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

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Abstract

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

Keywords

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

Introduction

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

The potential effects of fishing on mating system dynamics and recruitment success have rarely been incorporated into management, despite evidence fishing can affect these processes (Alonzo & Mangel, 2004; Kendall & Quinn, 2013; Rowe & Hutchings, 2003; Sørdalen et al., 2018). The effects of fishing on mating systems may be most important when fishing targets a specific size in sexually dimorphic species (Carroll & Lowerre-Barbieri, 2019; H.K. Kindsvater, Reynolds, Sadovy de Mitcheson, & Mangel, 2017; Sørdalen et al., 2018). In such cases, 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; Ingebrigt 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

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

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

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

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

Study species

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

Corkwing wrasse

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

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

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

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

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; Ingebrigt
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

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

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

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

Recruitment and population dynamics of both species

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

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

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

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

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

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

Lingcod

As in the wrasse, the yield to the fishery (in number of fish) decreased with the implementation of a harvest slot limit (Fig. 5), but did not vary with an effect of care capacity on 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*.

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

Lingcod

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

In our model, recruitment depended on a deterministic Beverton-Holt relationship between larval production and survival. Therefore, our model results regarding yield were not sensitive to our assumptions about feedbacks from male care (Fig. 3; Fig. 5), despite differences in larval production (SPR) arising under different management and harvest scenarios (Fig 4, Fig. 6). In reality, we expect that the relationship between larval supply and yield will fluctuate according to environmental conditions, though detecting this relationship is notoriously tricky (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

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

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

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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

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

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

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

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

Table 1. Fished species with male care.

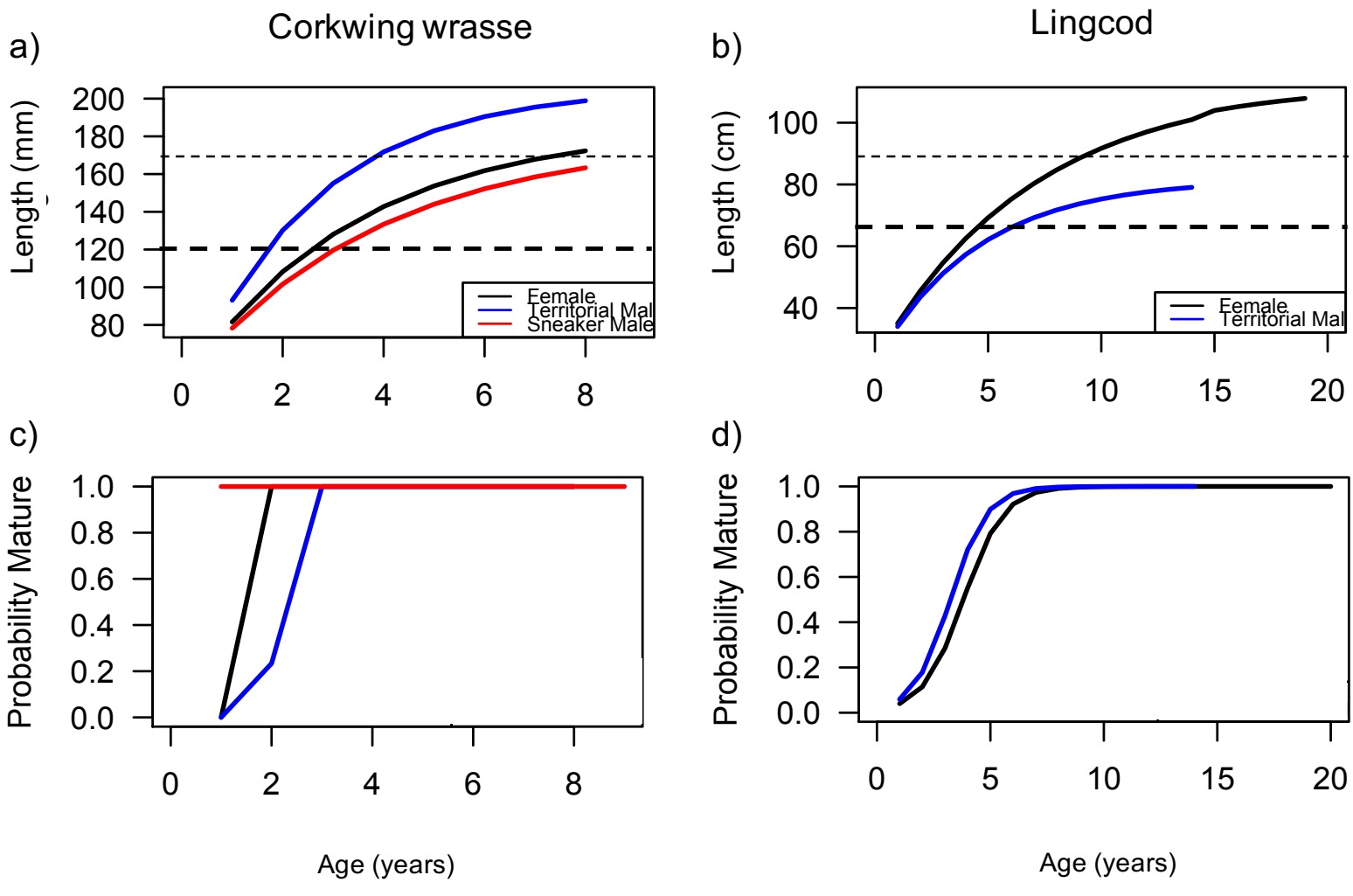
Species	Larger sex	Alternative male tactic	Hermaphroditism	Habitat	Fishery	Management includes slot limit (some populations)
Ballan wrasse (*Labrus bergylta*)	Male	No	Protogynous	Marine	Commercial and recreational	Yes
Cuckoo wrasse *(Labrus mixtus*)	Male	Yes	Protogynous	Marine	Commercial	Yes
Corkwing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

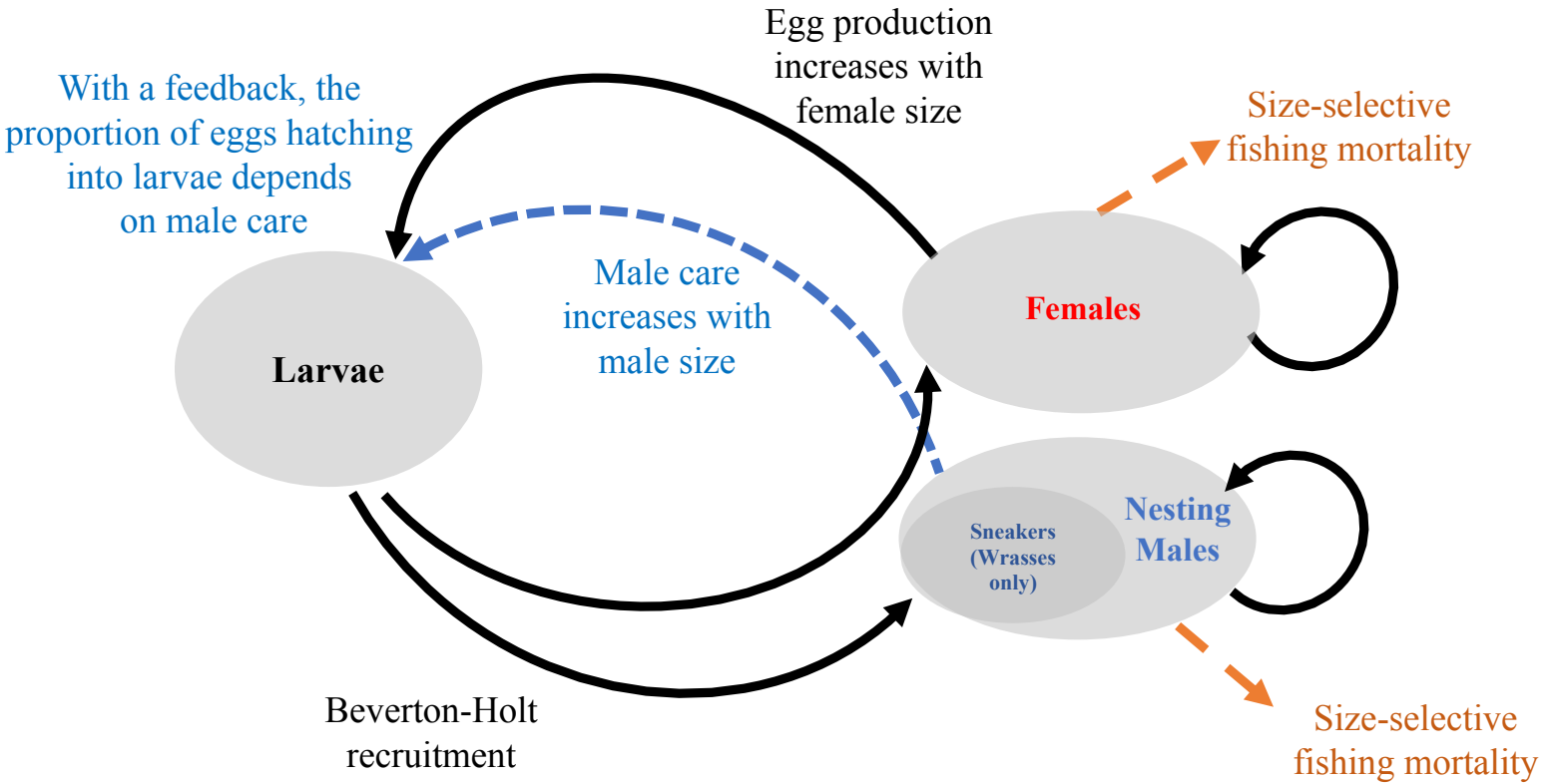
*Note Butterfly peacock bass has biparental care.

Table 2.

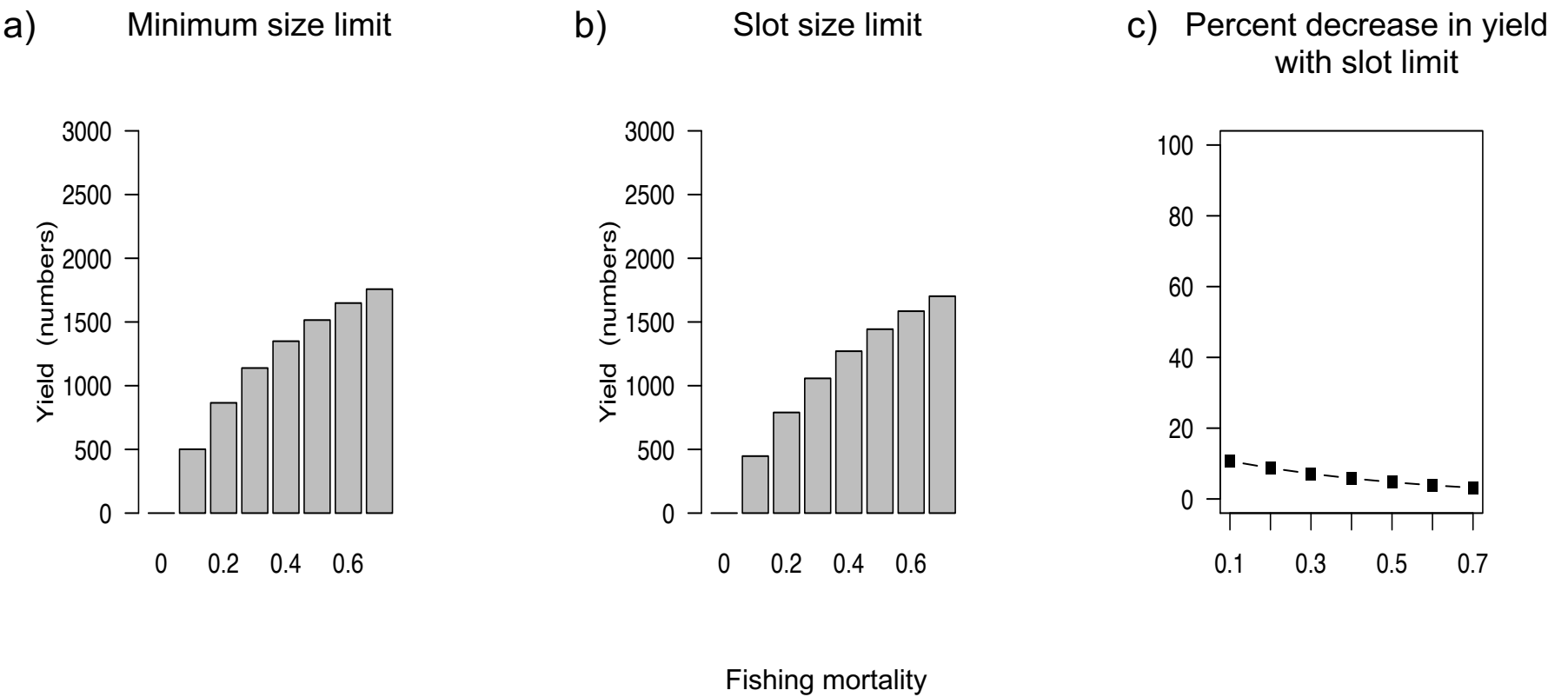
Process	Equation	Interpretation
Von Bertalanffy growth function	$L(i,a+1) = L(i,a)e^{-k} + L_{\infty,i}(1 - e^{-k_i})$.	$L_{\infty,i}$ and k_i determine size-at-age L of each life history type (in discrete time t)
Maturation probability function (wrasse nesting males)	$p_m(i = nm, a) = \frac{1}{1 + e^{(-\gamma + \rho L(i=nm,a))}}$	For $i = nm$, wrasse nesting males, maturation is based on length L and logistic parameters γ and ρ. 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	$W(i,a) = \nu_i L(i,a)^{\omega_i}$	ν and ω 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	$E(t) = \sum_a N(i=f,a,t)p_m(i=f,a)bW(i=f,a)^c$	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	$SPR = \frac{\sum_a^{a_{max}} P(a)e^{-M(i=f,a)-F(a))}}{\sum_a^{a_{max}} N(i=f,a,t)p_m(a)bW(i=f,a)\, e^{-M(i=f,a)}}$	Egg production in the fished population relative to the unfished population. Note that the maximum ages in each population may differ
Male Size Index	$\theta = mean\left(\frac{L(a)p_m(a)}{\bar{N}_T}\right)$	θ 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	$R = \frac{\theta^p_{fished} \Big/ \sum_a^{a_{max}} P(a)e^{-M(i=f,a)-F(a))}}{\theta^p_{unfished} \Big/ \sum_a^{a_{max}} N(i=f,a,t)p_m(a)bW(i=f,a)\, e^{-M(i=f,a)}}$	The parameter p shapes nonlinearity of the male size-care relationship (1 = linear). R is the proportional change in care-per-egg expected after fishing removes some males and females.
Population dynamics through time	$N(i,a+1,t+1) = \begin{cases} N_0(i,t) & if\ a = 0 \\ N(i,a,t)\, e^{-(M(a)+F(a))} & if\ a > 0 \end{cases}$	$N(i,a,t)$ 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

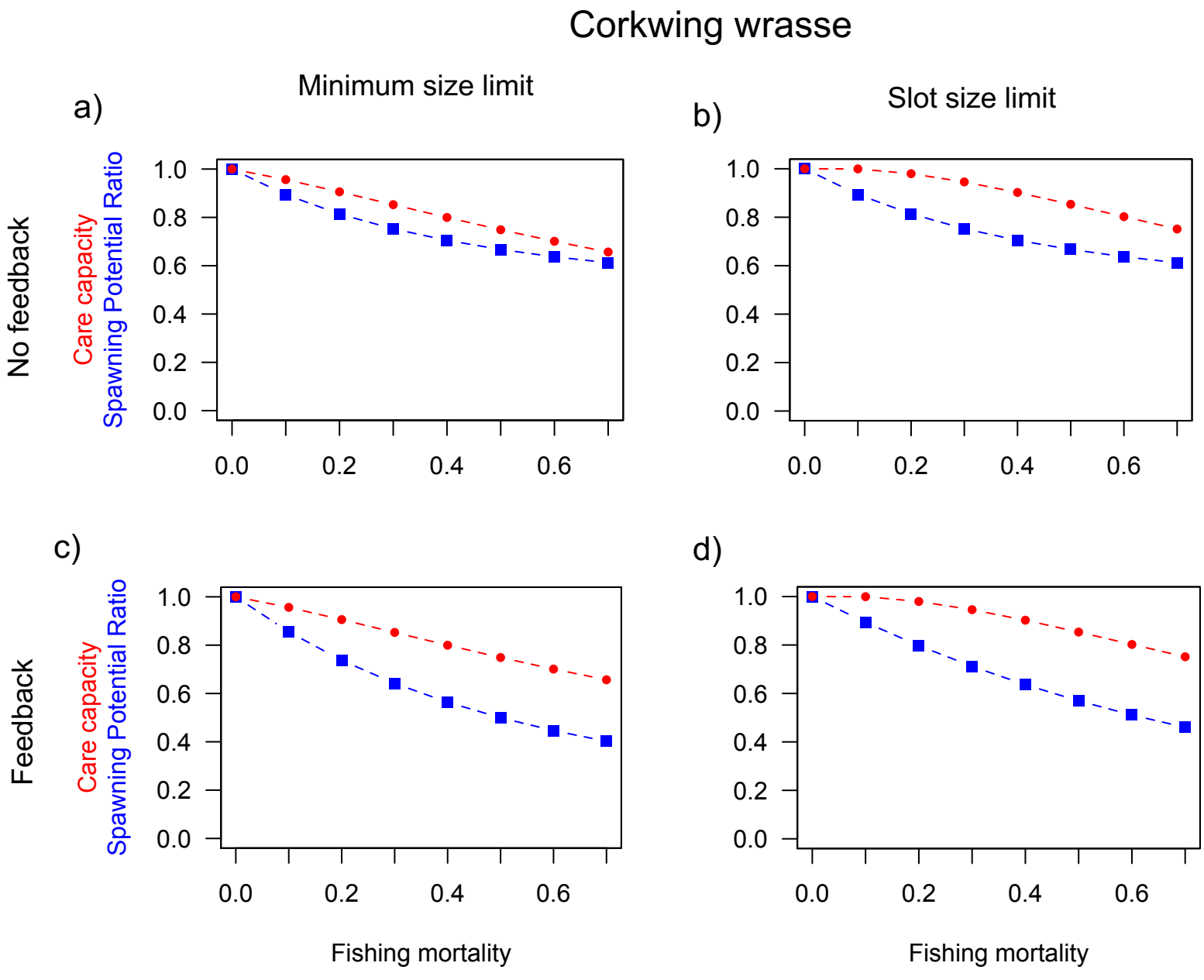
Table 3. Simulation parameters						
N	Initial population size (assumed 50:50 sex ratio, 25% of males assumed to be sneakers)	1000				
T_{max}	Number of years in our population simulation.	200				
$T_{fishing}$	Time when fishing mortality begins	100				
		Corkwing wrasse parameters			**Lingcod parameters**	
		Females	**Territorial males**	**Sneaker males**	**Females**	**Territorial males**
$M(a)$	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
ν	Scale coefficient relating length to body mass (in kg)	6.6×10^{-7}	9.3×10^{-7}	8.5×10^{-7}	1.7×10^{-3}	4.0×10^{-3}
ω	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	-	-
γ	Coefficient of length-based maturation function for wrasse nesting males	-	18.5836	-	-	-
ρ	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)	2.95×10^{5}	-	-	2.82×10^{-4}	-
c	Mass-specific fecundity exponent	1			3.0011	-
Recruitment parameters						
α	Steepness parameter of the Beverton-Holt recruitment function	0.05			0.1	
β	Parameter of the Beverton-Holt recruitment function	8×10^{-6}			1×10^{-5}	
Exploitation parameters						
-	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				

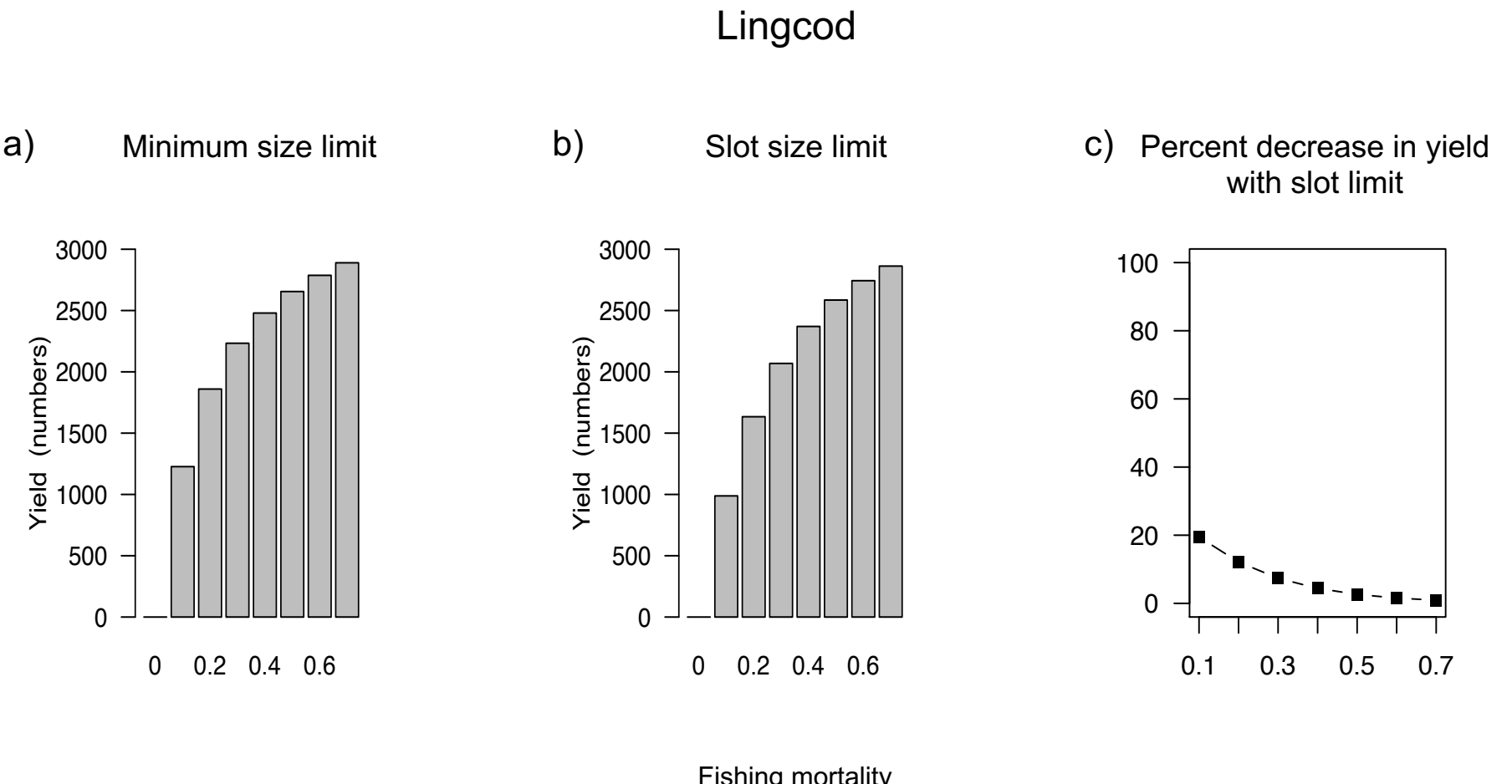

a)
Corkwing wrasse
Length (mm)
200
180
160
140
120
100
80
0
2
4
6
8
Female
Territorial Mal
Sneaker Male
b)
Lingcod
Length (cm)
100
80
60
40
0
5
10
15
20
Female
Territorial Mal
c)
Probability Mature
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
Age (years)
d)
Probability Mature
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
Age (years)

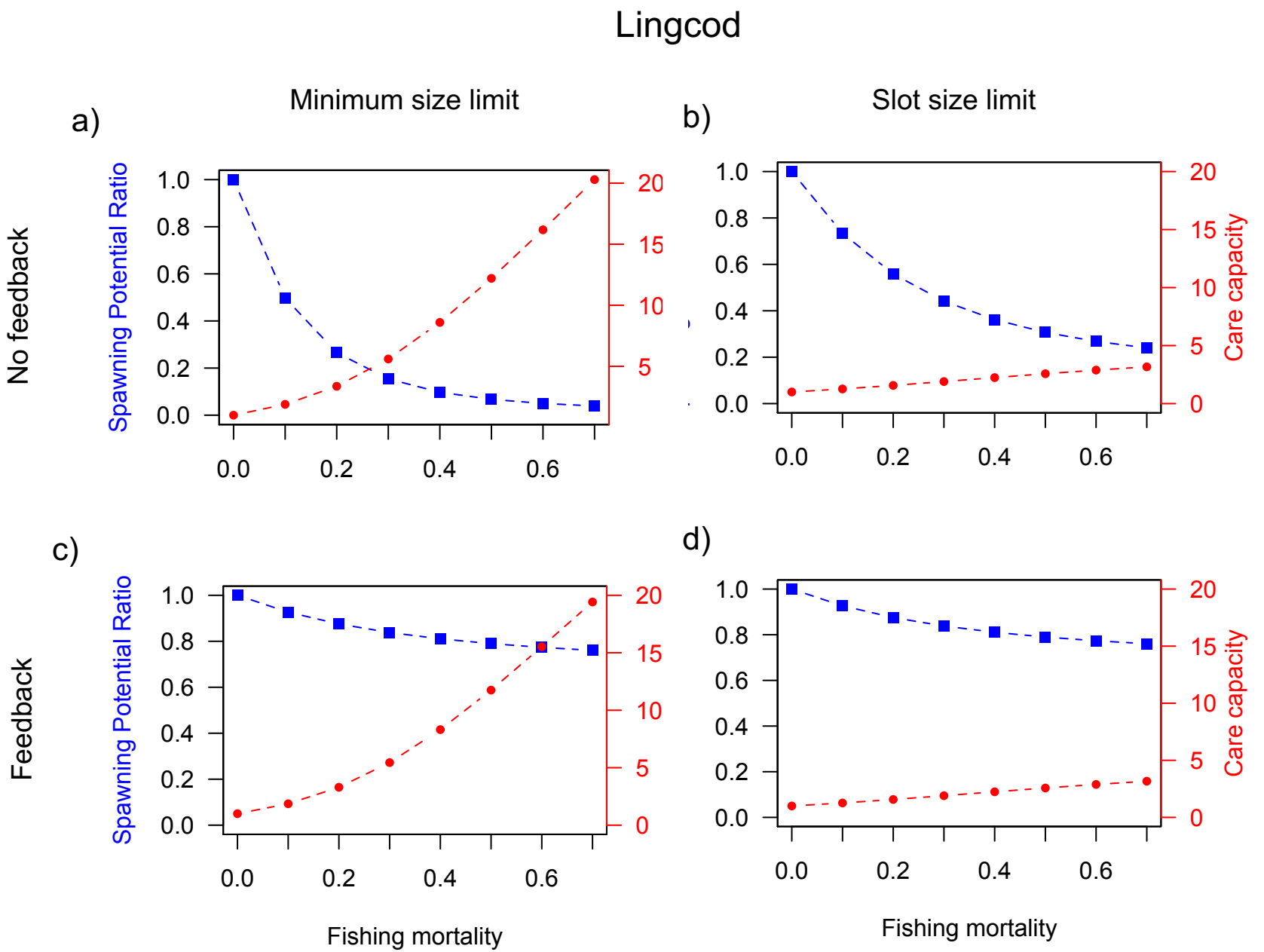

Egg production increases with female size
With a feedback, the proportion of eggs hatching into larvae depends on male care
Size-selective fishing mortality
Male care increases with male size
Larvae
Females
Sneakers (Wrasses only)
Nesting Males
Beverton-Holt recruitment
Size-selective fishing mortality

Corkwing wrasse




Corkwing wrasse
Minimum size limit
Slot size limit
a)
b)
c)
d)
No feedback
Feedback
Care capacity
Spawning Potential Ratio
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
Fishing mortality


Lingcod
a)
Minimum size limit
b)
Slot size limit
c)
Percent decrease in yield with slot limit
Yield (numbers)
3000
2500
2000
1500
1000
500
0
0
0.2
0.4
0.6
100
80
60
40
20
0.1
0.3
0.5
0.7
Fishing mortality


Lingcod
Minimum size limit
Slot size limit
a)
b)
c)
d)
No feedback
Feedback
Spawning Potential Ratio
Care capacity
Fishing mortality
1.0
0.8
0.6
0.4
0.2
0.0
20
15
10
5
0
0.0
0.2
0.4
0.6