

# Management of an Annual Fishery in the Presence of Ecological Stress: The Case of Shrimp and Hypoxia

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# Management of an Annual Fishery in the Presence of Ecological Stress: The Case of Shrimp and Hypoxia

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## Abstract

The emergence of ecosystem-based management suggests that traditional fisheries management and protection of environmental quality are increasingly interrelated. Fishery managers, however, have limited control over most sources of marine and estuarine pollution and at best can only adapt to environmental conditions. We develop a bioeconomic model of optimal harvest of an annual species that is subject to an environmental disturbance. We parameterize the model to analyze the effect of hypoxia (low dissolved oxygen) on the optimal harvest path of brown shrimp, a commercially important species that is fished in hypoxic waters in the Gulf of Mexico and in estuaries in the southeastern United States. We find that hypoxia alters the qualitative pattern of optimal harvest and shifts the season opening earlier in the year; more severe hypoxia leads to even earlier season openings. Failure to adapt to hypoxia leads to greater losses when the effects of hypoxia are more severe. However, rent gains from adapting fishery management to hypoxia are relatively small compared to rent losses from the hypoxia effect itself. This suggests that it is critical for other regulatory agencies to control estuarine pollution, and fishery managers need to generate value from the fishery resources through other means such as rationalization.

**Keywords:** bioeconomics; hypoxia; adaptive policy; ecosystem-based management

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## 20 1 Introduction

21 With the current shift towards ecosystem-based management, traditional natural resource  
22 management and protection of environmental quality are increasingly interrelated. Environ-  
23 mental quality affects the productivity of the natural resource base, and resource extraction  
24 can influence environmental quality. In spite of these feedbacks, natural resource extraction  
25 and environmental quality are typically managed by different agencies.

26 For fisheries resources, managers often have little or no control over environmental quality.  
27 Of particular importance for many fisheries is the degradation of estuarine habitat in which  
28 many fish spend critical life stages. Estuaries often experience hypoxia (low dissolved oxygen)  
29 and other environmental disturbances due to nutrient pollution from agricultural runoff and  
30 atmospheric deposition from fossil fuel combustion (NRC 2000). Hypoxia, in turn, can lead  
31 to juvenile mortality and a range of sub-lethal effects that have growth consequences. Several  
32 recent studies document the deleterious effects of hypoxia on fishery productivity by analyzing  
33 micro-level data from fishermen (Huang et al. 2010; Massey et al. 2006; Lipton and Hicks 2003).  
34 These studies quantify the increased value to the fishery from improved environmental quality,  
35 but they presume that a regulator would be able to influence pollution. Unfortunately, fishery  
36 managers cannot control the flows of nutrients into estuaries and can only react to pollution  
37 levels. In this paper, we explore how fishery managers can set optimal harvest policies that  
38 condition on fluctuating environmental conditions in estuaries.

39 Previous bioeconomic studies have examined related issues but have not considered how  
40 environmental conditions may influence harvest rates within a season. In a theoretical study,  
41 McConnell and Strand (1989) demonstrate that optimal management of the fishery is necessary  
42 to capture gains from water quality improvements. They compare only steady states under  
43 open access and optimal management. In a similar vein, Smith (2007) develops a bioeconomic  
44 model calibrated to the North Carolina blue crab fishery. He analyzes the full dynamic path  
45 of fishery rents and shows that gains from reduced hypoxia are higher when the fishery is  
46 rationalized. However, these gains are dwarfed by the gains from rationalization even with  
47 no water quality improvements. Most recently, Carson et al. (2009) theoretically model opti-  
48 mal harvest under cyclical population dynamics. They show that when ENSO cycles induce  
49 periodically fluctuating growth rates, optimal harvest is asynchronous with the ENSO cycle.  
50 Although they address related problems, these studies do not analyze within-season dynam-

51 ics, which are likely to be especially important for annual fisheries such as shrimp and squid;  
52 the size structure and hence available biomass for harvest of an annual species change dramati-  
53 cally over the course of a year. In this paper, we examine specifically how the path of optimal  
54 management changes in the presence of hypoxia.

55 We analyze the brown shrimp fishery. Brown shrimp (*Farfantepenaeus aztecus*) is one of  
56 the largest fisheries in the U.S. with nominal ex vessel landings over the past decade rang-  
57 ing from over \$156 million to nearly \$377 million.<sup>1</sup> Moreover, brown shrimp are fished in  
58 areas that experience seasonal hypoxia, most notably in the Gulf of Mexico. Like other shrimp  
59 species, brown shrimp have an annual life cycle and a weak stock recruitment relationship,  
60 i.e. recruitment is virtually uncorrelated with the previous years' stock. As a result of these  
61 reproductive features, shrimp are managed with seasonal closures rather than total allowable  
62 catches. Nonetheless, our results indicate that there are opportunities to design more efficient  
63 harvest policies by adjusting season closures to take environmental disturbances into consid-  
64 eration.

65 We develop a size-structured bioeconomic model that accounts for growth and aging of  
66 brown shrimp based on Clark (1990). We incorporate the effect of hypoxia directly into shrimp  
67 growth. In a numerical illustration, we calibrate the level of hypoxia to recent empirically-  
68 based growth effects from hypoxia in the Neuse River in North Carolina (Huang et al. 2010).  
69 Our results show that fishery managers should open the shrimp season earlier in years with  
70 more severe hypoxia. In a pristine year, there is a larger payoff from waiting to open the  
71 season and allowing shrimp to grow larger. However, greater environmental stress increases  
72 the opportunity cost of waiting. Moreover, the benefits of adaptating fishery management to  
73 hypoxia are greater when the effects of hypoxia are more severe.

## 74 **2 The Model**

75 In this section, we develop a stylized bioeconomic model to consider the optimal harvest strat-  
76 egy of an annual species in the presence of an environmental disturbance. Our motivating ex-  
77 ample and numerical results are based on brown shrimp subjected to hypoxia, but our model  
78 could apply more broadly to other annual species like squid and other seasonally varying pol-  
79 lution problems. Brown shrimp have annual life cycles, usually spawning in spring with very

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<sup>1</sup>See <http://www.st.nmfs.noaa.gov/st1/commercial/index.html>.

80 high fecundity rates and completing their life cycles in winter in deep offshore areas. How-  
 81 ever, they spend most of their lives growing in estuarine and inshore areas where many shrimp  
 82 fisheries occur. The features of annual life cycles and extremely high fecundity rates imply that  
 83 the annual shrimp stock recruitment could be regarded as being independent of the previous  
 84 year's stock and harvest. As such, it is reasonable to assume exogenous recruitment. We de-  
 85 rive the optimal policy from the perspective of a social planner and the planner's objective is  
 86 to choose the harvest path to maximize the total present value profits from harvesting.

## 87 2.1 The problem of optimal Harvest

88 Let  $p(t)$  indicate the price of fish per unit at time  $t$  and  $Q(t)$  be the harvest in weight at time  $t$ .  
 89 Let  $C$  denote the cost function depending on effort at time  $t$  ( $E(t)$ ). Then the social planner's  
 90 problem can be formally described as:

$$\max_{\{E(t)\}} \int_0^T (p(t) * Q(E(t), X(t)) - C(E(t)))e^{-rt} dt \quad (1)$$

$$s.t. \dot{X}(t) = f(X(t), t) - Q(t) \quad (2)$$

91 This equation illustrates that the planner is to maximize the total present value profits by  
 92 choosing the optimal effort path between 0 and  $T$  (a maximum time after which individuals  
 93 are dead or highly dispersed), where  $r$  is the instantaneous discount rate. The constraint de-  
 94 scribes the stock ( $X(t)$ ) dynamics consisting of a growth component ( $f(X(t), t)$ ) and harvest  
 95 ( $Q(t)$ ). Combining biological models for annual species (Fontaine and Neal, 1971; McCoy,  
 96 1968; Minello et al. 1989) and bioeconomic models for the hypoxia effect (Huang et al. 2010),  
 97 we can specify stock dynamics as the following:

$$\dot{X}(t) = X(t)[-m(t) - \phi A(t) + \frac{W(t)}{W(t)}] - Q(t) \quad (3)$$

98 Unlike the canonical bioeconomic model of the fishery that gives rise to the Fundamen-  
 99 tal Equation of Renewable Resource Economics (Clark and Munro 1975; Conrad 1999), this  
 100 state equation is non-autonomous and the stock dynamics are directly influenced by ecologi-  
 101 cal stress. Appendix A provides a detailed description of how this equation is developed, but

102 it is worth noting some details here. First, the natural mortality rate,  $m(t)$ , is time-dependent.  
 103 This feature can account for the fact that, *ceteris paribus*, smaller fish have more predators than  
 104 larger ones. Second,  $W(t)$  is the fish weight per individual. Although our model describes a  
 105 single cohort, we still must track how the cohort grows within the season. Third,  $\phi A(t)$  is the  
 106 instantaneous effect of environmental stress on stock dynamics. Like natural mortality, the  
 107 effect of environmental stress is proportional to stock size and time-dependent. This specifica-  
 108 tion allows for lethal effects such that the environmental stress increases natural mortality, but  
 109 it also accounts for sub-lethal effects. For example, environmental stress such as hypoxia can  
 110 reduce growth because animals expend energy avoiding low oxygen areas (Craig and Crow-  
 111 der 2005). A virtue of our specification is that one can use an empirical estimate of the total  
 112 effect of stress on the population without having to distinguish the lethal and sub-lethal effects  
 113 from observational data (something that has not been done in the literature on hypoxia).

114 Following Huang et al. (2010),  $A(t)$  is a binary indicator of whether there is environmental  
 115 stress (1 if stress exists at time  $t$  and 0 otherwise). For our case study of hypoxia,  $A(t)$  is coded  
 116 1 if bottom dissolved oxygen is below  $2 \text{ mg l}^{-1}$  (the standard measure of hypoxia). The coeffi-  
 117 cient,  $\phi$ , is the marginal effect of environmental stress on the fish stock. Note that we measure  
 118 the total stress effect by integrating stress events over time because they have a cumulative  
 119 effect (See Equation 18 in Appendix A). The intuition for a cumulative effect is the same as  
 120 having a dose-response relationship for a toxin or a carcinogen. Because the instantaneous  
 121 effect is the product of this constant and the occurrence of stress, the instantaneous effect is  
 122 time-dependent. In the analytical model and in our numerical simulations, we treat  $A(t)$  as if  
 123 it is known throughout the planning period. This is a simplification in order to gain analytical  
 124 and numerical insights about the potential for managers to adapt to environmental stresses. In  
 125 reality, managers would not know the exact timing of episodic environmental stresses like hy-  
 126 poxia *ex ante*, but they can often predict the seasonal concentration of stress events. Relaxing  
 127 the assumption of a deterministic  $A(t)$  could be a fruitful direction for future research.

128 Furthermore, we specify the catch and cost functions with standard assumptions from the  
 129 literature. More specifically,

$$Q(t) = q * E(t) * X(t) \tag{4}$$

130 where  $q$  is a constant, called the catchability coefficient. For the cost function, we assume that  
 131 the total cost is proportional to the effort:

$$C(t) = c * E(t) \quad (5)$$

132 In this expression,  $c$  is a positive constant. With all the expressions of the profit structure  
 133 and stock dynamics, we can fully characterize the social planner's problem in the following:

$$\begin{aligned} \max_{\{E(t)\}} \int_0^T (p(t)qE(t)X(t) - cE(t))e^{-rt} dt \quad (6) \\ \text{s.t. } X\dot{(t)} = X(t) * (-m(t) - \phi A(t) + \frac{W\dot{(t)}}{W(t)}) - qE(t)X(t) \\ m(t) = \beta(L(t))^\rho \\ W(t) = \omega L(t)^\eta \\ L(t) = L_\infty(1 - e^{\delta t}) \\ 0 \leq E(t) \leq \bar{E} \\ N_0 \text{ known} \end{aligned}$$

134 Where  $L(t)$  is the fish length,  $L_\infty$  is the maximum length and  $N_0$  is the initial stock number.  
 135 The biological equations and parameters are introduced and defined in the Appendix A.  $\bar{E}$  is  
 136 the capacity limit for each day's effort; i.e. the effort level is never greater than this limit. Note  
 137 that we use a finite-horizon model to characterize the annual fishery.

## 138 2.2 The solution to the social planner's problem

139 In this section, we derive the solution to the annual fishery in the presence of ecological stress.  
 140 With the model specification in the social planner's problem (Equation 6), the solution is the  
 141 admissible path  $\{E(t), X(t)\}$  that maximizes the total present value profit, where  $E(t)$  is the  
 142 control variable and  $X(t)$  is the state variable. As a practical matter, what comes out of the  
 143 optimization as well are season opening and closing times,  $T_0$  and  $T_1$  respectively, but it is  
 144 unnecessary to model them as choice variables.

145 We can use the current value Hamiltonian to derive the necessary conditions for the op-

146 timal paths of stock and effort. Let  $g(t)$  denote the expression for the non-autonomous stock  
 147 dynamics  $-m(t) - \phi A(t) + \frac{W(t)}{W(t)}$ . The current value Hamiltonian is:

$$\tilde{H} = p(t)qE(t)X(t) - cE(t) + \lambda(t)X(t) * (g(t) - qE(t)) \quad (7)$$

148 The current-value co-state variable  $\lambda(t)$  represents the shadow value of additional stock,  
 149 i.e. the benefit of increasing the stock marginally. Note that the Hamiltonian is linear in the  
 150 control. As a result, the first necessary condition is:

$$\frac{\partial \tilde{H}}{\partial E} = p(t)qX(t) - c - \lambda(t) * qX(t) = \sigma(t) \quad (8)$$

151 where  $\sigma(t)$  is the switching function as defined in Clark (1990). The problems in which the  
 152 Hamiltonian is linear in the control are characterized by a bang-bang solution such that the  
 153 control is at the maximum level, the minimum level, or follows a singular path (Spence and  
 154 Starrett 1975; Clark 1990). For our problem, the bang-bang solution is:

$$E(t)^* = \begin{cases} 0 & \text{if } \sigma(t) < 0 \\ E^{singular} & \text{if } \sigma(t) = 0 \\ \bar{E} & \text{if } \sigma(t) > 0 \end{cases} \quad (9)$$

155 where a '\*' indicates the optimal path. Although our problem is non-autonomous, the intuition  
 156 is the same as in other bioeconomic models in which stock growth and catch are balanced to  
 157 maximize total present value benefits. Analyzing Equations 8 and 9 together, if the co-state  
 158 variable is too high, we are better off allowing the stock to grow by not harvesting (exerting no  
 159 effort). If the co-state variable is too low, we are better off harvesting at the maximum rate.

160 In addition to Equation 8, a second necessary condition (by Pontryagin's Maximum Prin-  
 161 ciple) is:

$$\dot{\lambda}(t) - r\lambda(t) = -p(t)qE(t) - \lambda(t)[g(t) - qE(t)] \quad (10)$$

162 We also require the following transversality condition:

$$\lambda(T) = 0 \tag{11}$$

163 Lastly, because our environmental stress variable  $A(t)$  is not continuous, we require addi-  
164 tional conditions. Specifically, following Caputo (2005), we require:

$$\lambda^*(\tau^-) = \lambda^*(\tau^+) \tag{12}$$

165 where  $\tau$  is a switch point in  $A(t)$ . See Tomiyama (1985) Theorem 1, Remark 4 for a detailed  
166 treatment of this issue. Because  $A(t)$  is piecewise continuous, i.e. it is defined at every point  
167 along a continuous interval, Equation 12 holds at every switch point. Intuitively, by integrating  
168 Equation 10, the jumps in  $g(t)$  become kinks such that continuity holds. The optimal policy is  
169 the triplet  $\{X^*(t), E^*(t), \lambda^*(t)\}$  that solves equations 3, 8, and 10 by implementing the control  
170 rule in Equation 9 with the requirement that equations 11 and 12 hold. Pragmatically, this  
171 amounts to solving a system of ordinary differential equations (ODEs) in a piecewise fashion  
172 throughout the planning horizon.

173 For our particular problem, the optimal solution is characterized by three intervals:  $[0, T_0]$ ,  
174  $(T_0, T_1]$ ,  $(T_1, T)$ . The season is closed until time  $T_0$ . Then the season opens and maximum effort  
175 is exerted from  $T_0$  to  $T_1$ . Then the season closes and no more effort is exerted. Appendix B pro-  
176 vides analytical details and a description of our numerical routines. In addition to solving the  
177 ODEs for each combination of parameters in Matlab, we also discretize the problem and solve  
178 for the optimal path using Matlab's constrained optimization routine (FMINCON). The lat-  
179 ter is computationally intensive but produces the same results with only minor discrepancies  
180 from the discretization.

### 181 **3 Materials and numerical results**

182 In this section, we first use the known parameters for shrimp growth and real hypoxia data  
183 in the Neuse River of North Carolina to illustrate the optimal harvest path for brown shrimp.  
184 Then, using numerical simulations, we calculate the efficiency loss for the cases when the

185 policy has not taken hypoxia into account. The parameters in Equations 14 to 16 in Appendix  
186 A for brown shrimp are available in the scientific literature. Table 1 lists the parameter values  
187 and sources we use for the simulations. Among these parameters, the constant exponential  
188 discount rate is set to be 0.0005. Thus the daily discount rate is 0.05%, and the annual discount  
189 rate is about 17%.

190 The hypoxia data we use are collected by the USGS (The United States Geological Survey)  
191 for the Neuse River estuary. This area experiences moderate to severe and recurring hypoxia,  
192 mostly in the summer months, causing fish kills and other negative ecological damage (Paerl  
193 et al.1998, Lenihan et al. 2001, Eby et al. 2005). The USGS data record measurements of bot-  
194 tom and top dissolved oxygen and other water quality variables every 15 minutes from three  
195 moorings in the Neuse River. Since shrimp live near the bottom, we create the daily bottom  
196 dissolved oxygen values by taking an average of each day's bottom dissolved oxygen mea-  
197 surements from three moorings. However, these continuous dissolved oxygen values cannot  
198 be directly used since laboratory experiments show that a tolerable lower bound is a thresh-  
199 old for shrimp's normal growth. Specifically, Renaud (1986) shows that brown shrimp avoid  
200 areas with levels  $< 2 \text{ mgl}^{-1}$ . Therefore, we use  $2 \text{ mgl}^{-1}$  as a threshold to indicate whether it is  
201 a hypoxic day. Mathematically, if the daily dissolved oxygen measurement is  $< 2 \text{ mgl}^{-1}$ , the  
202 hypoxia indicator ( $A(t)$ ) is 1, otherwise 0. The average number of hypoxic days from 1999 to  
203 2005 is 61 days per year. We use 2004 hypoxia data since it is the worst hypoxia year between  
204 1999 and 2005 so that we can see the worst hypoxia effects in these years.

205 Before we analyze the hypoxia effect on the optimal harvest strategy, we first derive the  
206 optimal strategy when there is no hypoxia. Figure 3 shows the optimal harvest and stock  
207 paths with different parameter values. The optimal effort level is a constant over time and  
208 equal to the capacity limit ( $\bar{E}$ ) for these parameter values. The three panel rows in Figure 3  
209 describe three different scenarios with alternative catchability coefficients ( $q$ ), marginal cost  
210 coefficients ( $c$ ) and shrimp prices ( $p$ ), respectively. We assume a constant within-season price  
211 in our initial simulations as in Béné and Doyen (2000). The plain lines in all panels of Figure 3  
212 depict the baseline case with  $p = 2$ ,  $c = 100$ ,  $q = 0.001$  and hypoxia effect ( $\phi$ ) equal to 0.

213 The lines with diamonds in the first panel row of Figure 3 depict the cases with higher  
214 catchability. The left column of the first row describes the optimal harvest paths when the  
215 catchability coefficients are different, while the right column depicts the corresponding stock  
216 paths. We find that the baseline optimal harvest has an inverse U-shape with a peak in the

217 summer time, which is consistent with the actual seasonal shrimp fishery. In these two cases,  
218 the starting point of harvest is similar, while a higher catchability leads to a higher peak harvest  
219 and a later season closing date. Intuitively, higher catchability implies that it is profitable to  
220 fish the stock to a lower level.

221 The second row of Figure 3 depicts the scenarios when  $c$  varies. Specifically, the lines  
222 with diamonds describe the case when marginal cost,  $c$ , is higher. From this figure, we find  
223 that a higher marginal cost coefficient shortens the shrimp harvest season. It also suggests  
224 that the managers should delay the season opening date. Similarly, the last row of Figure  
225 3 illustrates the case when the shrimp price is higher at \$4 per pound. This figure suggests  
226 that if shrimp prices increase, the optimal fishing season extends for a longer period. The  
227 changes in marginal cost and price have similar effects on shifting the optimal harvest and  
228 stock paths. The intuition is that with lower shrimp price and higher fishing cost, it is more  
229 profitable to wait longer for the stock to grow larger. In the extreme case, if the marginal cost  
230 is extremely high or the price is extremely low, the season is only opened for a short amount of  
231 time or the season is not opened at all. An extremely short (or instantaneous) season could also  
232 occur if we removed the capacity constraint. In this case, the problem becomes like an optimal  
233 slaughter problem in aquaculture (Bjørndal, 1988). That is, the harvest sector waits until the  
234 resource growth is balanced by the time value of money and then harvests the entire year's  
235 catch instantaneously. This extreme interpretation is contingent on the weak stock recruitment  
236 relationship.

237 Overall, the results in Figure 3 are consistent with other bioeconomic models of shrimp  
238 fisheries. Most studies of the Gulf of Mexico shrimp fisheries use mathematical programming  
239 models that have far more parameters and equations to represent the fishery than our optimal  
240 control framework. Nevertheless, they find that optimal harvest paths peak in the middle of  
241 the season and recommend seasonal closures as part of optimal management (Önal et al. 1991;  
242 Nance et al. 1994; Önal 1996).

243 With regards to the hypoxia effect, we can derive different optimal harvest and stock paths  
244 with different hypoxia coefficients. These paths are illustrated in Figure 4. The hypoxia indexes  
245 are depicted in the top panel of this figure. Recall that if the dissolved oxygen is less than 2  
246  $mg\ l^{-1}$ , the hypoxia index is equal to 1, otherwise 0. From the figure, we see that most of the  
247 hypoxia days occur from May to August. The optimal harvest paths for three different hypoxia  
248 effects (i.e., no hypoxia effect,  $\phi=0.003$  and  $\phi=0.009$ ) are illustrated in the middle panel. As

249 usual, the plain lines are the baseline scenario with  $p = 2$ ,  $c = 100$ ,  $q = 0.001$  and  $\phi = 0$ . The  
250 lines with diamonds and the lines with triangles depict increasing hypoxia effects. Comparing  
251 these three cases, we find that a higher hypoxia effect makes the optimal harvest start and peak  
252 earlier. Correspondingly, the optimal stock level is lower with the earlier peak time (bottom  
253 panel). Thus with greater environmental stress, we need to start fishing earlier. The optimal  
254 harvest path is shifted to the left by the hypoxia because the pristine stock (stock without  
255 harvest) is shifted to the left by the hypoxia. Mathematically, the larger the shift in the pristine  
256 stock from greater hypoxia, the larger the shift in the optimal harvest path. More intuitively,  
257 hypoxia decreases the benefits of waiting to harvest.

258 From Figure 4, the optimal harvest paths suggest that we should set an earlier season open-  
259 ing date if there is hypoxia. In other words, ignoring hypoxia might lead to a suboptimal pol-  
260 icy, which again will lead to efficiency loss. In the shrimp fishery of North Carolina, one of  
261 the current adopted policies is to set the season opening date. Moreover, Texas uses a seasonal  
262 closure policy to allow shrimp to grow larger. Thus, it is interesting to compare some policy  
263 scenarios when hypoxia is partially or totally ignored in fishery management.

264 Figures 5 depicts the situations in which we follow different harvest strategies. The differ-  
265 ence between the top panel and the bottom panel is that they illustrate the cases of  $\phi = 0.003$   
266 (less severe hypoxia effect) and  $\phi = 0.009$  (more severe hypoxia effect), respectively. The pa-  
267 rameters other than  $\phi$  are all the same as the baseline scenario. The plain lines depict the  
268 optimal harvest paths that take hypoxia into account. If the social planner ignores the hypoxia  
269 effect, partially or totally, he could have two suboptimal policies. First, he only ignores the  
270 hypoxia in the beginning and sets the season opening date according to the no hypoxia case.  
271 After the suboptimal season opening, he realizes that hypoxia is a problem and adapts to it. It  
272 is too late to open the season early, but otherwise the regulator can follow the optimal strategy  
273 in the presence of hypoxia. We call this an “adaptive strategy”. This result is depicted by the  
274 line with triangles, which shows that the new adaptive strategy under the suboptimal season  
275 opening policy is a little higher than the optimal one. Though formally the model is still deter-  
276 ministic in this case, the adaptive strategy is a plausible reaction of the regulator to a stochastic  
277 environmental stressor. That is, having observed hypoxia, the regulator adjusts the harvest  
278 rate and season closing time.

279 Beyond the adaptive strategy, a second alternative occurs if the social planner totally ig-  
280 nores the hypoxia and treats the problem as if there is no hypoxia. In this case, he will naively

281 follow the baseline optimal effort path including opening and closing times. We call this a  
282 “non-adaptive strategy”. So the season opening date is the same with the case of “adaptive  
283 strategy”, and we use a dashed vertical line to show the same opening dates. The “non-  
284 adaptive strategy” is shown by the lines with diamonds in the figure.

285 In order to show clearly the magnitude of the efficiency loss due to suboptimal policies,  
286 we calculate the rents for different harvest strategies and report them in Table 2. This table  
287 describes sixteen combinations of parameters. While the line with “*Optimal*( $\phi = 0$ )” describes  
288 the baseline case where there is no hypoxia, the line with “*Optimal*( $\phi > 0$ )” reports the rent  
289 when there is hypoxia, the planner takes the hypoxia into account and derives the correct  
290 optimal strategy. The following lines denoted with “*Adaptive strategy*” and “*Non – adaptive*  
291 *strategy*” record results in two suboptimal policy cases described above. In this table, we  
292 calculate the hypoxia effect by dividing the rent under each cases by the baseline optimal rent  
293 with  $\phi = 0$  (no impact of hypoxia on the fishery). Policy loss is the difference between the  
294 adaptive strategy (or “Non-adaptive strategy”) and the optimal rent with  $\phi > 0$ . In addition,  
295 the policy loss percentage is derived by dividing the policy loss by the rent of “*Optimal*( $\phi >$   
296  $0$ )”. Given all these parameter combinations, the effort level is always binding and equal to  $\bar{E}$ .

297 Table 2 shows that the rent loss due to hypoxia is big in both absolute and relative magni-  
298 tude. For example, when  $\phi = 0.003, p = 2, c = 100$  and  $q = 0.001$ , the loss due to hypoxia is  
299 about 29.52% of the baseline optimal rent. If the hypoxic coefficient,  $\phi$ , increases to 0.009, the  
300 loss increases to 54.82%. The policy loss is mostly low relative to the economic loss of hypoxia.  
301 With the same parameter combinations, if we use the adaptive harvest strategy, the loss would  
302 reduce to only 0.77% of the potential maximum rent. If we use the non-adaptive strategy, we  
303 lose 5.62% of the maximum rent with hypoxia. For case 3 with a higher hypoxia effect, the  
304 rent for the non-adaptive strategy is negative. This outcome occurs because the non-adaptive  
305 strategy naively follows the fishing opening and closing dates for the case where there is no  
306 hypoxia. In fact, for many fishing dates, the profit is negative, which results in negative total  
307 profits for some of the simulations. We also note that the policy losses for cases 5 and 6 with  
308 lower hypoxia effects are the same. This outcome is due to  $T_1$  equaling to  $T$  (the terminal time  
309 in our numerical simulations) so that the opening and closing dates are all the same. Because  
310 effort binds and the season remains open throughout the planning period, both strategies pro-  
311 duce the same profits.

312 For the non-adaptive strategy, since there are negative fishing profits on some days and the

313 model is deterministic, the regulator could easily avoid these losses in reality. When negative  
314 profit days are discarded from the non-adaptive strategy, the non-adaptive strategy is very  
315 close to the adaptive strategy and even coincides with it in some cases as discussed above. As  
316 such, we focus on the policy loss from the adaptive strategy. In all the sixteen cases in Table  
317 2, the biggest policy loss relative to hypoxia loss for adaptive strategy is 13.55%. The fishery  
318 management gains from adapting to hypoxia are thus relatively small with these parameters.

## 319 **4 Discussion**

320 In this paper, we develop a stylized bioeconomic model for optimal harvest of an annual  
321 species (shrimp) in the presence of environmental degradation (hypoxia) that has growth con-  
322 sequences. In the absence of hypoxia, the optimal harvest path is longer or shorter depending  
323 on price and cost. Because of exogenous recruitment and the annual nature of the fishery, the  
324 problem is analogous to more controlled systems like rotationally managed forests or aqua-  
325 culture ponds (Bjørndal 1988; Guttormsen 2008). If one eliminates the capacity constraint, the  
326 optimal strategy for wild shrimp harvest would be to wait for the shrimp to grow and harvest  
327 all at once, balancing shrimp and price growth over time with the cumulative effects of natural  
328 mortality and discounting.

329 When hypoxia is introduced, we find that the optimal harvest path changes qualitatively.  
330 In particular, as hypoxia worsens, the optimal season opening shifts earlier. The intuition fol-  
331 lows from a standard capital-theoretic view of natural resources. Hypoxia slows the internal  
332 rate of return of the fish stock and thus shifts more harvest toward the present due to discount-  
333 ing. Conversely, in a pristine year managers are better off waiting longer to open the season.  
334 Under hypoxia, the path of optimal harvest also becomes adaptive. However, quantitatively  
335 the consequences are rather small. Previous empirical work finds that hypoxia in North Car-  
336 olina's Neuse River has sizable effects on shrimp harvest— in the range of 13% (Huang et al.  
337 2010)— and our bioeconomic model finds comparable rent losses from hypoxia under the opti-  
338 mal policy for some parameter combinations. Yet, when managers fail to adapt to hypoxia and  
339 instead implement what would be optimal under no hypoxia, the rent losses are small. That  
340 is, the difference between following the optimal policy under hypoxia and following a naive  
341 policy with respect to the season opening is small. An important caveat is that our hypoxia sce-  
342 narios are based on North Carolina's Neuse River and not the more sizable and notorious dead

343 zone in the Gulf of Mexico. The benefits of adaptation to hypoxia could be more substantial in  
344 this much larger fishery that is subject to more severe hypoxia. Indeed, our results show that  
345 more severe impacts of hypoxia increase the policy losses from following either sub-optimal  
346 strategy (adaptive or non-adaptive).

347 Our quantitative findings constitute a negative result of sorts; we set out to find how fish-  
348 ery managers can adapt to water pollution that they are unable to control and generate more  
349 value from fishery resources, but we find only small potential changes in aggregate outcomes.  
350 Nonetheless, our results suggest important policy implications. First, because fishery man-  
351 agers are extremely limited in their ability to adapt to water pollution, reducing pollution  
352 takes on greater importance for other regulatory agencies. Second, fishery managers must  
353 find ways to generate value through some other means. One possibility is generating value  
354 through rationalization. For instance, Smith (2007) finds that the benefits from rationalization  
355 for North Carolina blue crabs are more than an order of magnitude larger than the benefits  
356 from reducing nutrient pollution and the resulting hypoxia. Similarly, the gains from some  
357 form of rationalization of the shrimp fishery will likely outweigh gains from reduced nutrient  
358 pollution and almost certainly would be larger than gains from optimal adaptation to hypoxia.

359 Many caveats exist in our analysis. For example, all the prices in the numerical simulations  
360 are assumed constant over time as in Béné and Doyen (2000). However, in practice shrimp  
361 prices fluctuate during the season due in part to changing size structure within the season and  
362 the premium for larger shrimp. The bang-bang solution indicates that fluctuations of prices  
363 can switch the effort on and off over time, which complicates the problem. In addition, the  
364 capacity limit parameter potentially has normative implications. With a high enough capacity  
365 limit, a fishery that would most likely be highly overcapitalized, the solution moves toward  
366 an optimal slaughter problem in which all harvest is taken instantaneously. The temporal  
367 adaptation to hypoxia could become more important in this case. With a lower capacity limit,  
368 in contrast, we stretch the season out longer, and it may be less important to open the season  
369 early as a hypoxia adaptation strategy because the season already begins early in the fish's life  
370 history. Lastly, uncertainty about stock, catchability, and the cost function could change the  
371 nature of this problem, which we leave to future research.

372 Although our motivating example in this paper is hypoxia, the recent Deepwater Horizon  
373 Oil Spill presented fishery managers with an interesting parallel. The spill occurred before  
374 the shrimp season. Fishery managers decided to declare emergency early season openings to

375 allow shrimp fishermen to catch some shrimp before stocks were inundated with oil from the  
376 spill. Our model provides a theoretical justification for this action.

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458 **Appendix A:**

459

460 Our model is a size-structured single cohort model such that the state equation is a non-  
461 autonomous ordinary differential equation. We can decompose the growth component ( $f(X(t), t)$ )  
462 into biological growth rates that are available in the biology literature. Clark (1990) describes a  
463 similar model structure, and examples of recent work in fisheries bioeconomics using age- or  
464 size-structured models include Massey et al. (2006), Smith et al. (2008), and Tahvonen (2009).  
465 In general, the stock at time  $t$  can be represented as the following:

$$X(t) = N(t) * W(t) \tag{13}$$

466 In this function,  $N(t)$  is the number of individuals at time  $t$  and  $W(t)$  is the weight of each  
467 individual, so the total biomass ( $X(t)$ ) is the product of number and weight. Furthermore, the  
468 number of fish can be modeled as a function of initial number and the mortality rate:

$$N(t) = N_0 e^{\int_0^t -m(u)du} \tag{14}$$

469 Here,  $N_0$  is the initial number in each season, which is independent of last season's stock  
470 and determined by nature. That is, we assume exogenous recruitment at  $t=0$ . In addition,  $m(t)$   
471 is the instantaneous mortality rate, thus the total mortality at time  $t$  is an integration of  $m(t)$  over  
472 time. Because larger fish are typically subject to less predation,  $m(t)$  can be further modeled  
473 as:

$$m(t) = \beta(L(t))^\rho \tag{15}$$

474 In this equation,  $L(t)$  is the fish length and  $\beta$  and  $\rho$  are two parameters. We know that the  
475 number of fish decreases over time, so  $\beta > 0$ , and  $\rho < 0$  reflects the marginal mortality rate  
476 decreasing over time since  $L(t)$  is always positive. Jaw size of potential predators is the stan-  
477 dard justification for the latter assumption.  $L(t)$  itself can be modeled with a von-Bertalanffy

478 function:

$$L(t) = L_{\infty}(1 - e^{\delta t}) \quad (16)$$

479 In this von-Bertalanffy equation,  $L_{\infty}$  is the maximum length of an individual fish. The  
480 parameter  $\delta$  is less than zero to ensure that  $L(t)$  increases over time. Finally, we decompose  
481 the number of fish ( $N(t)$ ) to a function of  $t$ . Recall that Equation 13 has two components,  
482 number of fish and weight  $W(t)$ , which can also be modeled with an allometric function of  
483 fish length with parameters  $\omega$  and  $\eta$ :

$$W(t) = \omega L(t)^{\eta} \quad (17)$$

484 We require  $\omega > 0$  and  $\eta > 0$  to ensure that shrimp weight increases over time with an  
485 upper limit. Until now, the stock dynamics are due to natural growth without ecological stress.  
486 However, there might exist water pollution or some other stressor that influences growth.

$$X(t) = N(t) * W(t) * e^{\int_0^t -\phi A(u) du} \quad (18)$$

487 In this equation,  $A(t)$  is an indicator of whether there is ecological stress, specifically, hy-  
488 poxia in our case. The coefficient,  $\phi$ , is the marginal effect of stress on fish growth. Note that we  
489 measure the effect at time  $t$  by integrating the effects over time because water quality problems  
490 like hypoxia can have cumulative effects (Huang et al. 2010).

491 With all the above equations, we are able to take the derivative of  $X(t)$  with respect to  $t$ ,

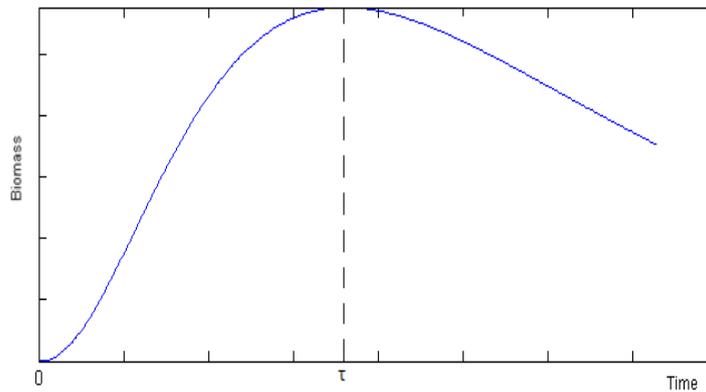
$$\begin{aligned}
\dot{X}(t) &= \frac{d(N(t) * W(t))}{dt} \\
&= \frac{d(N_0 e^{\int_0^t (-m(u) - \phi A(u)) du} * W(t))}{dt} \\
&= N_0 e^{\int_0^t (-m(u) - \phi A(u)) du} (-m(t) - \phi A(t)) * W(t) + N_0 e^{\int_0^t (-m(u) - \phi A(u)) du} * \dot{W}(t) \\
&= N(t)W(t) \left[ -m(t) - \phi A(t) + \frac{\dot{W}(t)}{W(t)} \right] \\
&= X(t) \left[ -m(t) - \phi A(t) + \frac{\dot{W}(t)}{W(t)} \right]
\end{aligned}$$

492 At this point, the stock is expressed as a differential equation of mortality rate, weight and  
493 the hypoxia effect without harvest. If we include harvest, this equation becomes:

$$\dot{X}(t) = X(t) \left[ -m(t) - \phi A(t) + \frac{\dot{W}(t)}{W(t)} \right] - Q(t) \quad (19)$$

494 This equation is exactly the one we use as Equation 3 in the text for the stock dynamics.  
495 The shape of the pristine stock dynamics is depicted in Figure 1:

Figure 1: **Biomass within the season**



Note: Depicts the time path of a shrimp biomass index when there is no harvest and no hypoxic effects. The path is based on the population parameters in Table 1.

496 **Appendix B:**

497

498 In this Appendix, we detail the numerical solution to the social planner's problem. An-  
 499 alytically, we can solve all of the ODEs such that only constants of integration are left to be  
 500 determined. To begin, we integrate the state equation (Equation 3) to obtain:

$$X(t)^* = cons_X * W(t) * e^{\int_0^t -m(u) - \phi A(u) - qE(u) du} \quad (20)$$

501 where  $cons_X$  is an unknown constant. This constant can be determined using the known  
 502 initial condition  $N_0$  (the number of individuals that recruit into the fishery in a given year).  
 503 Thus, according to  $X_0 = N_0 * W(0)$ , we can solve for  $cons_X$  to obtain:

$$X(t)^* = N_0 * W(t) * e^{\int_0^t -m(u) - \phi A(u) - qE(u) du} \quad (21)$$

504 To understand the evolution of the co-state variable, it is convenient to rewrite Equation 10  
 505 as:

$$\dot{\lambda}(t) = qE(t)[\lambda(t) - p(t)] + \lambda(t)[r - g(t)] \quad (22)$$

506 We now consider the extreme cases of when the control is at its maximum (Case A) and  
 507 when the control is 0 (Case B). To understand the control rule, we can combine Equations 8  
 508 and 9. When the control is at the maximum (Case A), the following is true:

$$\lambda(t) < p(t) - \frac{c}{qX(t)} \quad (23)$$

509 Note that because  $c$ ,  $q$ , and  $X(t)$  are always positive,  $\lambda(t) < p(t)$  in this case. And when the  
 510 control is 0 (Case B), the following is true:

$$\lambda(t) > p(t) - \frac{c}{qX(t)} \quad (24)$$

511 For Case A, the sign of the first term in square brackets in Equation 22 is always negative  
 512 as mentioned above. The sign of the second term in square brackets depends on whether  
 513 growth, natural mortality, and the effects of ecological stress are larger or smaller than the  
 514 discount rate. For our particular application of shrimp and hypoxia,  $r - g(t)$  will be negative  
 515 early in the season because shrimp are growing fast but positive late in the season once growth  
 516 slows down and losses from natural mortality and hypoxia dominate. Figure 1 illustrates how  
 517 growth slows and is overtaken by natural mortality even in the absence of hypoxia. If we  
 518 do not consider the transversality condition,  $\lambda(t)$  appears to decrease early in the season and  
 519 increase late in the season. However, we need to account for the transversality condition. It  
 520 turns out that transversality causes the rate of decrease of  $\lambda(t)$  to slow late in the season, but  
 521  $\dot{\lambda}(t)$  does not become positive.

522 Case B is more straightforward. The term in the first set of square brackets in Equation  
 523 22 drops out because the control is 0. Thus,  $\lambda(t)$  is decreasing early in the season. If not  
 524 considering transversality condition,  $\lambda(t)$  will increase late in the season. However, we need  
 525 to take account of the transversality condition.

526 To satisfy the transversality condition, first solve Equation 22 to obtain:

$$\lambda(t) = \frac{k - \int_0^t p(s)qE(s)e^{\int_0^s (-r+g(u)-qE(u))du} ds}{e^{\int_0^t (-r+g(u)-qE(u))du}} \quad (25)$$

527 in which  $k$  is an unknown constant. According to this equation,  $\lambda(T) = 0$  can only hold if  
 528  $\lambda(T_1) = 0$  because  $\lambda(t)$  can be expressed as  $\lambda(T_1) * \frac{e^{\int_0^{T_1} (-r+g(u)-qE(u))du}}{e^{\int_0^t (-r+g(u)-qE(u))du}}$  if  $t \geq T_1$ . Thus,  $\lambda(t)$  is  
 529 equal to 0 if  $t \geq T_1$ . Putting these cases together with the transversality condition satisfied  
 530 allows us to rule out a singular path for our application. At  $t = 0$ , the opportunity cost of  
 531 harvest is too high because the fish have not yet started to grow. Thus, we are in Case B  
 532 (Equation 24). As the stock grows, increased  $p(t) - \frac{c}{qX(t)}$  and decreased  $\lambda(t)$  eventually hit the  
 533 threshold level where  $\sigma(t) = 0$  that justifies the singular control. At this point, call it  $T_0$ , the

534 control turns on. However, by Equation 22, turning on the control will reinforce the decrease in  
535  $\lambda(t)$ . Consequently, the effort will switch to the maximum control (Case A). At the same time,  
536  $r - g(t)$  will grow and cut the decreasing speed of  $\lambda(t)$  until  $\lambda(t) = 0$ . As the season progresses,  
537  $X(t)$  becomes lower which decreases  $p(t) - \frac{c}{qX(t)}$ , eventually the threshold is reached again  
538 and the control passes through the singular control and goes straight to 0. Call this point  $T_1$ .  
539  $\lambda(t)$  becomes zero afterwards and the co-state permanently remains above the threshold and  
540 the control never turns on again.

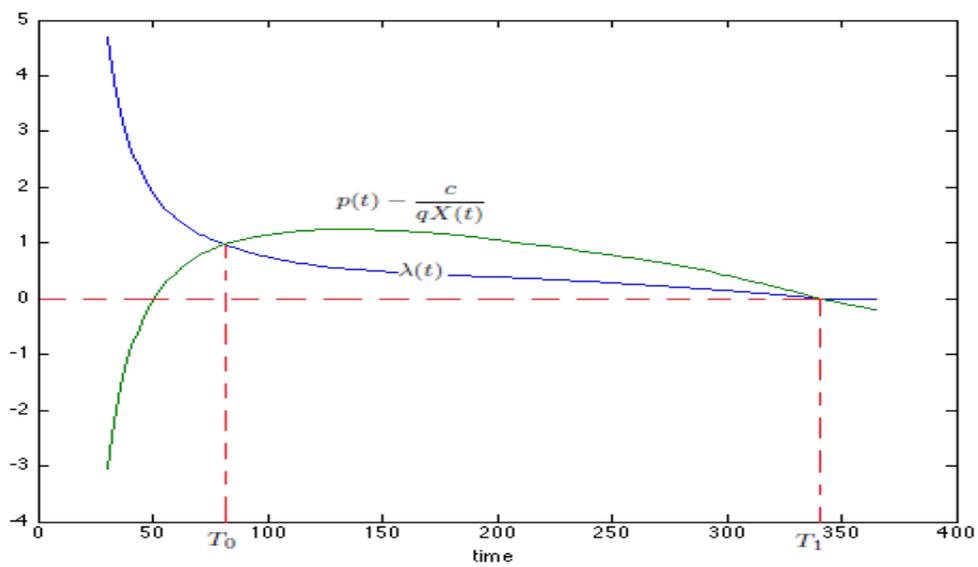
541 The following algorithm is used to determine the remaining constants of integration and  
542 the switch points in the control problem.

- 543 1) Conjecture a  $T_0$ ;
- 544 2) Solve the state equation assuming no effort between 0 and  $T_0$  to find  $X(T_0)$ ;
- 545 3) At  $T_0$ , use the fact that  $\lambda(t) = p(t) - \frac{c}{qX(t)}$  to obtain  $\lambda(T_0)$ ;
- 546 4) Substitute  $\lambda(T_0)$  into the solved co-state equation (Equation 25) and solve for the constant  
547  $k$ ;
- 548 5) Now simulate the state and co-state equations assuming effort is  $\bar{E}$  and find when  $\lambda$   
549 crosses the threshold. Call that "possible  $T_1$ ";
- 550 6) Simulate the co-state and state equations with  $E = 0$  from "possible  $T_1$ " and check that  
551 the threshold is not crossed again.
- 552 7) Choose the  $T_0$  that leads to the highest present value profits.

553 As a check on the above, we solve the problem without using optimal control theory and  
554 instead using Matlab's FMINCON and a discretization of the time and control space. Specifi-  
555 cally, we discretize  $E(t)$  from 0 to  $\bar{E}$ ,  $T_0$  from 0 to  $T$ , where  $T$  is 365 days, and  $T_1$  from  $T_0$  to  $T$  in  
556 each simulation. Then for each combination we calculate the total present value profits for ev-  
557 ery possible effort path. Lastly, we choose the highest profit level. The solutions are the same  
558 for all combinations of parameters that we report in Table 2; we find only slight differences  
559 that are attributable to the discretization.

560 Figure 2 exemplifies the dynamics of  $\lambda(t)$  and  $p(t) - \frac{c}{qX(t)}$  in a case.  $T_0$  and  $T_1$  are determined  
561 where these two lines meet.

Figure 2: **The Harvest Switch**



Note: Depicts the paths of  $\lambda$  and  $p(t) - \frac{c}{qX(t)}$ . The paths are based on the population parameters in Table 1 and  $p = 2, c = 150, q = 0.001$  and  $\phi = 0.003$ .

Table 1: **Parameter sources**

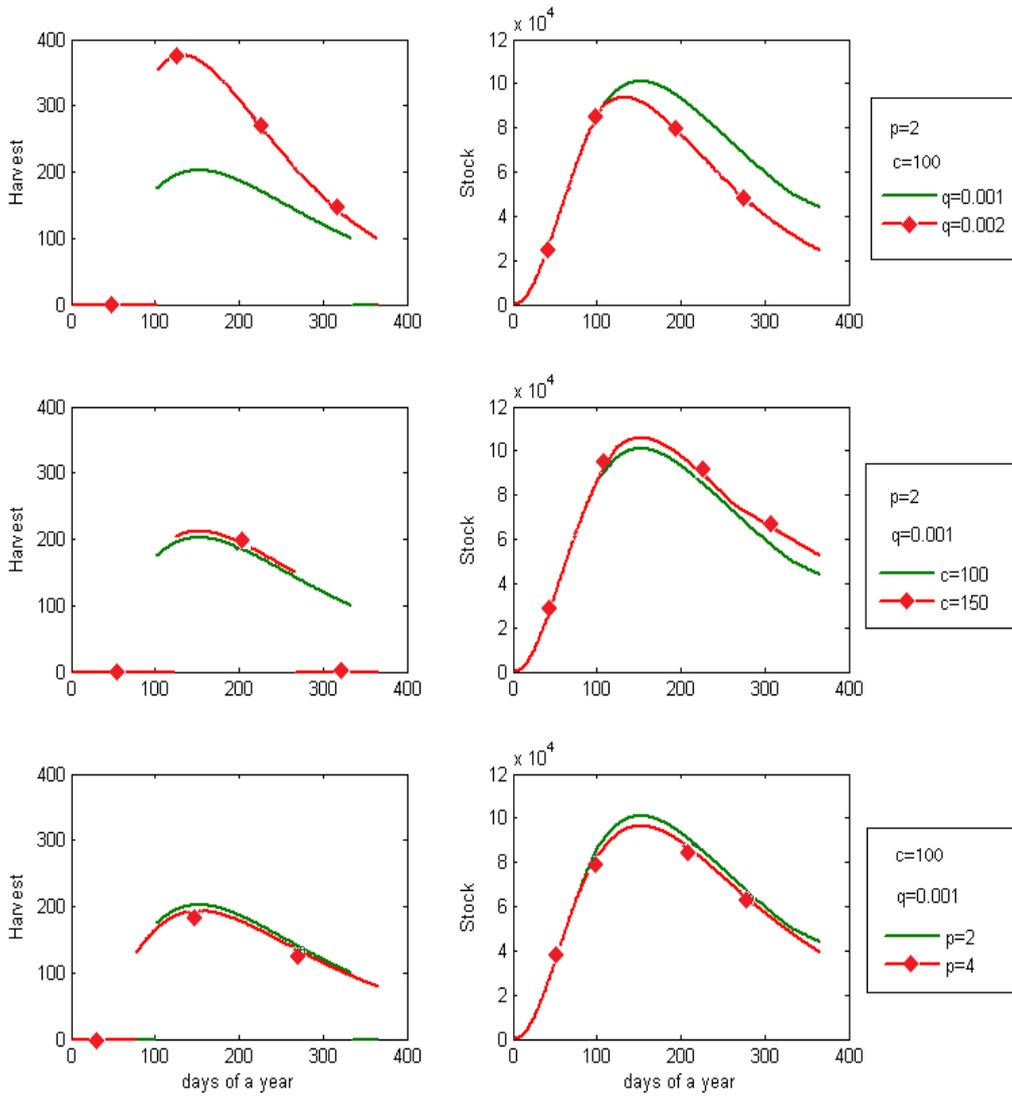
Parameter	Value	Note	Parameter source
$L_{\infty}$	177.7	Von-Bertalanffy growth function	McCoy 1968
$\delta$	-0.0104	Von-Bertalanffy growth function	McCoy 1968
$\beta$	1.4866	Natural mortality rate	Minello et al. 1989
$\rho$	-1.1163	Natural mortality rate	Minello et al. 1989
$\omega$	10.52*E-06	Allometric function(weight)	Fontaine and Neal 1971
$\eta$	2.94	Allometric function(weight)	Fontaine and Neal 1971
$N_0$	100 000	Initial number of shrimp	
$r$	0.0005	discount rate	
$c$	100	fixed cost of fishing	
$p$	2	price of per pound shrimp	
$q$	0.001	catchability coefficient	
$\bar{E}$	2	capacity limit	

Table 2: Efficiency loss due to hypoxia and suboptimal policies (US\$)

	$\phi=0.003$				$\phi=0.009$			
	Rent	Hypoxia effect	Policy loss percentage	$\frac{policy\ loss}{hypoxia\ loss}$	Rent	Hypoxia effect	Policy loss percentage	$\frac{policy\ loss}{hypoxia\ loss}$
Case 1: $p=2, c=100, q=0.001$								
Optimal( $\phi=0$ )	27734				27734			
Optimal( $\phi >0$ )	19546	29.52%			12531	54.82%		
Adaptive strategy	19395	30.07%	0.77%	1.84%	11742	57.66%	6.30%	5.19%
Non-adaptive strategy	18448	33.48%	5.62%	13.41%	4774	82.79%	61.90%	51.02%
Case 2: $p=2, c=100, q=0.002$								
Optimal( $\phi=0$ )	73189				73189			
Optimal( $\phi >0$ )	58875	19.56%			42685	41.68%		
Adaptive strategy	58350	20.27%	0.89%	3.67%	39907	45.47%	6.51%	9.11%
Non-adaptive strategy	57673	21.20%	2.04%	8.40%	34797	52.46%	18.48%	25.86%
Case 3: $p=2, c=150, q=0.001$								
Optimal( $\phi=0$ )	10911				10911			
Optimal( $\phi >0$ )	6277	42.47%			3640	66.64%		
Adaptive strategy	5992	45.08%	4.54%	6.15%	2853	73.85%	21.62%	10.82%
Non-adaptive strategy	4453	59.19%	29.06%	39.36%	-5363	149.15%	247.34%	123.82%
Case 4: $p=2, c=150, q=0.002$								
Optimal( $\phi=0$ )	52499				52499			
Optimal( $\phi >0$ )	40395	23.06%			29102	44.57%		
Adaptive strategy	39762	24.26%	1.57%	5.23%	25932	50.60%	10.89%	13.55%
Non-adaptive strategy	38753	26.18%	4.06%	13.57%	18229	65.28%	37.36%	46.47%
Case 5: $p=4, c=100, q=0.001$								
Optimal( $\phi=0$ )	103740				103740			
Optimal( $\phi >0$ )	83952	19.07%			56955	45.10%		
Adaptive strategy	83858	19.17%	0.11%	0.48%	56193	45.83%	1.34%	1.63%
Non-adaptive strategy	83858	19.17%	0.11%	0.48%	54815	47.16%	3.76%	4.57%
Case 6: $p=4, c=100, q=0.002$								
Optimal( $\phi=0$ )	194560				194560			
Optimal( $\phi >0$ )	165530	14.92%			124780	35.87%		
Adaptive strategy	165080	15.15%	0.27%	1.55%	121890	37.35%	2.32%	4.14%
Non-adaptive strategy	165080	15.15%	0.27%	1.55%	121620	37.49%	2.53%	4.53%
Case 7: $p=4, c=150, q=0.001$								
Optimal( $\phi=0$ )	78516				78516			
Optimal( $\phi >0$ )	59031	24.82%			38326	51.19%		
Adaptive strategy	58842	25.06%	0.32%	0.97%	37001	52.87%	3.46%	3.30%
Non-adaptive strategy	58151	25.94%	1.49%	4.52%	28402	63.83%	25.89%	24.69%
Case 8: $p=4, c=150, q=0.002$								
Optimal( $\phi=0$ )	170130				170130			
Optimal( $\phi >0$ )	140390	17.48%			103170	39.36%		
Adaptive strategy	139820	17.82%	0.41%	1.92%	99100	41.75%	3.94%	6.08%
Non-adaptive strategy	139810	17.82%	0.41%	1.95%	95123	44.09%	7.80%	12.02%

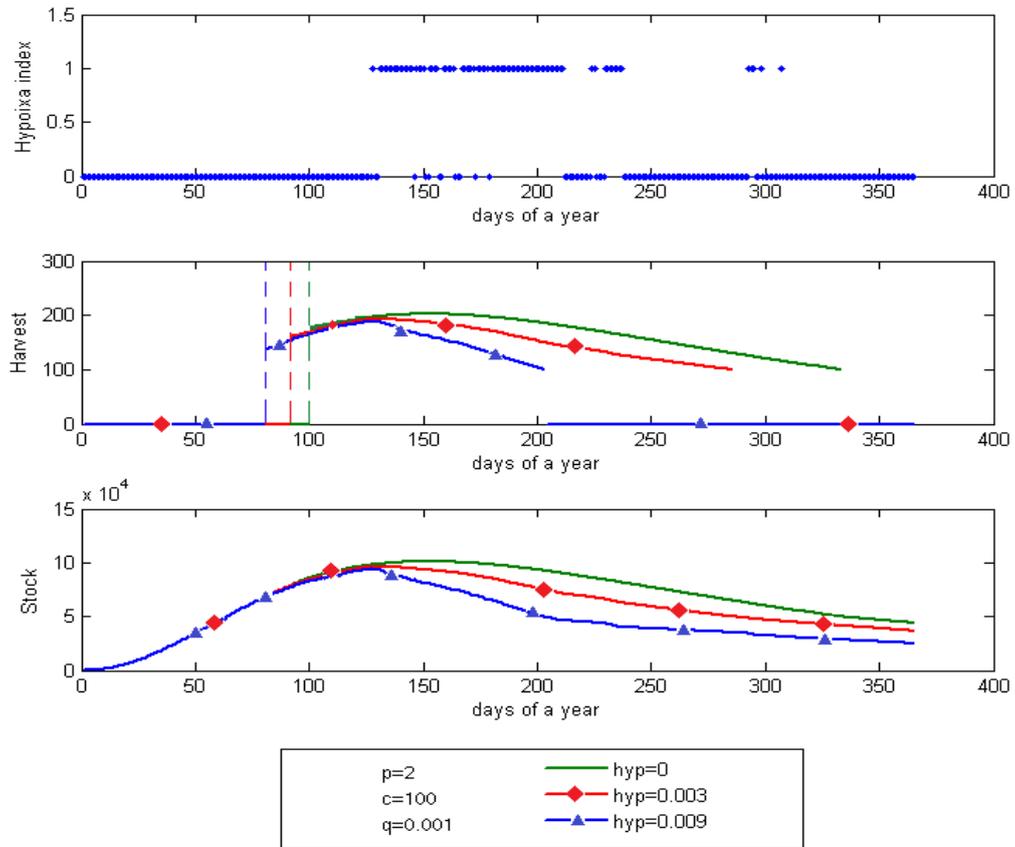
Note: Reports efficiency losses for different harvest strategies and parameter combinations, including low and high impacts of hypoxia ( $\phi$ ), two levels of catchability ( $q$ ), marginal harvest cost ( $c$ ), and shrimp price ( $p$ ).

Figure 3: Optimal harvest without hypoxia



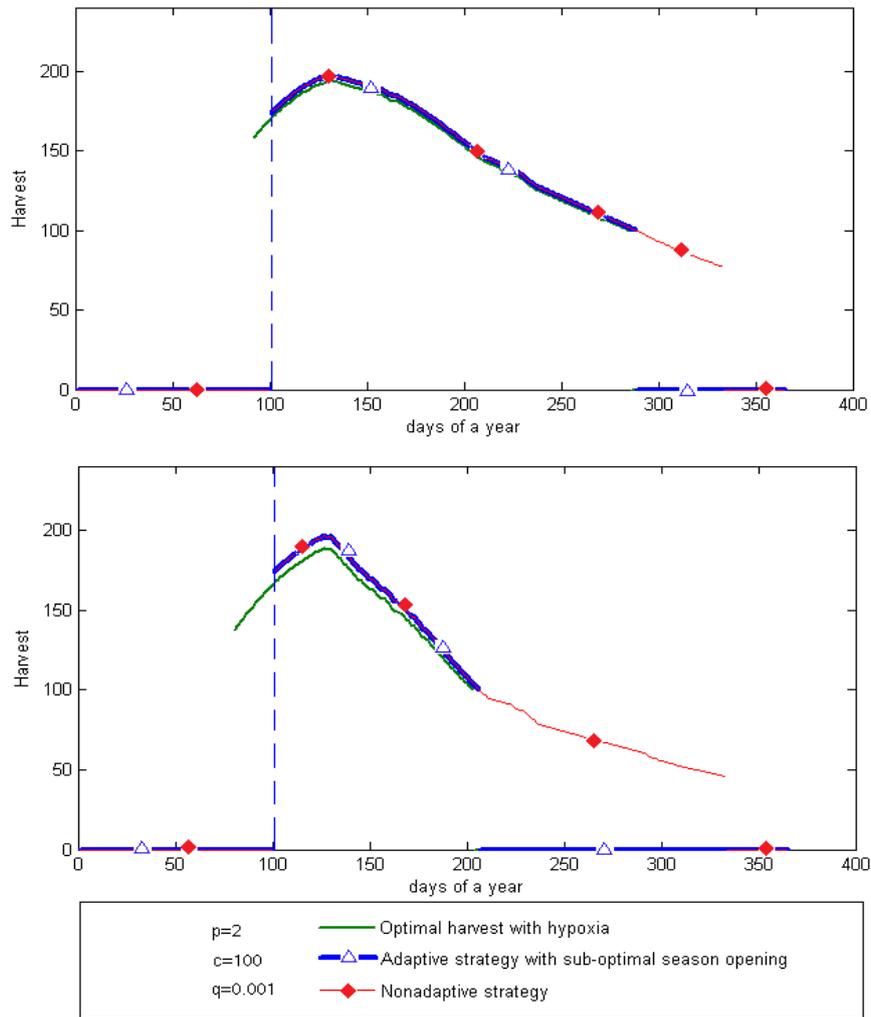
Note: Depicts the optimal harvest and corresponding stock paths when the catchability ( $q$ ), marginal harvest cost ( $c$ ) and shrimp price ( $p$ ) vary.

Figure 4: Hypoxia effects



Note: Depicts hypoxia indexes (top panel), optimal harvest paths (middle panel) and stock paths (bottom panel) at different levels of hypoxia ( $\phi$ ).

Figure 5: Harvest strategies under suboptimal policies



Note: Depicts four different harvest strategies for moderate impacts of hypoxia (top panel) and severe impacts of hypoxia (bottom panel).