

1 **Population outcome of an age-dependent maternal**
2 **effect depends on life-history context**

3 Yasmin Lucero, Ph.D. *

4 Northwest Fisheries Science Center

5 National Oceanic and Atmospheric Administration

6 2725 Montlake Boulevard East

7 Seattle, Washington 98112

8 (831) 332-4596

9 *yasmin.lucero@noaa.gov

Abstract

The discovery of age-dependent maternal effects in rockfish (genus *Sebastes*) has attracted attention to the truncated age-structure in harvested rockfish populations. Several researchers have suggested that, for some rockfish, population productivity is intertwined with population age-structure. This has raised the concern that fishing reduces population productivity even more than expected because of the elimination older age cohorts. However, little is known about the ecology of maternal effects. I use models to calculate the population impact of maternal effects. I measure population impact with two metrics: recruitment and time to recovery from an overfished state. To calculate recruitment, I employ a multivariate Beverton-Holt stock-recruitment model coupled with a maternal effects model. I then use this stock-recruitment model nested within a population simulation to calculate time to recovery. Both metrics are reported as a function of the the magnitude of the maternal effect and the survival and mortality rates of the pre-recruitment period. I demonstrate that maternal effects can have a significant population impact under a broad range of circumstances. However, the magnitude of the impact depends on the ecological context. Populations with low rates of productivity and slow rates of recovery from overfishing are those most likely to benefit from the restoration of maternal effects. Populations that are highly productive are the least likely to benefit, and in some cases may even be hindered by the increased population juvenile density that higher larval survival brings.

Keywords: rockfish; *Sebastes*; maternal effects; bipartite life history; pelagic larval stage; benthic juvenile stage; stage-structured models; rebuilding; time to recovery; stock-recruitment; multivariate stock-recruitment; multivariate Beverton-Holt; overfishing; age-structure

32 Introduction

33 On the U.S. west coast, several of the most troubled fish populations belong to the genus
34 *Sebastes*, commonly called rockfish. Low productivity, optimistic harvest plans and a string
35 of bad weather have contributed to placing seven rockfish stocks into rebuilding plans
36 (PFMC 2008). Recent observations of age-dependent maternal effects (Berkeley et al.
37 2004a, Sogard et al. 2008) have led several researchers to suggest that, for rockfish, pro-
38 ductivity is intertwined with age-structure. They hypothesize that a rockfish stock with a
39 full age-structure will be significantly more productive than a rockfish stock with the trun-
40 cated age-structure that is characteristic of an overfished stock (Palumbi 2004, Berkeley et
41 al. 2004b).

42 To persuade a fisheries management council to adopt the goal of restoring age-structure,
43 scientists must demonstrate that a truncated age-structure coupled with maternal effects is
44 detrimental. For example, we can model a maternal effect and use this in a population
45 simulation to calculate the change in population resilience with the addition of maternal
46 effects (Lucero 2008). However, this exercise cannot be conclusive because little is known
47 about the observed maternal effects and nothing is known about how the effects impact
48 survival of the early life history.

49 Here, I illustrate why these uncertainties prevent us from drawing specific conclu-
50 sions about the population impact of maternal effects. I use a simulation model to illus-
51 trate a range of realistic, potential consequences of the addition of a maternal effect. I
52 demonstrate that the expression of the maternal effect depends on the underlying pattern
53 of early life mortality rates. I identify four types of populations (Table 1) and show how
54 the same maternal effect can have a very different population impact in each of the pop-

55 ulations. I argue that to accurately predict the consequences of changing age-structure in
56 rockfish populations, we need to measure some basic features of the early life ecology.

57 I use two metrics to make this case: recruitment and time to recovery from an over-
58 fished state. Here, the term recruitment is used as it is in fisheries science; recruitment
59 occurs at the end of the juvenile period. The age of recruitment is defined as needed, al-
60 though vulnerability to fishing or reproductive maturity may be implied. Time to recovery
61 is a valuable metric because it integrates the entire history of a stock. Examining recovery
62 time allows us to overcome some of the limitations of considering recruitment alone.

63 **Maternal Effects in the Early Life History**

64 A maternal effect is defined as a non-genetic trait acquired from the mother (Lacey 1998).
65 An age-dependent maternal effect occurs when the acquisition of the trait depends on the
66 age of the mother. Working with *S. melanops* in laboratory tanks, Berkeley et al. (2004a)
67 demonstrated that larvae from older mothers grew 3–4 times faster and survived starva-
68 tion 2–3 times longer than larvae from younger mothers. In follow-up work, Sogard et al.
69 (2008) found either age or sized based maternal effects in larval oil globule volume (*S.*
70 *melanops*, *mystinus*, *flavidus*, and *carnatus*), parturition date (*S. melanops*, *mystinus*,
71 *flavidus*, and *atrovirens*), and weight specific fecundity (*S. mystinus* and *flavidus*). These
72 results, coupled with the high degree of similarity in reproductive physiology among rock-
73 fish, make it plausible that maternal effects are common in rockfish Love et al. (2002).

74 Rockfish have a bipartite life history, and they are live bearers who release larvae
75 fully formed into the pelagic environment. After several months, the larvae transition into

76 juveniles and settle into a benthic habitat (Figure 1). Mortality in the pelagic stage is
77 widely viewed to be density-independent (Ralston and Howard 1995, Hixon and Webster
78 (2002). However, in the benthic stage juveniles are faced with both density-independent
79 sources of mortality, such as the need to manage body temperature and locate food (Love
80 et al. 1991), and density-dependent sources of mortality, such as competition for shelter
81 space (Johnson 2006a) and density-cued predation (Adams and Howard 1996, Hobson et
82 al. 2001, Hixon and Jones 2005, Johnson 2006b).

83 Increases in weight specific fecundity should increase the rate of settlement (ϕ) by in-
84 creasing the initial number of larvae to enter the pelagic stage. Once in the pelagic stage,
85 larvae need to find food, avoid predators, avoid being swept offshore and maintain a body
86 temperature that is optimal for growth (Bakun 1996). All of these needs are facilitated by
87 the improved swimming ability that comes with larger body size. In this way, increased
88 larval oil globule volume and accelerated growth can both lead to increased body size and
89 then an increased settlement rate (ϕ). Additionally, large oil globule volume may extend
90 the amount of time the young larvae can survive before they must find food.

91 Furthermore, an early parturition date can lead to an early date of settlement (Pas-
92 ten et al. 2003), providing a refuge from competitive pressure during the initial benthic
93 stage and lowering the rate of density dependent mortality (γ). Additionally, accelerated
94 larval growth should lead to larger size at settlement (Pechenik et al. 1998, Shima and
95 Findlay 2002). As with larvae, the ability of juveniles to survive is improved by larger
96 body size. Larger juveniles are better able to manage their body temperature by managing
97 their depth, and they are better able to locate food, compete for shelter space and avoid
98 predators (Sogard 1997).

99 Previous analyses have modeled the impact of a maternal effect as equivalent to an
 100 increase in weight-specific fecundity (O’Farrell and Botsford 2006, Berkeley 2006). The
 101 model presented here diverges from this approach by incorporating stage structure and the
 102 potential for latent impacts on the benthic stage. There are two important reasons to con-
 103 sider the maternal effect on juvenile survival: (1) Variation in body size has a qualitatively
 104 different population impact in the pelagic and benthic stages because the benthic stage
 105 includes density-dependent processes. (2) In the past, much of the variation in pelagic sur-
 106 vival has been attributed to environmental variability (Ralston and Howard 1995) and not
 107 to variation in individual quality—i.e. it may be that the most important population im-
 108 pact of the maternal effect comes from its delayed impact on the benthic stage.

109 Methods

110 For convenience, I will use the term “maternal age” to refer to the age of an individual’s
 111 mother at the time of parturition.

112 To study productivity, I apply a multivariate Beverton-Holt stock-recruitment model
 113 developed to calculate recruitment in the presence of maternal effects (Lucero 2007). Re-
 114 cruitment is calculated by solving a system of differential equations for per-capita rate of
 115 mortality,

$$\text{diag}(\mathbf{n})^{-1} \frac{d\mathbf{n}}{d\tau} = -\boldsymbol{\mu} - \boldsymbol{\gamma}\mathbf{n} \quad (1)$$

116 where both \mathbf{n} and $\boldsymbol{\mu}$ are vectors of length a_{max} , and $\boldsymbol{\gamma}$ is a matrix of dimension $a_{max} \times$
 117 a_{max} . Here, $n_a(\tau)$ is the number of offspring with maternal age a at time τ , μ_a is the per-
 118 capita density-independent mortality rate of offspring with maternal age a , and γ_{aj} is the

119 per-capita density-dependent mortality rate of offspring with maternal age a due to their
 120 peers with maternal age j .

121 This system must be solved numerically and the solution requires the initial condi-
 122 tion

$$\mathbf{n} = \text{diag}(\boldsymbol{\phi})\mathbf{S} \quad (2)$$

123 where both \mathbf{S} and $\boldsymbol{\phi}$ are vectors of length a_{max} . Here, S_a is the spawning stock biomass of
 124 age a and ϕ_a is the rate of settlement per unit spawning stock biomass of age a .

125 Total recruitment, R , is the number of individuals summed across all of the maternal
 126 age classes at the end of the pre-recruitment period, T ,

$$R = \sum_a n_a(T) \quad (3)$$

127 I add a maternal effect by modeling the vector of rates with a sigmoidal curve, for example

$$\phi_a = \hat{\phi} \left(1 + \frac{p_\phi}{1 + e^{-c_\phi(a - a_{ME})}} \right) \quad (4)$$

128 where $\hat{\phi}$ is the baseline settlement rate, p_ϕ is percent increase in the settlement rate for the
 129 oldest mothers above the youngest mothers, c_ϕ controls how steeply the sigmoidal function
 130 increases, and a_{ME} is the inflection point of the sigmoid.

131 The most important parameter is p_ϕ , which effectively measures the strength of the
 132 maternal effect on the settlement rate. Similar sigmoidal functions are constructed for the
 133 two benthic mortality rates μ and γ . These are mortality rates, therefore the parameters
 134 p_μ and p_γ measure the percent *decrease* in the mortality rates due to the maternal effect.

135 When $p_\phi = p_\mu = p_\gamma = 0$, there is no maternal effect.

136 To examine the impact of a maternal effect on recruitment, I define the variable ΔR
 137 to be the relative change in recruitment due to a maternal effect.

$$\Delta R = \frac{R(\hat{\phi}, \hat{\mu}, \hat{\gamma} \mid p_\phi, p_\mu, p_\gamma) - R(\hat{\phi}, \hat{\mu}, \hat{\gamma} \mid p_\phi = p_\mu = p_\gamma = 0)}{R(\hat{\phi}, \hat{\mu}, \hat{\gamma} \mid p_\phi = p_\mu = p_\gamma = 0)} \quad (5)$$

138 While it is important to examine changes to recruitment, it can be difficult to assess the
 139 significance of these changes. In particular, the role of a maternal effect should be different
 140 in an overfished population with high productivity than an overfished population with low
 141 productivity. Additionally, recruitment is a function of the age-composition of the spawn-
 142 ing population. For simplicity, I have assumed a steady state age distribution for all of the
 143 recruitment calculations shown here, but this simplification limits the interpretability of
 144 these calculations. To overcome these complexities, I have defined the variable TTR , time
 145 to recovery from an overfished state. This metric is useful because it integrates across the
 146 entire history of a population and allows us to compare a single metric across numerous
 147 types of populations.

148 To calculate TTR , I simulate a population that begins with an arbitrary initial con-
 149 dition and is allowed to reach a steady-state biomass, also called the initial biomass. From
 150 the steady-state, the population is aggressively harvested until it reaches the overfish-
 151 ing threshold. The simulated population is then allowed to rebuild under various harvest
 152 rates. Finally, I measure the number of years the simulated population requires to recover
 153 (Figure 2).

154 The population simulation is age-structured. It includes length-based fishing mor-
 155 tality and natural mortality, von Bertalanffy growth and an age-based probability of ma-

156 turity. Wherever possible, parameters are based on the stock-assessment for *S. melanops*
 157 (Ralston and Dick 2003). Recruitment is calculated with the multivariate Beverton-Holt
 158 stock-recruitment function defined above. The simulation is entirely deterministic and
 159 *TTR* is capped at 100 years. A fully explicit description of the simulation is in Lucero
 160 (2008).

161 In the simulation, the overfishing threshold is defined as 15% of initial biomass (B_{15})
 162 and the recovery level is defined as 40% of initial biomass (B_{40}). For U.S. fisheries, if the
 163 biomass of a managed stock falls below the overfishing threshold, then a rebuilding plan
 164 is required by law. The overfishing threshold is set on a stock by stock basis as a function
 165 of the inherent productivity of the stock. These values tend to range between 10%–35% of
 166 initial biomass. Rebuilding plans for west coast rockfish use the rebuilding target of 40%
 167 of initial biomass (B_{40}), this is used as a proxy for the biomass that produces maximum
 168 sustainable yield (Haltuch et al. 2008, PFMC 2008).

169 Additionally, I define the variable ΔTTR to be the change in recovery time when a
 170 maternal effect is added:

$$\Delta TTR = TTR(\hat{\phi}, \hat{\mu}, \hat{\gamma} \mid p_{\phi}, p_{\mu}, p_{\gamma}) - TTR(\hat{\phi}, \hat{\mu}, \hat{\gamma} \mid p_{\phi} = p_{\mu} = p_{\gamma} = 0) \quad (6)$$

171 The relative metric ΔTTR allows us to consider changes independent of overall speed of
 172 population recovery.

173 Results

174 In Figures 3 and 4, I show solutions of the stock-recruitment model. Each of these time
175 series begin with the initial cohort of larvae released into the pelagic stage and concludes
176 with recruitment. There is a significant transition at the time of settlement. Pre-settlement
177 mortality is strictly density-independent, and thus linear, but post-settlement mortality
178 is a combination of density-independent and density-dependent processes, and thus non-
179 linear.

180 In Figure 3, I show outcomes for the *LH* case in the presence of a pelagic mater-
181 nal effect. All four time series use the exact same mortality rates for the benthic juvenile
182 stage. We can see that the benthic stage reduces variation among the four time series; this
183 is consistent with observations of rockfish in nature (Ralston and Howard 1995). Here, the
184 maternal effect causes large differences in the size of the settlement class, but these dif-
185 ferences are dampened by the high mortality in the benthic stage. In this case, a strong
186 pelagic maternal effect increases settlement by 160%, this yields a seemingly substantial
187 56% increase in recruitment, but adds only 270 recruits to the population.

188 In Figure 4, I show time series' for all four types of population with three examples
189 of a benthic maternal effect applied to each. Although I applied the same maternal effects
190 to each case, the effects have very different impacts. In the *HH* case, a maternal effect has
191 a very large impact on recruitment. The same maternal effect has only a moderate impact
192 on recruitment in the *HL* and *LH* cases, and almost no impact on the *LL* case.

193 A large settlement class does not necessarily lead to a large recruitment class. The
194 two cases where juvenile mortality is high (*LH* and *HH*) yield very similar recruitment
195 classes, despite large differences in size of the settlement class. However, in the two cases

196 where juvenile mortality is low (HL and LL), the size of the recruitment class is very close
197 to the size of the settlement class.

198 In Figure 5, I show the relative change to recruitment as a function of the magni-
199 tude of the maternal effect. Here, I have used the parameter p_γ , but the pattern is similar
200 for the other types of maternal effects parameters. When the effect is weak, there is little
201 difference among the population types. This is true even when the maternal effect creates
202 a non-negligible change to recruitment, e.g. a 12% increase in recruitment when $p_\gamma = 0.2$.
203 But as the magnitude of the effect increases, the differences among the populations grow
204 increasingly important. For example when $p_\gamma = 0.6$, ΔR is about twice as large for the
205 HH population as the LL population. The magnitude of ΔR depends first on the benthic
206 mortality rate and only secondarily on the settlement rate.

207 In Figure 6, I show time to recovery for the four population types. Each boxplot
208 summarizes eighteen calculations of TTR based on eighteen cases of the maternal effect.
209 Therefore, the trends are robust across our significant uncertainty about the maternal ef-
210 fect.

211 Similar to the recruitment values shown in Figure 4, populations with low settlement
212 and high post-settlement mortality (LH) are the least productive and populations with
213 a high settlement and low post-settlement mortality (HL) are the most productive. On
214 average, the least productive LH populations recover the slowest and the most productive
215 HL populations recover the fastest. Here, the settlement rate is the best predictor of the
216 rate of recovery. The benthic mortality rate is a secondary factor.

217 Finally in Figure 7, I show the change in time to recovery for the four types of pop-
218 ulations. The magnitude of ΔTTR depends first on the settlement rate, while the benthic

219 mortality rate is a secondary factor. The *LH* populations are prone to dramatic improve-
220 ments in recovery time with the addition of maternal effects. The improvements observed
221 in *LL* and *HH* populations are more modest, but can still yield significant improvements
222 of as many as twelve years.

223 The populations who recovery most quickly are of type *HL*. These do not generally
224 benefit from the addition of a maternal effect, and can actually take slightly longer to re-
225 cover with maternal effects. This is due to the high levels of competition associated with
226 the high juvenile densities in these populations. The addition of a subclass of juveniles
227 with superior competitive ability (due to their older mothers) serves to reduce the success
228 of the remaining majority of juveniles.

229 **Discussion**

230 Rockfish have a complex early life history that is representative of the early life history of
231 many marine fishes. Due to maternal effects, when we change the age-structure of these
232 populations we may also be changing the ecological properties of the larval cohorts being
233 produced. The two ecological properties of complex early life history and maternal effects
234 interact so that the consequences of the changed age-structure cannot be easily predicted.
235 To make confident predictions, we need to measure some basic properties of the early life
236 ecology. Specifically, we need to know the relative importance of the pelagic and larval
237 stages for survival.

238 We also know very little about the magnitude of the maternal effect themselves. In
239 my simulation analysis, I chose parameter values in the maternal effects model that pro-

240 duced realistic values for recruitment. Fortunately, it seems that these parameters do not
241 need to be known with very much precision; It is more important to know the context in
242 which the maternal effect plays out. For example, in Figure 4 the same maternal effect pa-
243 rameters applied to the four different population types produced a recruitment increase of
244 65% (*HH*), 22% (*LH*), 2.3% (*HL*) and 0.6% (*LL*).

245 Interestingly, we come to slightly different conclusions depending on how we choose
246 to frame the problem (Table 2). If we focus on recruitment success alone, we conclude that
247 the rate of juvenile mortality is the most important factor determining the impact of ma-
248 ternal effects on recruitment. However, if we are concerned with recovery time, we come
249 to the opposite conclusion. It is the settlement rate that drives the ability to recover from
250 overfishing, and juvenile mortality becomes the secondary factor.

251 In either case, we observe an inverse relationship between the effect size and the ba-
252 sic metric. In the case of recruitment, the two least productive populations (*LH* and *HH*)
253 are also the two most helped by the restoration of a maternal effect. In the case of recov-
254 ery time, there is a one to one inverse relationship between average speed of recovery and
255 the positive impact of restoring a maternal effect. It is those populations that are slowest
256 to recovery who stand the most to gain from the addition of maternal effects.

257 The general observation to be made is that for the maternal effect to be helpful, it
258 must resolve a problem that the fish actually have; i.e., a maternal effect that improves
259 survival of the pelagic stage is very important if pelagic survival is a limiting factor. How-
260 ever, if settlement is already high and recruitment is largely driven by dynamics in the
261 benthic stage, then such an effect would have little impact. Highly productive populations
262 are driven by competitive dynamics, and thus increasing survival rates only serves to in-

263 crease competition. This is useful for those individuals who are now more competitive, but
264 fails to improve overall cohort success.

265 The most productive populations are those that are least likely to be aided by the
266 addition of more old fish. Conversely, it is the least productive populations that are most
267 damaged by the removal of old fish. For example, the populations most aided by the restora-
268 tion of maternal effects are the *LH* type populations. These population have significant
269 room for improvement in both their rate of settlement and their rate of survival of the
270 benthic stage.

271 Maternal effects have significant populations impacts under a broad range of ecologi-
272 cal circumstances. This alone should draw the attention of fisheries managers, even in the
273 absence of more specific predictions. To be more specific, we require knowledge of the sur-
274 vival rates for the pelagic and benthic stages. These measurements will not only help us
275 specify the consequences of changing population age structure, they will also help us pre-
276 dict the consequences of many other dynamic features of fish ecology. Uncertainty of the
277 stock-recruitment relationship is a fundamental limiting factor in fisheries science. Better
278 knowledge of the early life ecology of fishes will improve our ability to predict the conse-
279 quences of a changing climate, changing ocean conditions, changing food webs and chang-
280 ing competitors.

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285 **References**

- 286 Adams, P. B. and D. F. Howard. 1996. Natural mortality of blue rockfish, *Sebastes mysti-*
287 *nus*, during their first year in nearshore benthic habitats. Fish. Bull., **94**:156–162.
- 288 Bakun, A. 1996. Patterns in the ocean: Ocean processes and marine population dynamics.
289 California Sea Grant College System, National Oceanic and Atmospheric Administration
290 in cooperation with Centro de Investigaciones Biologicas del Noroeste.
- 291 Berkeley, S. 2006. Pacific rockfish management: are we circling the wagons around the
292 wrong paradigm? Bull. Mar. Sci., **78**:655–667.
- 293 Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004*a*. Maternal age as a determinant of
294 larval growth and survival in a marine fish, *Sebastes melanops*. Ecology, **85**:1258–1264.
- 295 Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004*b*. Fisheries sustainability
296 via protection of age structure and spatial distribution of fish populations. Fisheries,
297 **29**:23–32.
- 298 Haltuch, M., A. Punt, and M. Dorn. 2008. Evaluating alternative estimators of fishery
299 management reference points. Fisheries Research, **in press**.
- 300 Hixon, M. A. and G. P. Jones. 2005. Competition, predation, and density-dependent mor-
301 tality in demersal marine fishes. Ecology, **86**:2847–2859.

- 302 Hixon, M. A. and M. S. Webster. 2002. Density dependence in reef fish populations. In
303 P. F. Sale, editor, Coral Reef Fishes. Academic Press, San Diego.
- 304 Hobson, E. S., J. R. Chess, and D. F. Howard. 2001. Interannual variation in predation on
305 first-year *Sebastes* spp. by three northern california predators. Fish. Bull., **99**:292–302.
- 306 Johnson, D. W. 2006a. Density dependence in marine fish populations revealed at small
307 and large spatial scales. Ecology, **87**:319–325.
- 308 Johnson, D. W. 2006b. Predation, habitat complexity, and variation in density-dependent
309 mortality of temperate reef fishes. Ecology, **87**:1179–1188.
- 310 Lacey, E. P. 1998. What is an adaptive environmentally induced parental effect? In T. A.
311 Mousseau and C. W. Fox, editors, Maternal Effects as Adaptations, pages 54–66. Oxford
312 University Press, New York.
- 313 Love, M. S., M. H. Carr, and L. J. Haldorson. 1991. The ecology of substrate-associated
314 juveniles of the genus *Sebastes*. Environ. Biol. Fishes., **30**:225–243.
- 315 Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. The rockfishes of the northeast
316 Pacific. University of California Press, Berkeley.
- 317 Lucero, Y. 2007. Population consequences of an age-dependent maternal effect in rockfish
318 (genus *Sebastes*). Ph.D thesis in Ocean sciences, University of California Santa Cruz,
319 1156 High Street, Santa Cruz CA 95064.
- 320 Lucero, Y. 2008. Maternal effects and time to recovery. Bulletin of Marine Science, **83**.

- 321 O'Farrell, M. R. and L. W. Botsford. 2006. The fisheries management implications of
322 maternal-age-dependent larval survival. *Can. J. Fish. Aquat. Sci.*, **63**:2249–2258.
- 323 Palumbi, S. R. 2004. Fisheries science—why mothers matter. *Nature*, **430**:621–622.
- 324 Pasten, G. P., S. Katayama, and M. Omori. 2003. Timing of parturition, planktonic du-
325 ration, and settlement patterns of the black rockfish, *Sebastes inermis*. *Environmental*
326 *Biology Of Fishes*, **68**:229–239.
- 327 Pechenik, J. A., D. E. Wendt, and J. N. Jarrett. 1998. Metamorphosis is not a new begin-
328 ning. *BioScience*, **48**:901–910.
- 329 PFMC. 2008. Pacific coast groundfish fishery management plan for the California, Ore-
330 gon and Washington groundfish fishery as amended through amendment 17. URL
331 www.pcouncil.org.
- 332 Ralston, S. and E. J. Dick. 2003. The status of black rockfish (*Sebastes melanops*) off Ore-
333 gon and northern California in 2003. Technical report, SWFSC, NOAA.
- 334 Ralston, S. and D. F. Howard. 1995. On the development of year-class strength and cohort
335 variability in 2 northern California rockfishes. *Fish. Bull.*, **93**:710–720.
- 336 Shima, J. S. and A. M. Findlay. 2002. Pelagic larval growth rate impacts benthic settle-
337 ment and survival of a temperate reef fish. *Mar. Ecol. Prog. Ser.*, **235**:303–309.
- 338 Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A re-
339 view. *Bulletin of Marine Science*, **60**:1129–1157.

- ³⁴⁰ Sogard, S. M., S. A. Berkeley, and R. Fisher. 2008. Maternal effects in rockfish (*Sebastes*
³⁴¹ spp.): a comparison among species. *Mar. Ecol. Prog. Ser.*, **360**:227–236.

Table 1: Definitions of the four types of populations being compared

	<i>HH</i>	<i>HL</i>	<i>LH</i>	<i>LL</i>
settlement rate	high	high	low	low
juvenile mortality rate	high	low	high	low
$\hat{\phi}$	2	2	0.5	0.5
$\hat{\mu}$	0.01	0.001	0.01	0.001
$\hat{\gamma}$	5e-6	1e-7	5e-6	1e-7
recruitment with no effect	864	7,488	485	1,989

Table 2: Comparison of average metric rankings for each population type.

R	more productive	$HL > LL > HH > LH$	less productive
ΔR	less benefit	$LL < HL < LH < HH$	more benefit
TTR	faster recovery	$HL < HH < LL < LH$	slower recovery
ΔTTR	less benefit	$HL > HH > LL > LH$	more benefit

342 **Figure Legends**

343 **Figure 1** Schematic of the stage-structured stock-recruitment model. The age-composition
344 of the spawning stock biomass is used to calculate the number of larvae to enter the pelagic
345 stage. The maternal age composition of the larval cohort is used to calculate the number
346 of larvae that survive to become juveniles. The maternal age composition of the juvenile
347 cohort is used to calculate how many individuals recruit.

348 **Figure 2** An example time series from the population simulation. The simulated popu-
349 lation begins at an arbitrary initial condition and runs until it reaches a steady-state. Ag-
350 gressive harvest is applied until the population falls below the overfishing threshold, B_{15} .
351 Fishing pressure is reduced to recover the population to the rebuilding target, B_{40} . The
352 dashed lines show recovery trajectories under various fishing levels. This is an *HH* type
353 population with no maternal effect.

354 **Figure 3** A time series of numbers of pre-recruits in the presence and absence of a ma-
355 ternal effect on the pelagic stage. The examples shown are for an LH type population (de-
356 fined in Table 1) and three example maternal effects. Note the break in the *y*-axis.

357 **Figure 4** A time series of numbers of pre-recruits in the presence and absence of a ma-
358 ternal effect on the benthic stage. Three examples of a maternal effect are shown applied
359 to four types of populations (defined in Table 1). Note the break in the *y*-axis.

360 **Figure 5** Relative change in recruitment after the addition of a maternal effect as a
361 function of the strength of the effect. The four types of populations are defined in Table

362 1. $p_\phi = 1$ and $p_\mu = 0$.

363 **Figure 6** Boxplots of time to recovery for eighteen different examples of a maternal ef-
364 fect applied to the four population types.

365 **Figure 7** Boxplots of change in time to recovery for eighteen different examples of a ma-
366 ternal effect applied to the four population types.

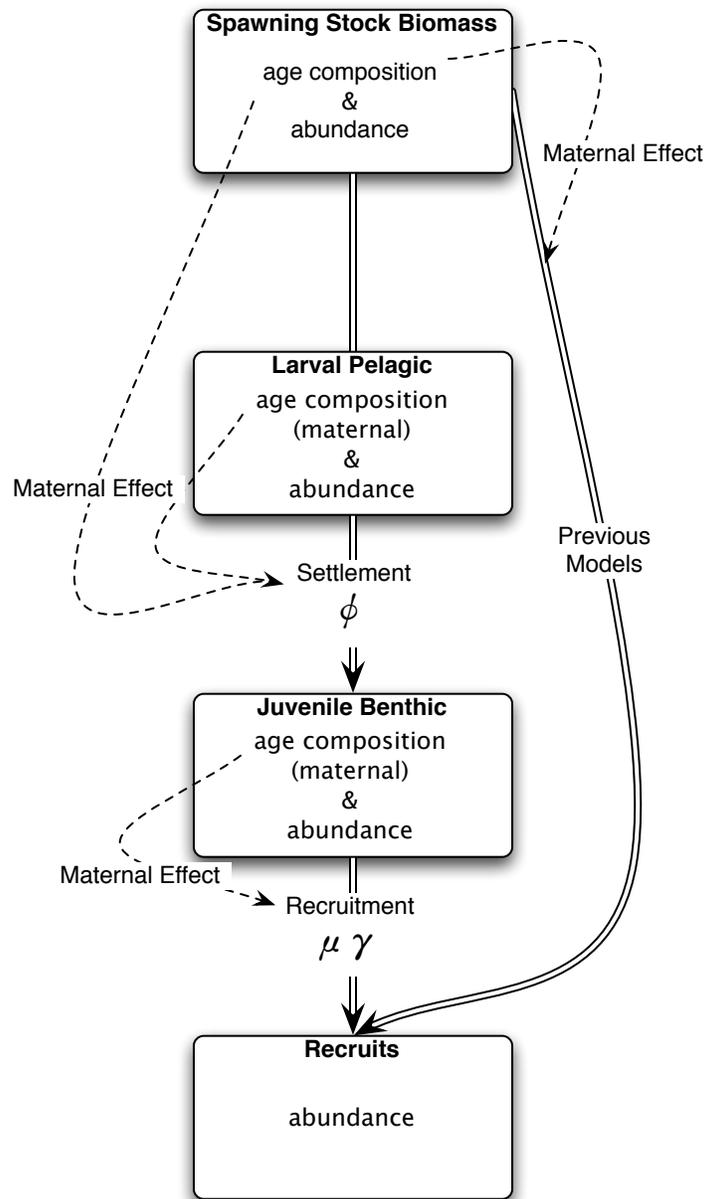


Figure 1

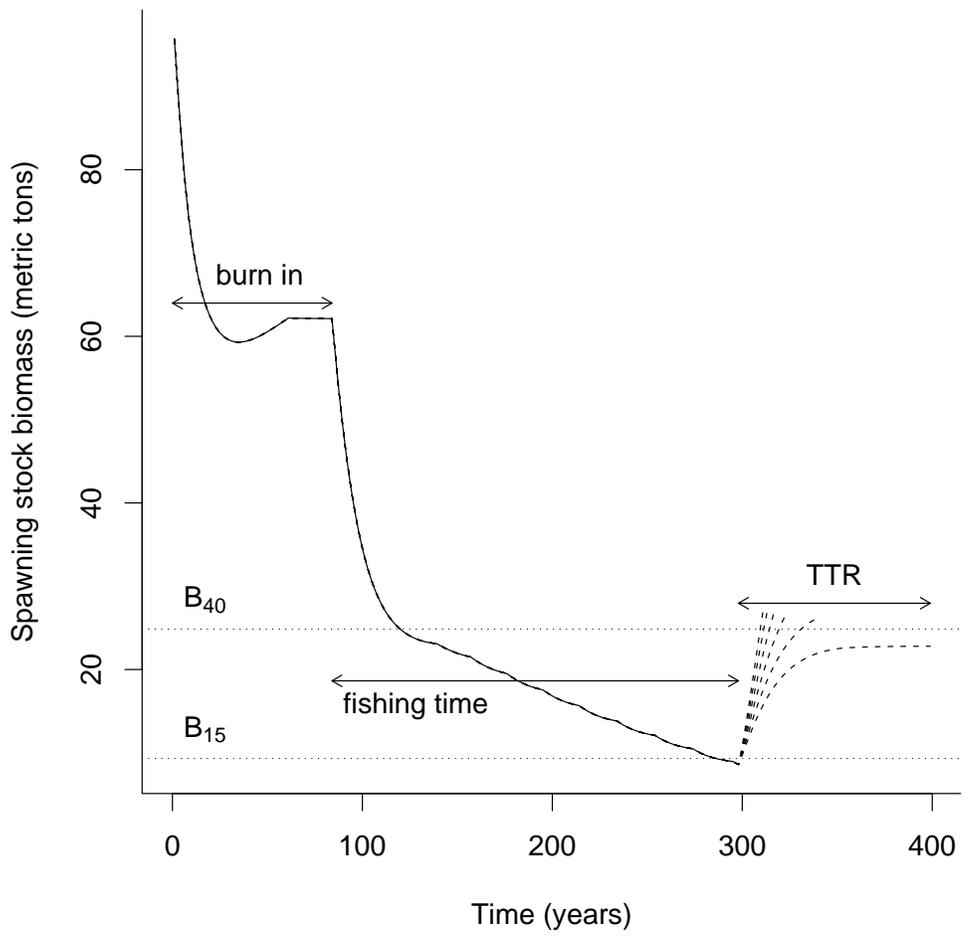


Figure 2

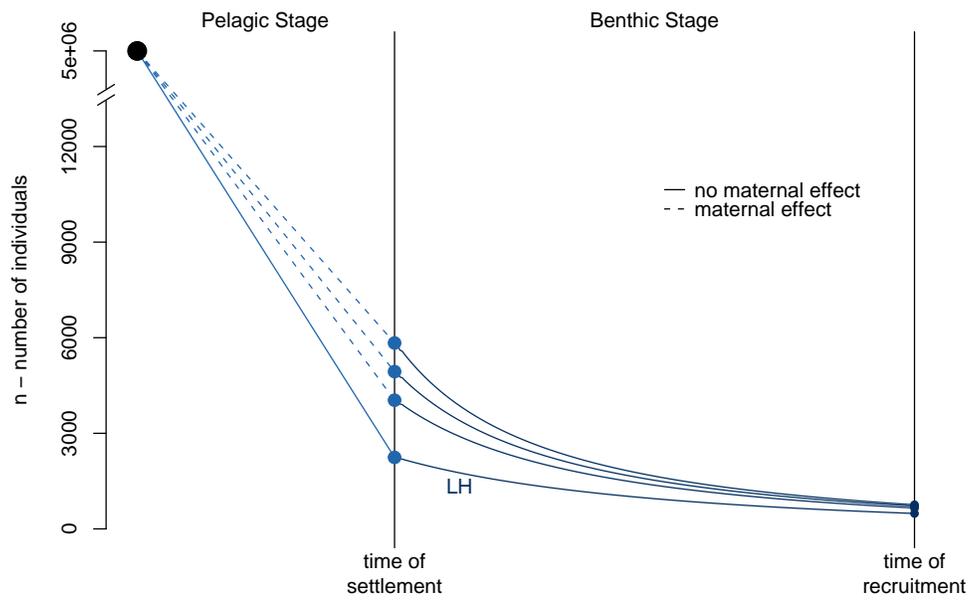


Figure 3

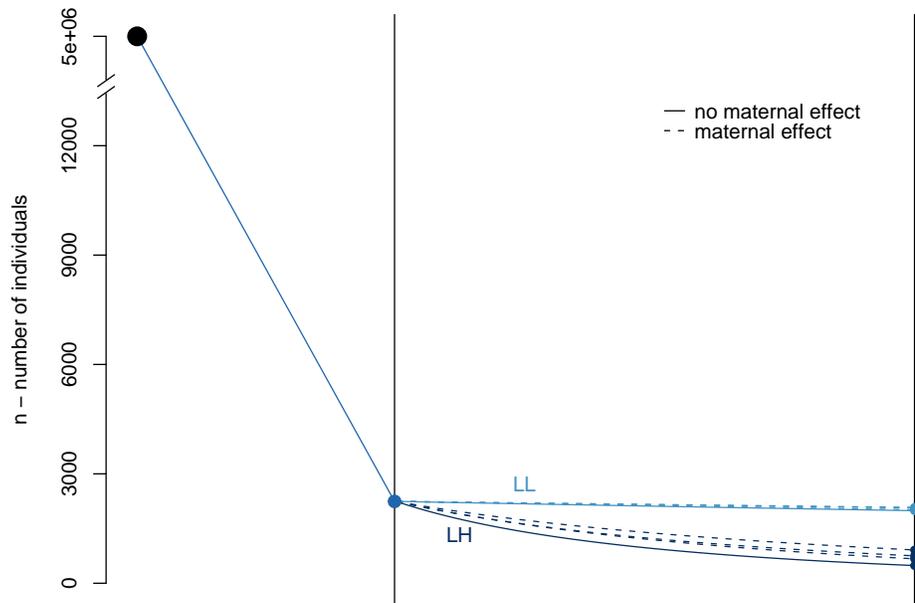
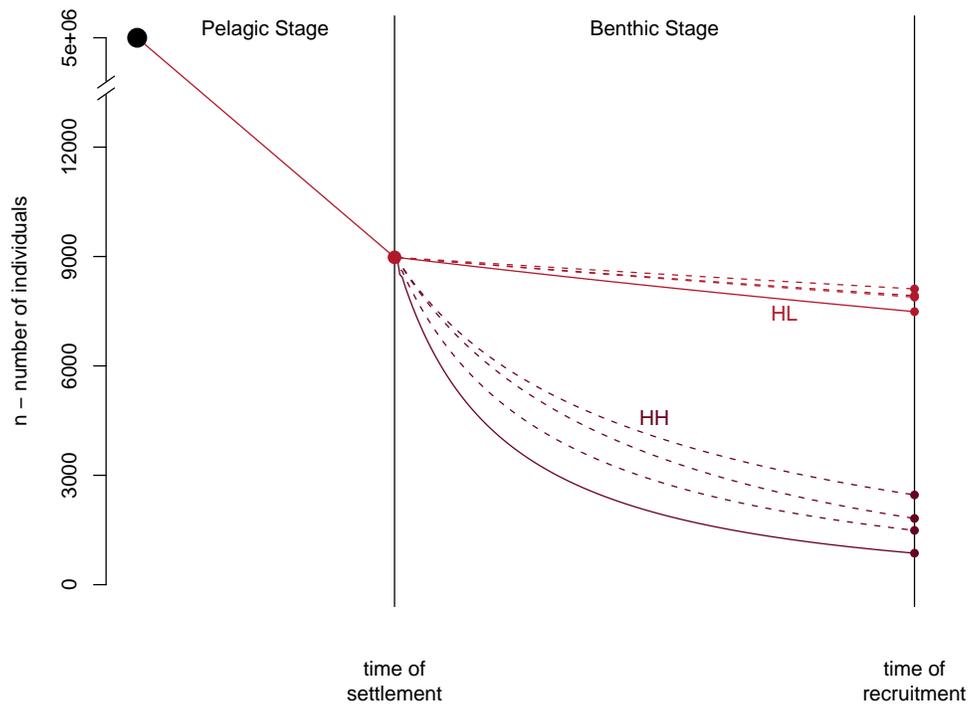


Figure 4

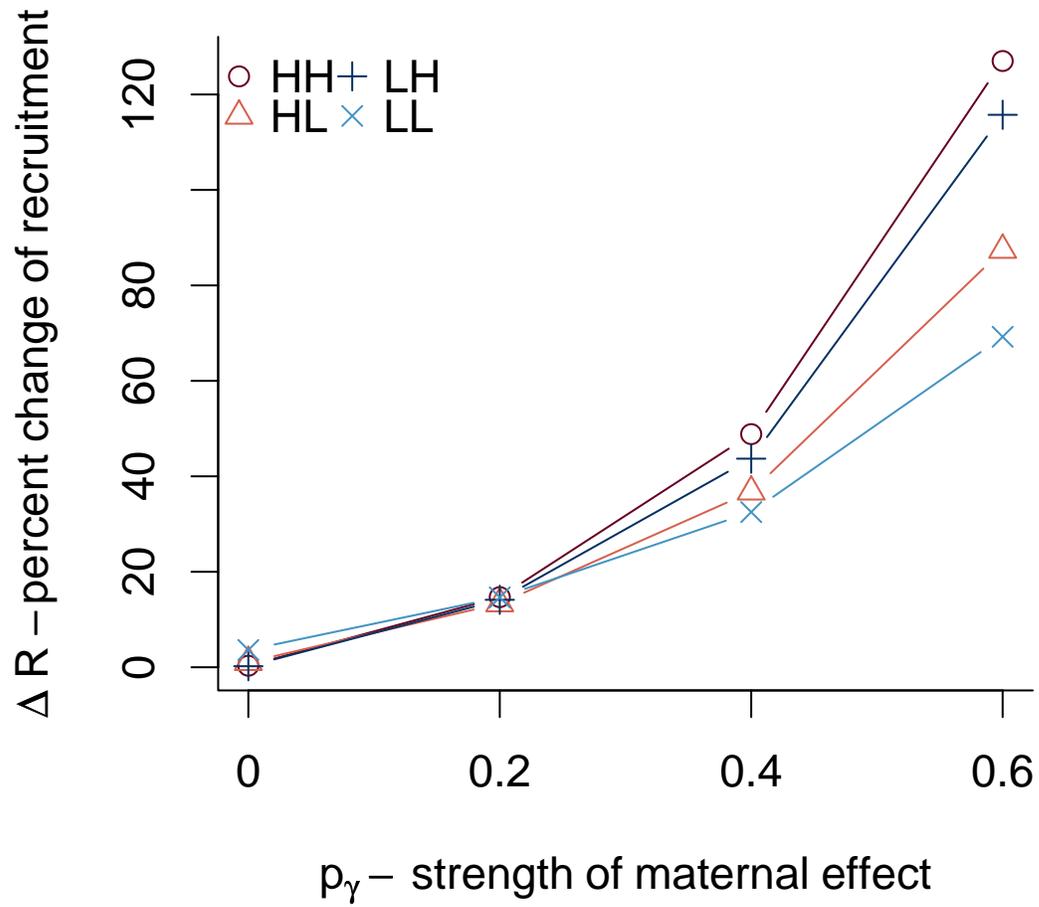


Figure 5

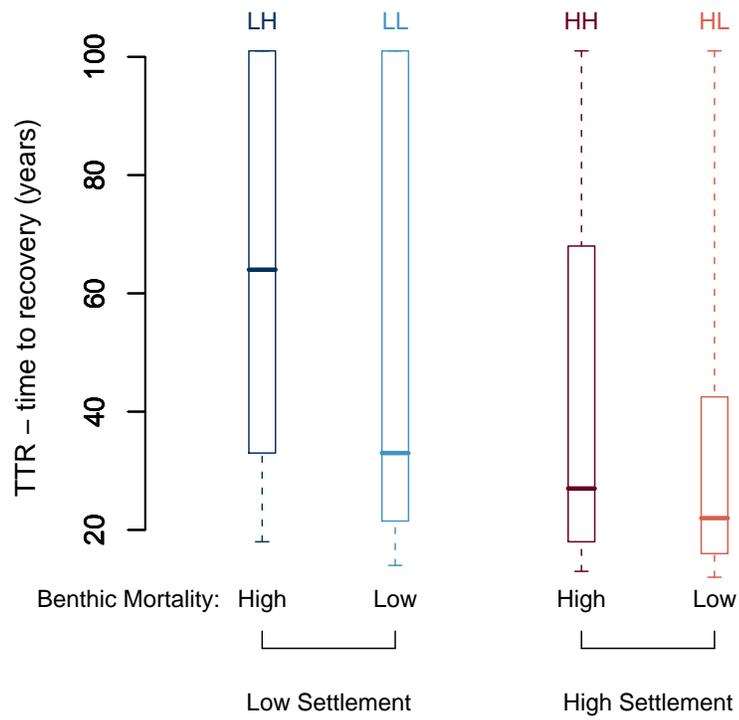


Figure 6

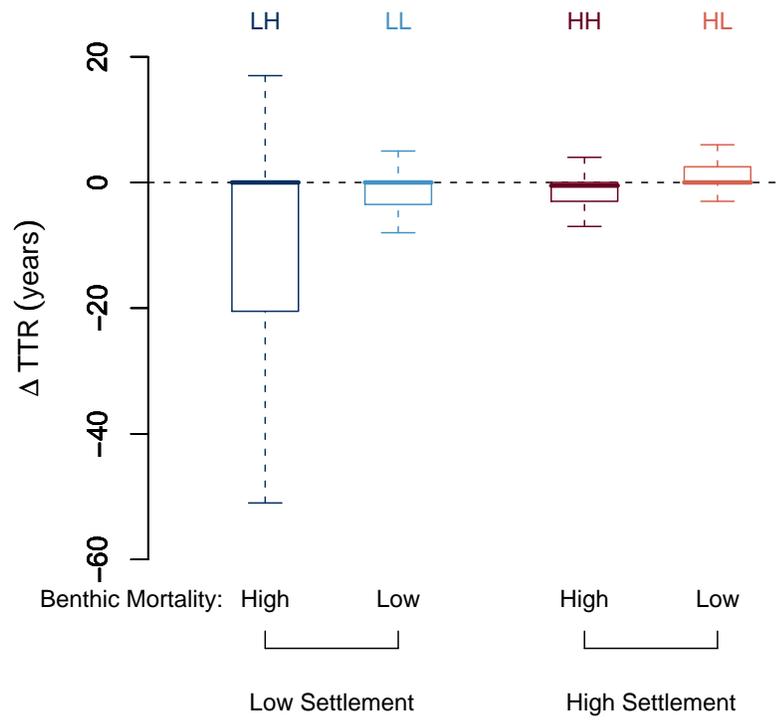


Figure 7