No	Protogynous	Marine	Commercial and recreational	Yes
Cuckoo wrasse ( <i>Labrus mixtus</i> )	Male	Yes	Protogynous	Marine	Commercial	Yes
Corkwing wrasse ( <i>Symphodus melops</i> )	Male	Yes	No	Marine	Commercial	Yes
Black bream ( <i>Spondyliosoma cantharus</i> )	Male	No	Protogynous	Marine	Recreational	No
Bluegill sunfish ( <i>Lepomis macrochirus</i> )	Male	Yes	No	Fresh water	Recreational	No
Largemouth bass ( <i>Micropterus salmoides</i> )	Monomorphic	No	No	Fresh water	Recreational	Yes
Smallmouth bass ( <i>Micropterus dolomieu</i> )	Monomorphic	No	No	Fresh water	Recreational	Yes
Atlantic wolffish ( <i>Anarhichas lupus</i> )	Monomorphic	No	No	Marine	Commercial	No
Butterfly peacock bass ( <i>Cichla ocellaris</i> )*	Monomorphic	No	No	Fresh water	Recreational	No
Lingcod ( <i>Ophiodon elongatus</i> )	Female	No	No	Marine	Commercial and recreational	Yes
Lumpfish ( <i>Cyclopterus lumpus</i> )	Female	No	No	Marine	Commercial	No

\*Note Butterfly peacock bass has biparental care.

**Table 2.**

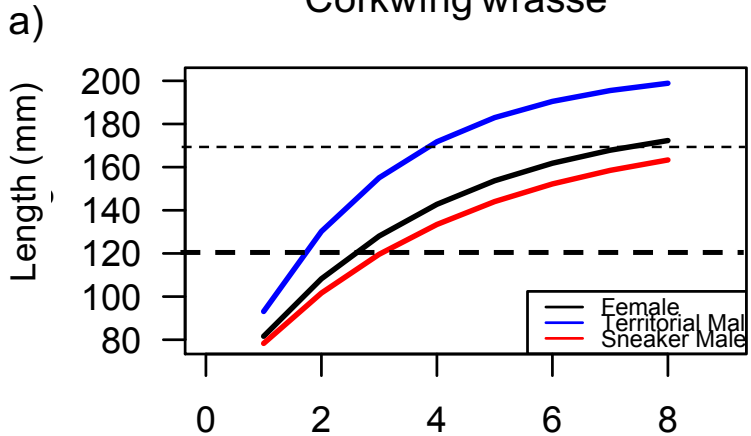
Process	Equation	Interpretation
Von Bertalanffy growth function	$L(i, a + 1) = L(i, a)e^{-k} + L_{\infty,i}(1 - e^{-k_i}) .$	$L_{\infty,i}$ and $k_i$ determine size-at-age $L$ of each life history type (in discrete time $t$ )
Maturation probability function (wrasse nesting males)	$p_m(i = nm, a) = \frac{1}{1 + e^{(-\gamma + \rho L(i=nm,a))}}$	For $i = nm$ , wrasse nesting males, maturation is based on length $L$ and logistic parameters $\gamma$ and $\rho$ . All females and sneaker males mature in years 2 and 1, respectively, which we denote as $a_{100}$
Maturation probability function (lingcod)	$p_m(i, a) = \frac{1}{1 + e^{-q(a-a_{mat,i})}}$	For lingcod $a_{mat,i}$ is the age at which 50% of individuals mature; $q$ determines the steepness ogive.
Body mass	$W(i, a) = v_i L(i, a)^{\omega_i}$	$v$ and $\omega$ are scale and shape parameters for each life history type $i$
Natural mortality	$M(i, a)$	$M$ assumed constant for all ages after age 1
Fishing mortality	$F(a) = \begin{cases} 0 & L(a) < \text{min size limit} \\ F & \text{min size limit} < L(a) < \text{max size limit} \end{cases}$	Depends on fishing mortality rate $F$ and selectivity (size limit or harvest slot limit)
Total annual egg production	$E(t) = \sum_a N(i = f, a, t) p_m(i = f, a) b W(i = f, a)^c$	Where $i = f$ is the female population. Mass and fecundity depend on length, which depends on age. Mass- specific fecundity parameters are $b$ and $c$
Density dependent recruitment	$N_0(t + 1) = \frac{\alpha P(t)}{1 + \beta P(t)}$	Beverton-Holt recruitment function
Spawning Potential Ratio	$SPR = \frac{\sum_a^{a_{max}} P(a) e^{-M(i=f,a)-F(a)}}{\sum_a^{a_{max}} N(i = f, a, t) p_m(a) b W(i = f, a) e^{-M(i=f,a)}}$	Egg production in the fished population relative to the unfished population. Note that the maximum ages in each population may differ
Male Size Index	$\theta = \text{mean} \left( \frac{L(a) p_m(a)}{N_T} \right)$	$\theta$ is the mean probability a territorial male is mature given its length, weighted by the number of territorial males of that size alive in the steady state population
Care Ratio	$R = \frac{\theta_{fished}^p / \sum_a^{a_{max}} P(a) e^{-M(i=f,a)-F(a)}}{\theta_{unfished}^p / \sum_a^{a_{max}} N(i = f, a, t) p_m(a) b W(i = f, a) e^{-M(i=f,a)}}$	The parameter $p$ shapes nonlinearity of the male size-care relationship ( $1 = \text{linear}$ ). $R$ is the proportional change in care-per-egg expected after fishing removes some males and females.
Population dynamics through time	$N(i, a + 1, t + 1) = \begin{cases} N_0(i, t) & \text{if } a = 0 \\ N(i, a, t) e^{-(M(a)+F(a))} & \text{if } a > 0 \end{cases}$	$N(i, a, t)$ is the number of individuals of each life history type $i$ at age $a$ alive at time $t$ . $N_0(i, t)$ is made up of equal numbers of males and females. Male tactics (for the wrasse) occur in equal proportions at birth



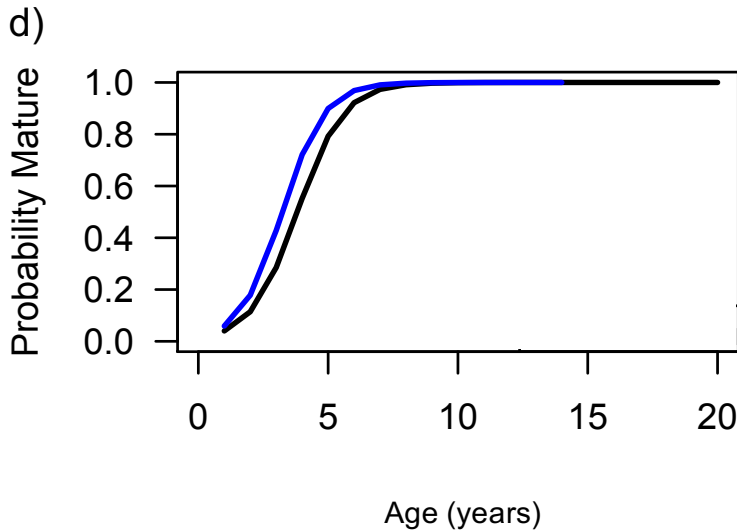
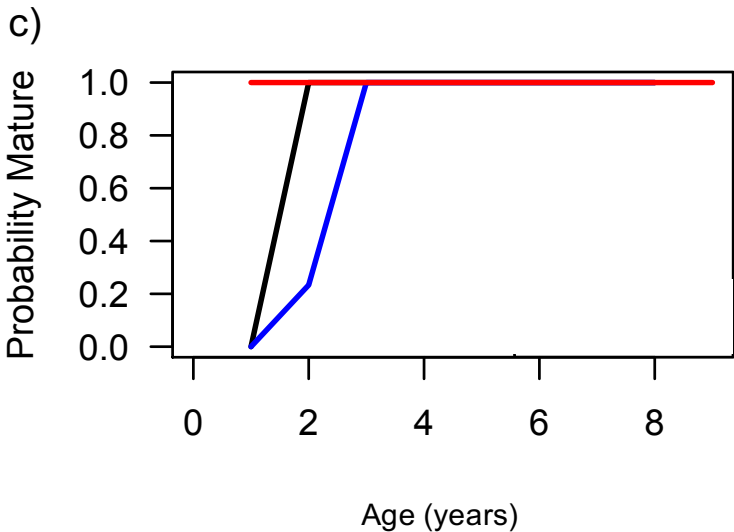
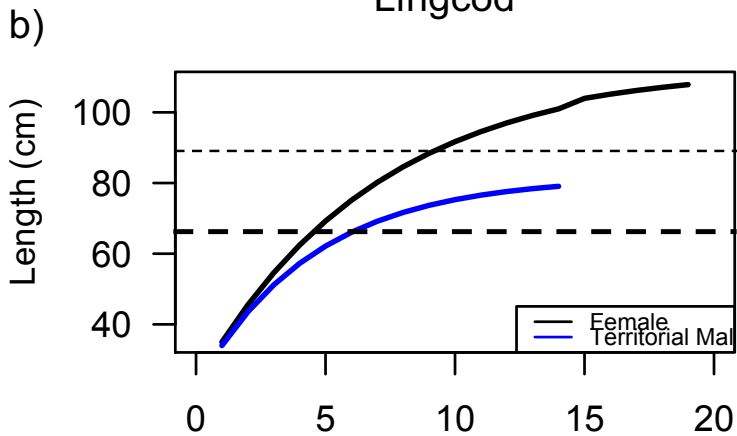
$N$	Initial population size (assumed 50:50 sex ratio, 25% of males assumed to be sneakers)	1000				
$T_{max}$	Number of years in our population simulation.	200				
$T_{fishing}$	Time when fishing mortality begins	100				
		<b>Corkwing wrasse parameters</b>			<b>Lingcod parameters</b>	
		<b>Females</b>	<b>Territorial males</b>	<b>Sneaker males</b>	<b>Females</b>	<b>Territorial males</b>
$M(a)$	Natural mortality rate (assumed constant)	0.54	0.54	0.40	0.18	0.32
$A_{max}$	Maximum age (years)	8	8	9	20	14
$L_{inf}$	Asymptotic size in von Bertalanffy growth function	177.5 mm	199.72 mm	180.8 mm	112.8 cm	81.87 cm
$k$	Growth coefficient in von Bertalanffy growth function	0.2972	0.3994	0.2625	0.145	0.223
$L$	Length-at-age; L(1) is reported here as the initial size at recruitment	81.6 mm	93.1 mm	78.3 mm	35 cm	34 cm
$\nu$	Scale coefficient relating length to body mass (in kg)	$6.6 \times 10^{-7}$	$9.3 \times 10^{-7}$	$8.5 \times 10^{-7}$	$1.7 \times 10^{-3}$	$4.0 \times 10^{-3}$
$\omega$	Shape exponent relating length to body mass	3.176	3.089	3.115	3.40	3.21
$a_{100}$	Age at maturation (wrasse females/sneaker males)	2	-	1	-	-
$\gamma$	Coefficient of length-based maturation function for wrasse nesting males	-	18.5836	-	-	-
$\rho$	Shape coefficient of length-based maturation function for wrasse nesting males	-	0.13361	-	-	-
$a_{mat}$	Age when 50% of lingcod are mature	-	-	-	1.129	1.124
$q$	Steepness of age-based maturation function for lingcod	-	-	-	3.814	3.233
$b$	Mass-specific fecundity coefficient (mass in kg)	$2.95 \times 10^5$	-	-	$2.82 \times 10^{-4}$	-
$c$	Mass-specific fecundity exponent	1	-	-	3.0011	-
<b>Recruitment parameters</b>						
$\alpha$	Steepness parameter of the Beverton-Holt recruitment function	0.05			0.1	
$\beta$	Parameter of the Beverton-Holt recruitment function	$8 \times 10^{-6}$			$1 \times 10^{-5}$	
<b>Exploitation parameters</b>						
-	Minimum size limit (mm)	120			26 inches (66.04 cm)	
-	Maximum size limit (slot)	170			36 inches (91.44 cm)	
$F$	Fishing mortality rate	Ranged from 0 to 0.7				

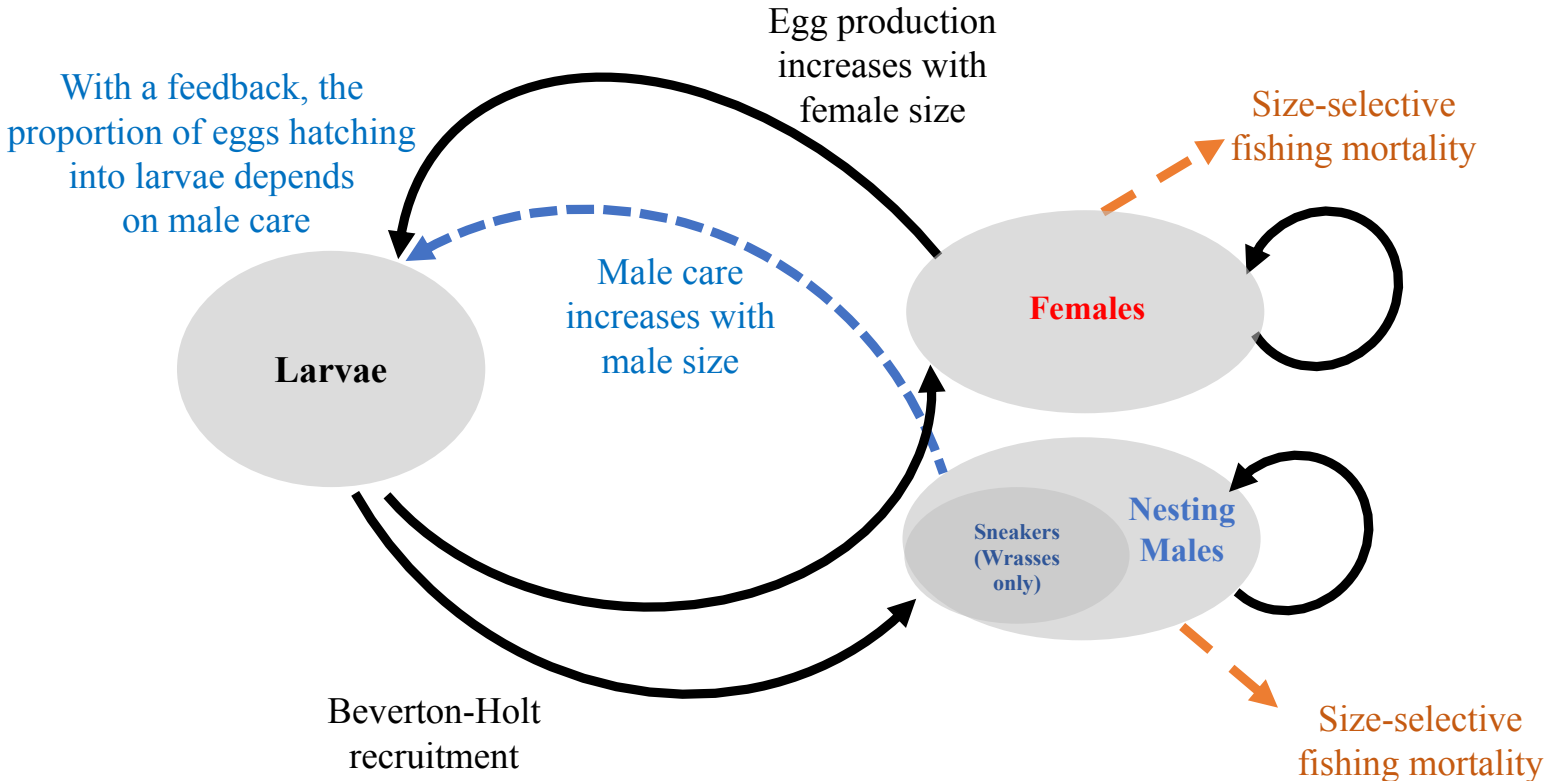


Corkwing wrasse



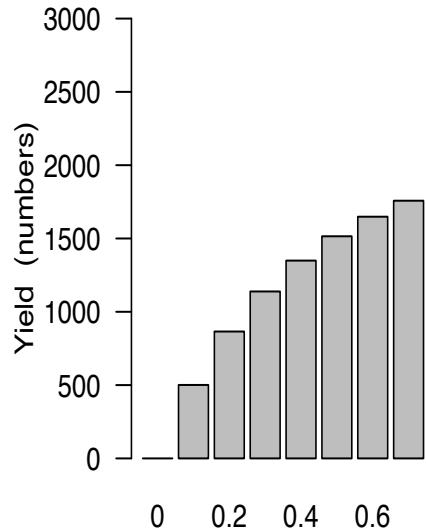
Lingcod



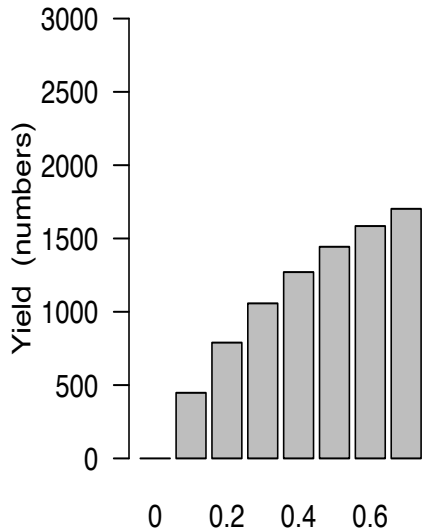


# Corkwing wrasse

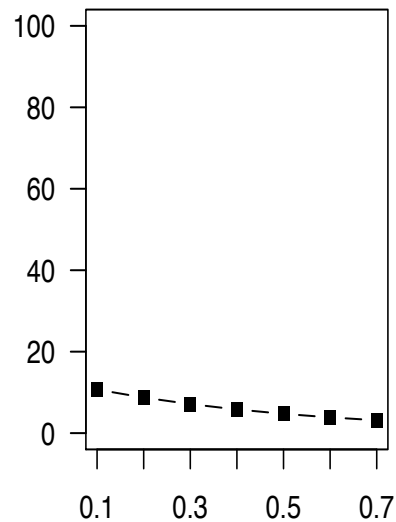
a) Minimum size limit



b) Slot size limit

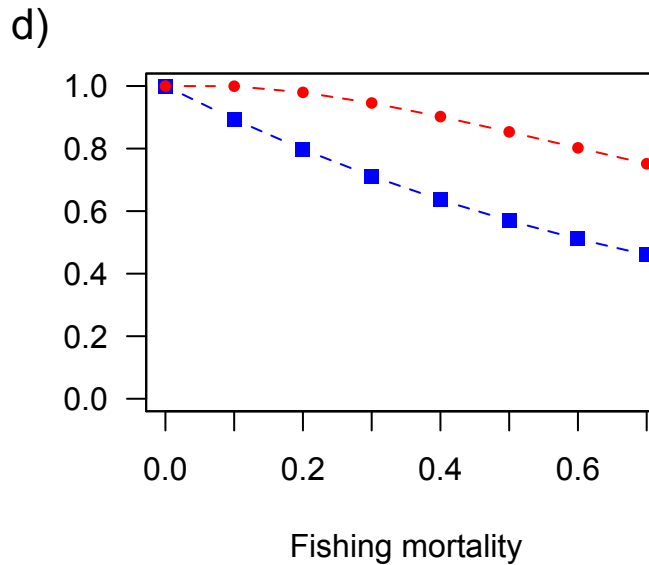
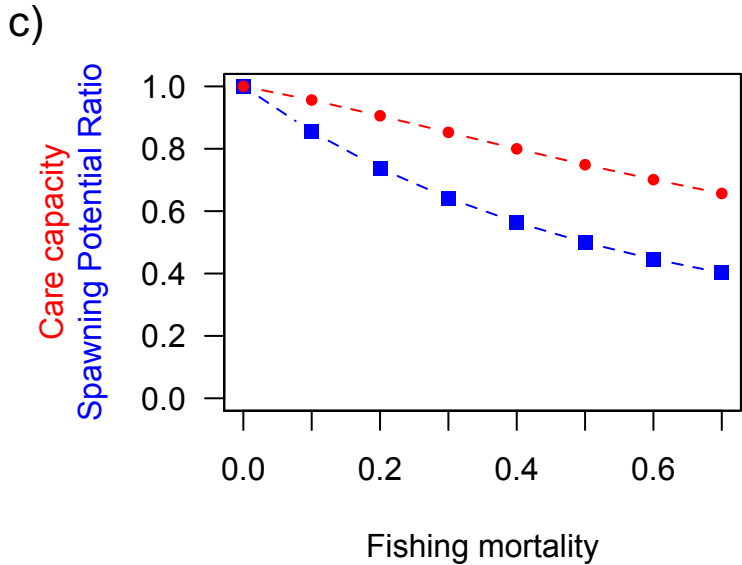
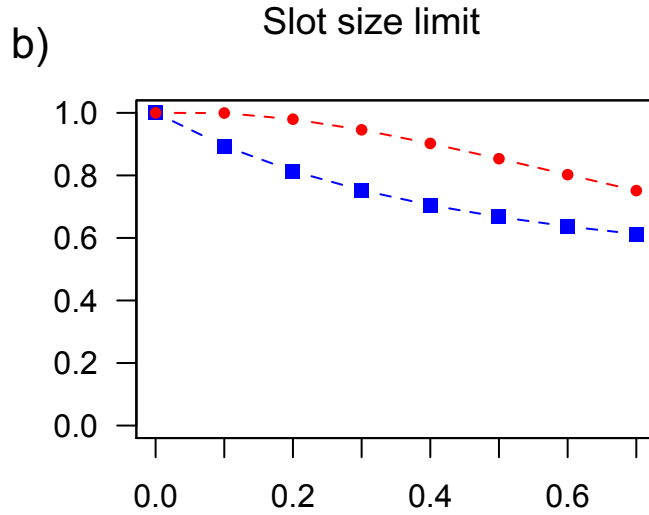
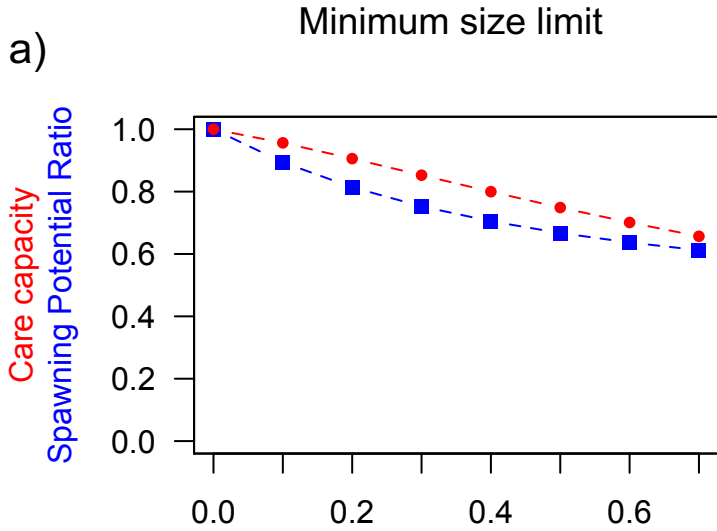


c) Percent decrease in yield with slot limit



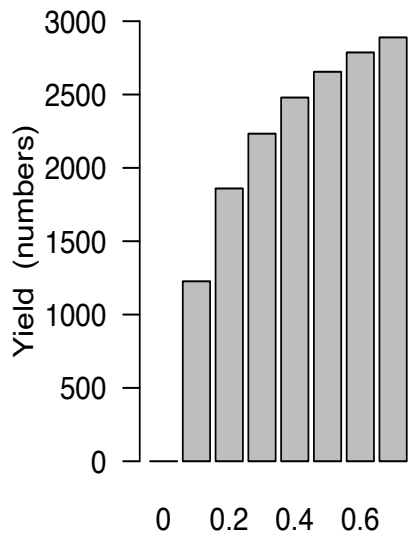
Fishing mortality

# Corkwing wrasse

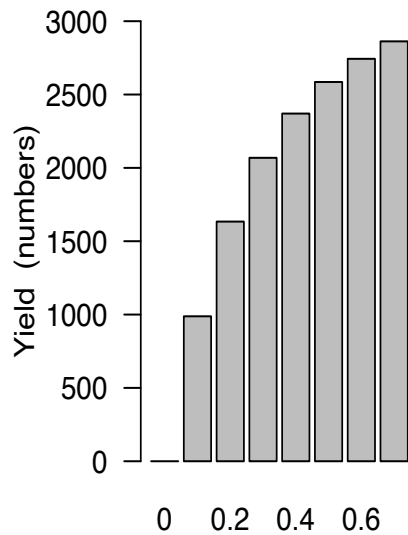


# Lingcod

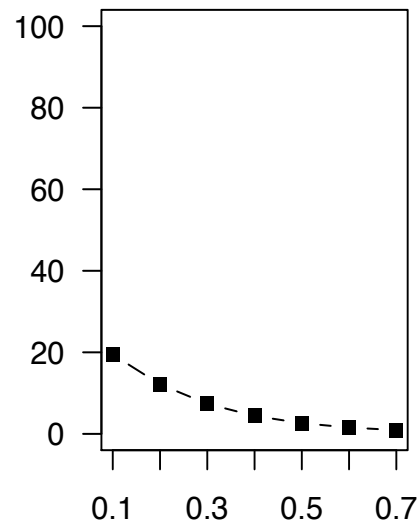
a) Minimum size limit



b) Slot size limit



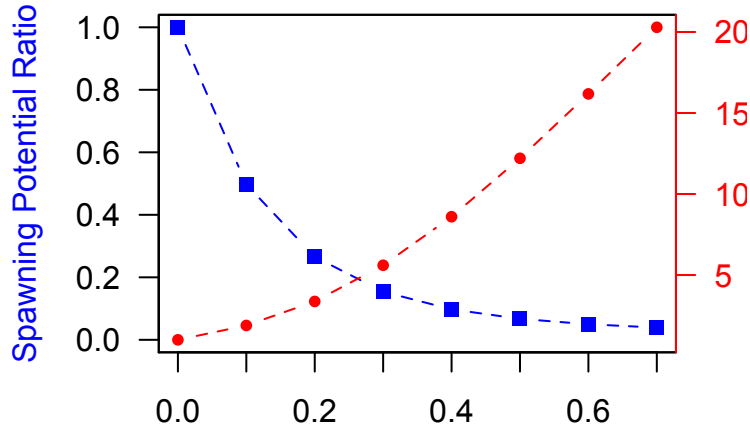
c) Percent decrease in yield with slot limit



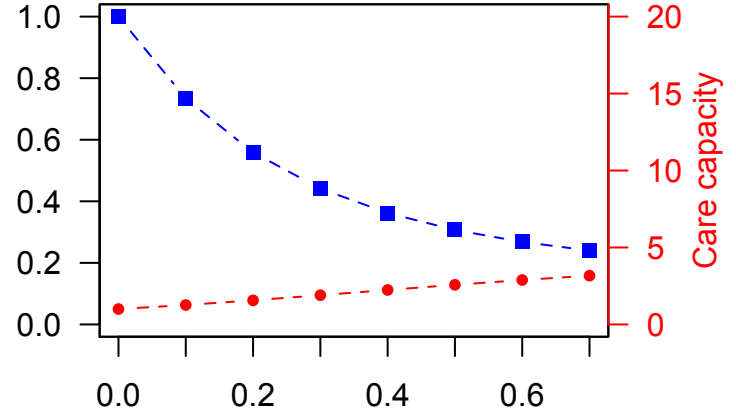
Fishing mortality

# Lingcod

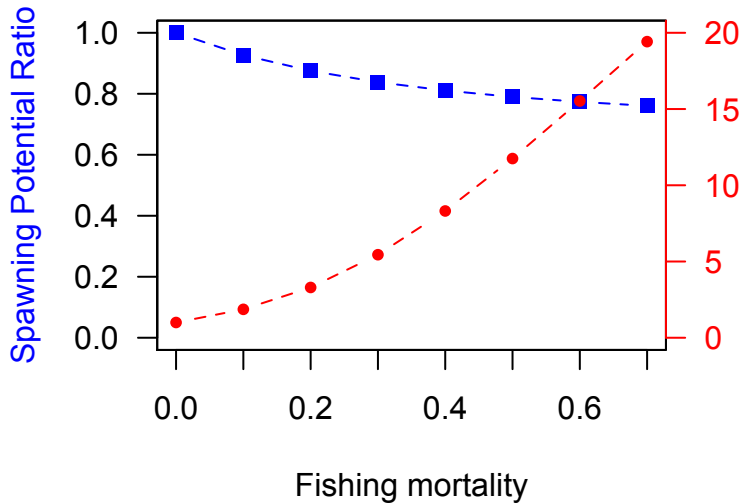
a) Minimum size limit



b) Slot size limit



c)



d)

