

1 **Examining the performance of alternative harvest regulations for short-lived**
2 **taxa; a case study of Florida Bay Scallop Management**

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20 **Highlights**

- 21 • Recreational fisheries for annual species are not often evaluated quantitatively
- 22 • Harvest regulations that are matched to life history can improve expected outcomes
- 23 • A later harvest season or a “rolling” bag limit would benefit this scallop fishery
- 24 • Rolling bag limits mirror escapement policies like those in commercial fisheries

25 **Abstract**

26 The life history schedule of short-lived species compresses the temporal window available for
27 harvest and exacerbates harvest timing decisions. For annual species whose populations are
28 made up of a single year class, it is challenging yet essential to limit harvest to a level that will
29 allow sufficient spawning escapement to sustain the population. Unexpectedly, intense harvest
30 prior to reproduction could extirpate a population in a single season. Larger-scale commercial
31 fisheries for annual or semelparous species are often managed using sophisticated pre-season
32 abundance forecasts or in-season depletion estimates combined with intensive monitoring of
33 catches and enforcement of catch limits. However, sufficient monitoring and harvest control are
34 rarely feasible in recreational fisheries. We demonstrate the use of an age-structured simulation
35 model to identify robust management regulations for recreational harvest season and bag limits
36 applied to the Florida bay scallop fishery. We compared the outcomes of current harvest
37 regulations with a suite of alternative harvest regulations in a recreational fishery for Florida bay
38 scallops. To account for uncertainty in the stock status and dynamics of the fishery, we evaluated
39 alternative harvest options across three levels of initial stock exploitation and two scenarios for
40 future fishing effort. Our results show that biologically-informed regulations, which allowed for
41 more bay scallops to spawn prior to harvest, such as a later harvest season and daily harvest limit
42 increasing over the season, performed well across all treatments, and outperformed many of the
43 current regulations when the initial stock state was more exploited, as well as when future effort
44 doubled. These results suggest that (1) harvest regulations that more closely match the biology
45 and life history are likely to perform better for short-lived, annual taxa than simpler regulations
46 that may not explicitly consider these factors, and (2) simpler regulations can perform well, but

47 require precise, annual monitoring to prevent potentially catastrophic overharvest or costly

48 underutilization.

49 **Keywords:** *Argopecten irradians concentricus*, recreational fisheries, harvest season, bag limits,

50 population simulation

51 **1. Introduction**

52 Fisheries for short-lived or annual species pose challenges for harvest management.
53 Annual species have a simpler (single mode) size structure and truncated age structure compared
54 to most managed fish species. This compression of age and size structure as a function of
55 comprising but a single year class means that these species are highly sensitive to effects of
56 human exploitation. Larger-scale commercial fisheries for such species are often managed using
57 sophisticated pre-season abundance forecasts or in-season depletion estimates (e.g., Rosenberg et
58 al., 1990; Arkhipkin et al., 2015) combined with intensive monitoring of catches and
59 enforcement of catch limits to ensure sufficient spawning escapement. Although recreational
60 fisheries for short-lived species are common and socioeconomically important (Lellis-Dibble et
61 al., 2008; Taylor, 2017; Aguilera, 2018; Ben-Hasan, 2018; Sydeman et al., 2020), these fisheries
62 are more difficult to monitor, assess, and manage than major commercial fisheries. The large,
63 unrestricted pool of potential recreational fishers entering from numerous access points along
64 with limited traditional means of restricting catch (such as using season, length, or bag limits)
65 constrain the available means to manage recreational fisheries for short-lived or annual species.

66 Precision is necessary for the amount and timing of harvest for short-lived species with
67 essentially a single age or size class, e.g., small-bodied fish, some crabs, many shrimp, and many
68 cephalopods (Robert et al., 2010; Arkhipkin et al., 2015; Sauer et al., 2021; Žák et al., 2021).
69 Most traditional fisheries models were developed for longer-lived fish and invertebrate species
70 because these models assume the existence of multiple year classes and population dynamics
71 associated with iteroparity (Arkhipkin et al., 2021). Compression of age and size structure in
72 annual species entails a meaningful proportion of the population need to spawn each year to
73 ensure sustainable harvest as population replenishment and viability is highly dependent on

74 spawning success of a sole cohort (and not buffered by any carry-over of spawning stock year to
75 year; Rosenberg et al., 1990). However, harvesting also needs to occur before rapid post-spawn
76 senescence, which renders the organism unpalatable or undesirable to catch (notably occurs in
77 some semelparous species such as pacific salmon and octopus). Additionally, delaying harvest
78 until after their peak spawning period will likely decrease overall socioeconomic utility as most
79 of the stock would succumb to natural mortality without being harvested. Conversely, high
80 fishing mortality rates before most of the spawning has occurred, in addition to the potential for a
81 critical reduction in spawning potential, could result in growth overfishing that would undercut
82 harvestable biomass.

83 Common harvest regulations in recreational fisheries include season length and bag
84 limits. Effects of season timing and length may interact with bag limits (Melnychuk et al., 2021);
85 liberal bag limits may especially function to “shorten” the season by quickly removing the
86 available stock, whereas very conservative bag limits may constrain harvest-based utility.
87 However, there are very few studies quantitatively evaluating the biological sustainability and
88 harvest utility tradeoffs resulting from the more unique aspects of these annual species life-
89 histories.

90 Most research on fisheries for such species has focused on commercial take (Rosenberg
91 et al., 1990; Hoshino et al., 2012; Ben-Hasan et al., 2018), with fewer studies evaluating
92 recreational fisheries (Reid and Montgomery, 2005), and very few evaluating the harvest season
93 and bag limit regulations that are important to sustaining the socioecological system of these
94 fisheries (Forbes et al., 2019). Among the reasons for this is the large number of active and
95 potential participants in recreational fisheries given essentially unrestricted access (fishing
96 licenses are required but are cheap and their number is not limited) and the dispersed nature of

97 access points which make monitoring difficult and unprecise while also limiting the ability of
98 managers to effectively constrain harvest. Typically, such fisheries are harvest-oriented and cease
99 outside of the harvest season (e.g., Taylor et al., 2017; Ben-Hasan et al., 2018; Arkhipkin et al.,
100 2022), but while participating, fishers attain utility from both catch-related and non-catch-related
101 attributes of the fishing experience. Popular recreational fisheries of these species also support
102 economically important visitation and tourism activities, and thus are vital to local communities.
103 The extent to which local economies depend on these fisheries emphasizes the importance of
104 setting appropriate season and bag limits. Shorter seasons will limit annual market activity, but a
105 single year of overly intense harvest from lenient season lengths and bag limits could collapse
106 the entire fishery. Successful local governance requires evaluations of social and ecological
107 dynamics to set reasonable and sustainable regulations.

108 Here we consider a case study of a recreational fishery for a short-lived species that has
109 high socioeconomic value locally: the bay scallop (*Argopecten irradians concentricus*) fisheries
110 of the Gulf coast of Florida, USA. Many different types of regulations have been adopted across
111 counties, but little management evaluation exists to determine which of these regulations
112 optimize ecological and socioeconomic sustainability. The goals of this work are to evaluate
113 current and alternative management strategies for managing this species and provide applicable
114 management advice to a local fishery. We address these goals by building upon the initial
115 empirical work done by Granneman et al. (2021), developing a simulation model representing a
116 local Florida bay scallop fishery, and discussing the implications our results have for trade-offs
117 between current harvest regulations, like bag and season limits, and similar regulations tweaked
118 to be more biologically-informed by considering the life history schedule.

119 *1.1 Case Study*

120 Bay scallops are distributed from Massachusetts to Northern Mexico throughout the Gulf
121 and Atlantic coasts in the US, where they support commercial and recreational fisheries
122 (Mackenzie, 2008; Bert, 2011). The Florida bay scallop (*Argopecten irradians concentricus*) is a
123 subspecies currently found from St. Andrew Bay to Pine Island Sound along the Florida Gulf
124 coast (Geiger et al., 2006). Florida bay scallops rarely live longer than 12-18 months (Barber
125 and Blake, 1983; Arnold et al., 2005) and spawn in late summer or early fall (Geiger et al.,
126 2010), however there is evidence of some protracted spawning throughout the year (Sastry,
127 1963; Geiger et al., 2010). This makes Florida bay scallops effectively an annual species and the
128 prevailing theory across the entire species range is that they reproduce usually only once, what
129 has been characterized as “interrupted iteroparity” since individuals may undergo multiple
130 spawning events however usually do not survive long enough for the second and senescence
131 does not appear to be directly related to spawning (Bricelj and Krause, 1992; Estabrooks, 2007;
132 Abele et al., 2009).

133 The fishery for bay scallops on the Gulf coast of Florida is exclusively recreational and
134 hand-harvest, with fishers swimming (usually snorkeling) over shallow sea grass flats and
135 locating scallops by sight. The species’ occurrence in nearshore, shallow waters and the simple
136 harvest techniques has made the fishery especially popular with people who otherwise might not
137 engage in recreational fishing (Granneman et al., 2021). These traits also make the fishery a
138 social affair, with large, *ad-hoc* aggregations of scallop harvester vessels forming on the water,
139 and little indication of negative utility associated with crowding (as is common in other
140 recreational fisheries; Hunt et al., 2019). The popularity of this fishery attracts thousands of
141 visitors for day or overnight trips to coastal communities that rely on the additional revenue and
142 market activity (Hall-Scharf et al., 2018). Because the fishery is harvest oriented, essentially no

143 scalloping trips (and associated market activity) occur outside of harvest season. The fishery is
144 currently managed by bag limits (per individual and vessel per day) and by harvest seasons, but
145 the length and timing of the harvest season and bag limits are regulated differently in each of the
146 spatial management zones (Figure 1). While all harvest seasons occur generally during the
147 summer (and thus largely before or overlapping with scallop spawning), changes to the length of
148 the harvest seasons are perceived to have important implications for local economies (Hall-
149 Scharf et al., 2018). Despite this, quantitative assessments of harvest season efficacy and effect
150 on scallop population and socioeconomics are largely unexplored (Geiger et al., 2006;
151 Granneman et al., 2021).

152

153 **2. Methods**

154 *2.1 Approach*

155 We used a simulation approach to evaluate the effects of harvest regulations on bay
156 scallop population dynamics as well as metrics considered important to the socioeconomic utility
157 of scallopers. We developed an age structured simulation model for a hypothetical population of
158 bay scallops and subjected this population to alternative harvest regulations.

159 *2.2 Population model*

160 All analyses were conducted in R (R Core Team, 2022), and all data and code needed to
161 replicate our study are available from github.com/lidach/CampLabScallop. We built a single
162 area, single sex, age structured population model that simulates the monthly dynamics of a
163 hypothetical bay scallop fishery under different management actions. Where possible, we
164 parameterized the model using the most recent information from the literature (Table 1). We
165 chose a single sex model given bay scallops are functional hermaphrodites (Barber and Blake,

166 1985). We modeled bay scallop ages from 1 to 18 months, as 18 months is generally thought to
 167 be the maximum age achieved in Florida (Barber and Blake, 1983). The model is initialized at an
 168 unfished equilibrium age structure using:

$$169 \quad (1) \quad N_{a,t=1} = \begin{cases} R_0 & \text{if } a = 1 \\ N_{a-1,t=1} e^{-M_{a-1}} & \text{if } a > 1 \end{cases}$$

170 where R_0 denotes unfished recruitment, M_a references the monthly instantaneous natural
 171 mortality at age a , and t denotes the time step in months ($t = 1$ references the beginning of
 172 model). Natural mortality was calculated using the length-inverse Lorenzen M , which assumes
 173 that natural mortality declines with age until the maximum age of $a = 18$ months (T2.3;
 174 Lorenzen, 2000, 2022). Upon reaching that maximum age, scallops are subject to infinite M , i.e.,
 175 no scallops survive beyond $a = 18$ months. Shell height, measured from the hinge to the shell
 176 margin, was calculated using the von Bertalanffy growth function (T2.1, Figure 2). We modeled
 177 the weight at age of a scallop as a power function of shell height (T2.2), and the maturity-at-age
 178 as a logistic function of age (T2.4).

179 The monthly scallop population simulates forward in time according to:

$$180 \quad (2) \quad N_{a,t} = \begin{cases} R_t & \text{if } a = 1 \text{ and } t = \text{every 12 months} \\ N_{a-1,t-1} e^{-(M_{a-1} + F_{a-1,t-1})} & \text{if } a > 1 \end{cases}$$

181 where $F_{a,t}$ represents the fishing mortality in a given month for a given age and R_t denotes
 182 recruitment. Given the monthly time-step, spawning only takes place in select months
 183 corresponding to the start of the year (every twelfth time step). Recruitment in each year (y) was
 184 calculated deterministically using the Beverton and Holt function (Beverton and Holt, 1957):

$$185 \quad (3) \quad R_t = \frac{\alpha S_{y-1}}{1 + \beta S_{y-1}} \text{ if } t = \text{every 12 months}$$

186 where $S_{y-1} = \sum_{t \text{ in } y-1} \sum_a N_{a,t} * Mat_a * \psi_{month(t)} * \omega_a * Fec_a$

187 The accumulated spawning biomass for the year prior to recruitment, S_{y-1} , attempts to account
 188 for the individuals that may have spawned prior to the 12th month in each year (December). This
 189 quantity was calculated by summing the monthly spawning biomass produced by scallops within
 190 a year (where the $\sum_{t \text{ in } y-1}$ summation symbol denotes summation over a year). The vector ψ
 191 denotes the probability of spawning in each month ($\psi_{month(t)}$, where $month(t)$ references the
 192 particular month depicted at time t), which accounts for the seasonality of spawning. This vector
 193 was parameterized using relative values obtained from Figure 5 in Geiger et al. (2006), which
 194 depicts the mean gonadal-somatic indices of bay scallops each month from the Homosassa area
 195 of Florida’s Gulf coast. The ability to spawn only once was enforced using ω_a , which describes
 196 the proportion of individuals alive in a cohort at age a that are available to spawn (have not yet
 197 spawned). This vector was derived according to

198
$$\omega_a \begin{cases} 1 & \text{if } a = 1 \\ \omega_{a-1} (1 - Mat_{a-1} * \psi_{month(a-1)}) & \text{if } a > 1 \end{cases}$$

199 where now $month(a-1)$ references the specific month associated with age $a-1$ in a cohort (e.g.,
 200 age 1 and age 13 both reference January). For example, all individuals of age 1 are available to
 201 spawn in January, since none spawned in the previous month. In February, the percentage of
 202 individuals age 2 that are available to spawn is equal to the percentage of age 1s that were
 203 available to spawn in the previous month multiplied by the percentage of age 1 individuals that
 204 did not spawn in the previous month ($1 - Mat_{a-1} * \psi_{month(a-1)}$). This assumes randomness with
 205 respect to which scallops (spawned or not) died over the course of the year. We chose to assume
 206 bay scallops were only able to spawn once in our model as the majority of the population in

207 Florida is assumed to (Barber and Blake, 1983), and the likelihood of surviving to a second
208 spawn is low (Estabrooks, 2007; Abele et al., 2009). The parameters α and β of the stock recruit
209 function were converted from the compensation ratio, CR (the relative improvement in juvenile
210 survival rate as the spawning stock biomass approaches zero, Goodyear, 1980), and the spawning
211 biomass produced per recruit in the unfished condition, ϕ_0 (T2.7-2.9). We assumed fecundity-at-
212 age was proportional to weight-at-age with an arbitrary scalar of 0.1.

213 *2.3 Fishery*

214 Fishing mortality per month is calculated as:

$$215 \quad (4) \quad F_{a,t} = s_a q E_t$$

216 where s_a denotes the fishery selectivity of scallops at age, q the catchability of scallops in the
217 fishery, and E_t the effort expended in each month, measured as the number of scallopers. The
218 fishery selectivity of scallops was modeled as a simple two-parameter logistic function of the
219 length (i.e., shell height) of scallops at age (T2.6). Since empirical size-based selectivity
220 information is lacking and there is no minimum size limit, the length at 50% vulnerability was
221 set at 35mm (pers comm, J. Granneman) -- roughly 60% of the average maximum size, and the
222 slope of the logistic function was assumed 0.5.

223 *2.4 Model Calibration/Initialization*

224 *2.4.1 Effort*

225 Harvest and effort data are largely unavailable for the Florida bay scallop fishery, and
226 thus there are no existing stock assessment models for the fishery. To initialize our population
227 model, we used effort estimates from Granneman et al. (2021), who estimated vessel effort at
228 different dates throughout the course of the 2018 scallop season in the Steinhatchee area of
229 northwest Florida (Region C, Figure 1). This data was used to estimate the total vessel effort in a

230 given month. To aggregate the daily effort counts into monthly total effort, we first fit a model to
231 the observed vessel effort as a function of the days since the first sampled effort count for that
232 month and with a random effect for the weekday of the observation (Figure S1) to account for
233 both the general decline of effort throughout the season and the weekday/weekend pattern. We
234 then predicted the effort for 90 days since the start of the scalloping season to approximate the
235 three-month season Granneman et al. (2021) observed and accounted for every possible day of
236 the week. This allowed us to calculate the total expected effort for each month in a hypothetical
237 three-month season regardless of the weekday/weekend pattern. Vessel effort was then
238 multiplied by the average persons per vessel (3.8; Granneman et al., 2021) to get the total
239 number of scallopers. The baseline catchability was also obtained from Granneman et al. (2021)
240 and divided by 3.8 to scale to average persons per vessel.

241 2.4.2 R_0

242 With seasonal effort and baseline catchability estimates, we then estimated the starting
243 number of recruits in the population (R_0) by minimizing the difference between model-estimated
244 average gallons (1 US liquid gallon is equivalent to 3.785 liters) of scallops caught per person at
245 equilibrium and the estimate from Granneman et al. (2021) (0.81 gallons of scallops per person).
246 To ensure our model was in equilibrium, we ran the model for 25 years and estimated (tuned) R_0
247 based on the last year's average gallons of scallops per person. For comparison purposes, we also
248 generated model results for an unfisher scenario assuming $E_t = 0$.

249 2.5 Scallop bag limit calculations

250 The bag limit was factored into the calculation of fishing mortality by changing the
251 catchability of scallops by individual fishers. First, we calculated the catch rate of scallops in a

252 given month if there were no bag limit. We call this the catch-per-unit-effort (CPUE) and
 253 calculated it by dividing the unregulated catch (not accounting for bag) by effort using:

$$254 \quad (5) \quad I_t = \frac{\sum_a \frac{F_{a,t}}{F_{a,t} + M_a} N_{a,t} \left(1 - e^{-(F_{a,t} + M_a)}\right) * \%Gal_a}{E_t}$$

255 Given the bag limits are specified in gallons, the numerator describing the catch at age (using the
 256 Baranov catch equation; Baranov, 1918) was converted to gallons using:

$$257 \quad (6) \quad \%Gal = \left[\frac{(-6.704 * L_a + 480.96)}{2} \right]^{-1}$$

258 Where L_a is the length at age defined by the von Bertalanffy growth curve (T2.1). This equation
 259 describes the proportion of a gallon occupied by a scallop at a given age. This formula was
 260 obtained from Granneman et al. (2021) and Geiger et al. (2006). We assumed catch rates
 261 followed a truncated normal distribution with a coefficient of variation of 0.455 calculated from
 262 distributions of catch rates obtained in Granneman et al. (2021). We then obtained the
 263 probabilities of catching any number of scallops under this distribution from 0- N , where N is set
 264 at some sufficiently large number (where probability of catching N scallops approaches 0 and the
 265 sum of the probabilities of catching 0- N scallops is approximately 1). The expected catch rate
 266 under the bag limit (\tilde{I}_t) was then calculated by multiplying the probability of attaining each
 267 catch rate by the number of scallops that would be retained under that catch rate (for $N > bag$,
 268 number retained is equal to bag), and summing the values. We then searched for an adjusted
 269 catchability value using Newton-Raphson iterations (Brent, 1973) that would produce a catch
 270 rate equal to that expected under the bag limit. Note that this adjusted catchability can be thought
 271 of as a realized catchability or harvestability, which represents the proportion of the population
 272 harvested per unit of effort (as opposed to the catch or search efficiency for scallops). We do not

273 model any discard mortality as this is thought to be negligible in bay scallops (Benoît et al.,
274 2015).

275 *2.6 Alternative harvest regulations assessed*

276 In total, we explored ten harvest scenarios. The primary harvest regulations we evaluated
277 include the duration of the scalloping season (longer vs shorter), the timing of the season (earlier
278 vs later), and the size and nature of the bag limit (more vs less, and rolling vs fixed). A full suite
279 of management regulations that were tested is included in Table 3. In the simulation model,
280 changing the season dates changes the months which experience E_t and thus F_t . For our
281 baseline scenario, we approximated the management regulations currently in place in Citrus,
282 Hernando, and Levy Counties (Region D, Figure 1), as well as regulations similar to those used
283 in surrounding counties (Figure 1) and some novel regulations (Table 3). The size of the bag
284 limits refers to the quantity of scallops (in gallons) legally allowed per scalloper on each day, and
285 the nature of the bag limit refers to whether this amount was constant over the course of the
286 scalloping season (the same each month) or “rolling”. We defined a “rolling” bag limit as one in
287 which the bag limit for the initial months of the season was lower than the limit in the final
288 months. We varied bag limits of scallops from 1, 2, and 3 gallons per scalloper per day within
289 the constant bag limit (with two gallons being the “baseline” regulation applied in most areas)
290 and explored rolling limits allowing for 1 gallon in the first month of the season to 2 gallons in
291 the final two months. We also explored the effects of lengthening the season by one month and
292 shifting the season earlier or later in the year. If an additional month was to be added to the
293 harvest season, we kept total effort for the year equivalent and reallocated it across the months
294 following the exponential decay function in subsection 2.4.1.

295 *2.7 Uncertainty in starting conditions and effort trajectory*

296 For Florida bay scallops, and likely for other annual species fisheries that are rarely
297 subjected to stock assessments, there is substantial uncertainty regarding the current exploitation
298 status as well as the trajectory of effort in the past and future. To explore the sensitivity to the
299 population starting condition, we adjusted the catchability value to generate three levels of initial
300 exploitation. Low, moderate, and high levels of initial exploitation were defined for which the
301 initial spawning escapement equaled 50%, 35%, and 20% of that in the unfished simulation after
302 the 25-year initialization period, respectively. These levels were chosen to encompass a range
303 below which different fisheries may be considered overexploited (Caddy and Mahon, 1995;
304 Clark 1991; Goodyear, 1993). Initial spawning escapement was defined as the spawning biomass
305 in the last year of the initialization period for a given simulation divided by the spawning
306 biomass produced over a year in the unfished simulation. For reference, the initial spawning
307 escapement in our model which resulted from using the catchability value from Granneman et al.
308 (2021) was 63%, and the region evaluated in Granneman et al. (2021) generally produces the
309 greatest densities of scallops ([https://myfwc.com/research/saltwater/mollusc/bay-](https://myfwc.com/research/saltwater/mollusc/bay-scallops/season/)
310 [scallops/season/](https://myfwc.com/research/saltwater/mollusc/bay-scallops/season/)). The new catchability values for each population starting condition were then
311 used in the process model to project the population forward under the different management
312 regulations.

313 An additional but related uncertainty in the Florida bay scallop fishery is how future
314 fishing effort will change—either in response to alternative management actions or independent
315 of them. While not well-monitored, some evidence suggests substantial increases over the last
316 decade (Granneman et al., 2021). To assess the sensitivity of harvest regulation performance to
317 future effort dynamics, we created two levels of future effort: 1) effort remained at its current
318 level for the whole simulation and 2) effort linearly increased after the initialization period such

319 that it doubled by the end of the time series relative to the starting conditions. Together, these
320 two treatment axes of initial exploitation conditions (three levels) and future effort (two levels)
321 resulted in six treatments that each harvest scenario was assessed on. Note however that these
322 scenarios do allow for effort to respond differently to the different regulations evaluated,
323 implications of which are described in the Discussion.

324 *2.8 Performance metrics*

325 Each management regulation scenario and uncertainty treatment were simulated for an
326 additional 25 years beyond the 25-year initialization period. To compare the regulation scenarios
327 across the uncertainty treatments, we compared two metrics at the end of the 50-year time series:
328 1) spawning output, and 2) harvest per unit of effort (HPUE). For the calculation of spawning
329 output, we took the mean of the total spawning biomass from the last five years of the simulation
330 (years 46-50) and divided by the spawning biomass produced over one year in the unfished
331 simulation (i.e., spawning biomass unfished). Thus, low values at the end of the simulation
332 period represent low spawning output from the population, and vice versa. For HPUE, we
333 calculated the mean harvest per unit effort of the last five years of the simulation using the
334 expected catch rate under the bag limit. We specifically used harvest per unit effort as opposed to
335 CPUE because there is no indication of socioeconomic value of catch and release in this fishery,
336 and because HPUE explicitly accounts for the imposition of bag limits, which was a key harvest
337 regulation we sought to examine.

338 *2.9 Sensitivity analysis and additional management regulations*

339 We focus mainly on results of ten main management regulations tested within the main
340 text (Table 3). However, we tested an additional 24 regulations, closer to a full factorial of all our
341 regulation treatments, and these are presented in the supplemental file. In addition, we also

342 examined the sensitivity of our results to the specification of the reference natural mortality rate
343 (M_r) and steepness (h) by increasing and decreasing them by 25% and rerunning the model and
344 management regulations (resulting in an additional 4x24 runs; Figures S2-7). We used steepness
345 instead of compensation ratio as increasing and decreasing steepness by 25% exhibits a greater
346 difference in the stock-recruit relationship than would altering CR by 25%. The base value of CR
347 = 8 converts to $h = 0.66$ ($h = CR / (CR + 4)$), and the sensitivity values of $h = 0.5$ and $h = 0.83$
348 correspond to CR = 4 and CR = 20. We also present results for the metric CPUE in Figures S6-7.

349

350 **3. Results**

351 We evaluated the two performance metrics separately for all combinations of harvest
352 regulations, effort assumptions, and initial exploitation assumptions. The effects of these
353 treatments on spawning output are depicted in Figure 3, and the effects on HPUE are shown in
354 Figure 4.

355 *3.1 Effects of harvest regulations on biological performance*

356 The differences in spawning output between scenarios were larger when initial
357 exploitation was high (i.e., 20% of the initial unfished escapement rather than 50%) as well as
358 under assumptions of greater effort (row 2 [panels d, e, f], Figure 3). The effects of the scenarios
359 can be divided into three main groups. The first group contains the harvest scenario 2: increased
360 bag limit, scenario 3: decreased bag limit, scenario 4: extending the harvest season later, and
361 scenario 8: a rolling bag limit applied to the current season. This group had little effect relative to
362 the base scenario (status quo), with decreased bag limit generating more spawning output. The
363 second group includes the three scenarios involving an earlier season, scenario 5: extending the
364 harvest season earlier, scenario 7: earlier season, and scenario 10: a rolling bag with an earlier

365 season. This group resulted in a lower spawning output relative to the baseline. The third group
366 includes scenario 6: a later season and scenario 9: a rolling bag with a later season that resulted
367 in higher spawning output relative to the base scenario. Of these, the rolling bag with the later
368 season (scenario 9) resulted in the most spawning output. However, under the assumptions of
369 baseline effort and low initial exploitation (50% of the initial unfished escapement), no harvest
370 regulations resulted in substantial differences in spawning output, i.e., spawning output was
371 always greater than 40% of the unfished level.

372 As the levels of initial exploitation increased to moderate and high (35%, 20% of the
373 initial unfished escapement, respectively), the differences between the different harvest
374 regulations increased. The second group (scenarios 5, 7, and 10) noticeably resulted in much
375 lower spawning output at the end of the time series (<10% unfished) under the high initial
376 exploitation. In contrast, the third group (scenarios 6 and 9) still allowed for near or greater than
377 50% spawning output at the end of the time series. However, at this high initial exploitation level
378 (20% of the initial unfished escapement), the later season approach was the most robust, which
379 performed essentially as well as the decreased bag limit scenario, and was improved when
380 coupled with a rolling bag limit (Figure 3, panel c).

381 The patterns of our results described above were mirrored for the treatment of increased
382 effort, which effectively decreased the spawning output (e.g., the effective spawning output for
383 the baseline management regulations for panel d in Figure 3 is about 30%, due to the doubling of
384 effort that is only slightly muted by bag limits). The second group (three harvest regulations
385 involving earlier seasons) showed even less spawning output as expected, and the third group
386 (two scenarios involving a later season) showed little difference from the base regulations.
387 Applying the assumption of increased future effort caused three key differences in results: (i) the

388 “rolling bag, later season” (scenario 9) performed better than all other scenarios when under high
389 exploitation (20% of the initial unfished escapement); (ii) under this same assumption, decreased
390 bag limit (scenario 3) was no longer providing any real improvement relative to the baseline
391 scenario; and finally (iii) the later season (without a rolling bag) actually outperformed the other
392 rolling bags measures that did not feature a later season (scenarios 8 and 10). Thus, when the
393 doubling in effort effectively reduced the spawning output values further, the later harvest season
394 became increasingly better than other measures.

395 *3.2 Effects of harvest regulations on harvest per unit of effort*

396 Similar to spawning output at the end of the time series, HPUE was nearly equivalent
397 across different management strategies until initial exploitation increased (Figure 4). Under
398 assumptions for baseline effort and initial low or moderate exploitation (50% or 35% of the
399 initial unfished escapement; Figure 4, panels a and b), most strategies resulted in similar HPUE,
400 owing to the imposition of bag limits (as CPUE did change, Figures S6-7). However, when the
401 initial exploitation was high (20% of the initial unfished escapement; Figure 4, panel c), four
402 regulations stood out as providing greater HPUE: a decreased bag limit (scenario 3), a later
403 season (scenario 6), and the two scenarios with rolling bag limits (scenarios 8 and 9). Thus, when
404 the population is more exploited, decreasing the bag or life history-matched regulations (later
405 season or rolling bag) maintain higher harvest rates than other regulations. The pattern was
406 similar under the assumption of doubled effort (Figure 4, panels d, e, f).

407 *3.3 Sensitivity*

408 Altering the reference natural mortality rate or steepness by 25% up or down did not alter
409 which management regulations performed optimally (Figures S2-7). Of the additional 24
410 management regulations tested, scenarios 13 and 23-24 performed optimally with respect to both

411 spawning output at the end of the time series and HPUE. These refer to management regulations
412 which delay the season one month and reduce the bag limit to 1 gallon (scenario 13) or delay the
413 season one month and have rolling bag limits of 1, 1, 2 (scenario 23), and 1, 2, and 2 gallons for
414 months in the season (scenario 24) respectively. These scenarios represent a fine-tuning of the
415 best performing regulations out of the initial 10 scenarios.

416 *3.4 Summary of Results*

417 The results reveal three main findings. First, if a scallop population is known to be
418 relatively less exploited (i.e., greater spawning output, lesser effort, or both), then nearly any of
419 the harvest regulations assessed here perform similarly well. The converse of this constitutes the
420 second point: in cases where the scallop population status is either known to be more exploited,
421 or is largely unknown, harvest regulations like later seasons and rolling bag limits that are more
422 aligned with the biology and, specifically, the spawning times of this short-lived, annual species
423 will result in better biological and fishery performance (as measured by spawning output and
424 HPUE). Finally, the third finding is that there are some harvest regulations which are likely to
425 perform poorly under greater exploitation (whether from lower spawning output, greater effort,
426 or both). Specifically, any regulations that move the season earlier, and thus results in more
427 scallops being harvested prior to their spawning, risks both the lowest egg production and HPUE
428 returns.

429

430 **4. Discussion**

431 Fisheries for short-lived, annual taxa are likely to be particularly sensitive to harvest
432 timing relative to spawning. In the case of the Florida bay scallop, biologically-designed
433 regulations (e.g., later season or rolling bag) ensured some scallops spawn prior to harvest and

434 performed well across all initial exploitation levels and effort treatments in both the ecological
435 and socioeconomic metrics. Under greater initial exploitation and effort, these regulations
436 outperformed others, where they performed no worse than the others under lower initial
437 population exploitation and effort scenarios. Moreover, these regulations were much more robust
438 in our worst-case scenarios (explored as sensitivities), those being when natural mortality was
439 higher or steepness lower, coupled with higher initial exploitation and when effort increasing
440 over the time series (Figures S2-S7). This is generally consistent with the long history of
441 fisheries regulations attempting to protect some spawning individuals (Lackey, 2005), and we
442 have shown that for short-lived, annual species like the Florida bay scallop, doing so may be
443 achieved through specific timing of the harvest season.

444 The efficacy of delayed and rolling bag limits in the Florida Bay scallop fishery is
445 supported by findings of better-studied annual and/or semelparous species, as well as the few
446 studies focusing on bay scallops. While not exclusively annual species, the most well-known
447 commercially harvested semelparous species include some of the Pacific salmon and pelagic
448 squid species (Eggers, 1993; Arkhipkin et al., 2015). These populations are often managed under
449 escapement policies that require annual monitoring (Rodhouse, 2001), which is more precise but
450 conceptually similar to the harvest strategies we found performed well for the Florida bay scallop
451 fishery. Whereas escapement-based management typically relies on monitoring to determine
452 when the targeted amount of reproduction has occurred, our model identified regulations that
453 delayed much of the harvest until after spawning. Studies evaluating the harvest of bay scallop
454 populations are more sparse. One of the most comparable studies is bioeconomic investigation of
455 the North Carolina commercial bay scallop fishery (Kellogg et al., 1988). Although it did not
456 include a detailed population dynamics model and focused on commercial rather than

457 recreational objectives, it similarly concluded that delaying harvest seasons would optimize
458 profits. Additionally, Granneman et al. (2021) estimated bay scallop pre- and post-season
459 population size, harvest, and effort for 2018 in the Steinhatchee area of the Florida Gulf Coast,
460 although they also did not include a population dynamics model with stock and recruitment.
461 They evaluated various management strategies with respect to season lengths and effort levels
462 and found similar results to this study where under the current management regulations, a
463 doubling of effort would likely extirpate the population. In addition, they estimated that rolling
464 bag limits would also lead to increased post-season bay scallop populations.

465 The main management implication of this work is that biologically designed harvest
466 regulations provide better outcomes, especially under uncertainty (e.g., actual population size
467 and effort levels). The results emphasize that there are essentially two management strategies for
468 sustaining the egg production of scallops. The first is to maintain a fishery at relatively low
469 levels of exploitation. Though requiring substantial, more costly annual monitoring to assess, this
470 would allow for the imposition of a broad range of harvest regulations. The second approach
471 would be to employ biologically designed harvest regulations that specifically delay some
472 harvest until more scallops have likely spawned. The outcomes in the biological and
473 socioeconomic metrics show that a biologically-designed approach performs well under nearly
474 all exploitation scenarios. This implies that biologically-designed harvest approaches will likely
475 be effective even in absence of a substantial monitoring program by ensuring a sufficient
476 proportion survive to spawn. If the actual exploitation is low but also unknown, these harvest
477 regulations will at worst perform barely below other approaches, whereas if the exploitation is
478 higher, they will perform substantially better. However, this harvest approach notably does not
479 reduce effort capacity, leaving the fishery vulnerable to increases in total effort (Mullon et al.,

480 2005). Thus, the primary finding of our work aligns with Young et al. (2006); there is little
481 reason to not apply biologically designed regulations to short-lived and annual fisheries.
482 However, what these biologically designed regulations should be may differ across species and
483 fisheries. For many annual species, it is likely a delayed harvest season and rolling bag limit will
484 work well, but the specific harvest strategy and timing should be investigated on a case-by-case
485 basis.

486 The approach we used provides a blueprint for evaluating management regulations for
487 other short-lived, annual recreational fisheries where catch and effort data are sparse.
488 Recreational fisheries for these types of species are common and popular (e.g., Lellis-Dibble et
489 al., 2008; Taylor 2017; Aguilera, 2018; Ben-Hasan, 2018; Sydeman et al., 2020), but harvest
490 regulations are not often evaluated (Forbes et al., 2019). Quantitative evaluation of these
491 fisheries can be complicated by at least two factors, and we demonstrate how both may be
492 addressed. The first challenge is that annual species life histories are not generally well-
493 represented by modern fisheries population dynamics modeling (Martell et al., 2008), in which
494 spawning is generally iteroparous and occurs once per modeled time step. Complete or partial
495 semelparity and corresponding periodic recruitment can be achieved by using monthly time steps
496 (as opposed to annual) with simple timing skips (spawning ever n th time step) and incorporating
497 this into recruitment calculations (T2.3 and T2.9). The second complication is that recreational
498 fisheries for these types of short-lived species will often involve bag limits (Hartill et al., 2005;
499 Reid and Montgomery, 2005; Obregón, 2020). Bag limits are easy to implement in individual-
500 based models (IBMs) but challenging in the population and fishery-level models that are most
501 commonly employed (Martell et al., 2008). Our approach provides a more mechanistic

502 description of how changing bag limits will translate to altered total harvest, which builds off
503 what has been used in earlier recreational fisheries evaluations (Forbes et al., 2019).

504 Application of our approach should consider several assumptions that could not be
505 verified, and which could affect outcomes. An important one is the implicit assumption that the
506 HPUE metric is sufficient to represent socioeconomic objectives of the fishery. This assumption
507 would be inappropriate for many, if not most, longer-lived finfish recreational fisheries, where
508 the size and rate of catch and harvest are critical components of utility (Hunt et al., 2019), but is
509 probably more appropriate for Florida bay scallops that are gathered (not angled) at a more
510 uniform size compared to most finfish (Granneman et al., 2021). Furthermore, the
511 recommendations we made are conservative with respect to any (unknown) preference for size in
512 that the average size of harvested scallops is likely to increase under the biologically-designed
513 regulations we have recommended. If this modeling approach is applied to other fisheries with
514 perhaps more diverse motivations or types of fishers, multi-attribute utility per trip metrics
515 (Camp et al., 2019; van Poorten and Camp, 2019) or some measure of satisfaction (Birdsong et
516 al., 2021) should be considered. Those approaches should also be applied to future bay scallop
517 work if emerging evidence suggests non-harvest utility or satisfaction is affected by harvest
518 regulations (e.g., regulations increasing congestion or leading to harvest seasons overlapping
519 with less enjoyable weather).

520 Two other important considerations not assessed in this study include scallops
521 metapopulation structure and the political economy of local scallop management. This work
522 considered a single population that supplies its own spawning biomass and thus recruits because
523 this simple approach increases the clarity of the results and matches the current regional scallop
524 management approach. However, there is some evidence that more complex metapopulation

525 dynamics exist, with local populations being subsidized by larvae from other populations
526 (Arnold et al., 1998; Bert et al., 2014). If in the future such metapopulation structure can be
527 understood well enough to assess the probabilities of larvae spawned in one region settling in
528 another, spatial population modeling should be used to assess population sources and sinks.

529 Regardless of metapopulation structure, future studies should assess how harvest
530 regulations implemented differently across the region could directly or indirectly affect effort
531 and the potential landscape consequences of this. By testing scenarios in which overall effort
532 increased in the future, we account for long-term changes in effort independent of regulations,
533 but not for effort dynamics driven directly by regulations or indirectly by regulatory-induced
534 population changes. Empirical (Johnson and Carpenter, 1994; Beard et al., 2003; Post and
535 Parkinson, 2012) and theoretical (Hunt et al., 2011; Allen et al., 2013) studies suggest that
536 altered harvest restrictions can affect fishing effort in some fisheries, though the direction of the
537 effect is not always intuitive (Hurley and Jackson, 2002). Thus, it is possible that the alternative
538 regulations we explore could differently affect scallop fishing effort, which could instigate
539 effort-population feedbacks and alter our results. Future work studying this should assess, such
540 as by stated preference choice experiment, the part-worth utility functions influencing scalloper
541 decision-making. Borrowing those estimated for fin-fisheries (reviewed in Hunt et al., 2019) may
542 be inappropriate because of differences between often challenge-motivated fin-fisheries and
543 scallop fisheries that are more gathering. Such models could consider not only consumer demand
544 for scallops but also the political economy governing regional management decisions. Here, we
545 have implicitly assumed a shift in the harvest season is sufficiently palatable to decision-makers.
546 In reality, shifting towards a later harvest season, including one that occurs after the current
547 summer season closes, may reduce the demand for scallop fishing and alter the economic

548 contribution of the fishery. Recreational scalloping is a family-oriented activity, with peak
549 participation in the summertime holidays and on the weekends (Granneman et al., 2021). As the
550 season progresses, there are fewer scallop trips, which may be attributable to the start of the
551 school year, hunting season, and hurricane season. Evaluating the socioeconomic effects of a
552 later-shifted season would require assessing the economic contribution to local economies and
553 how fishers are likely to behave under the new regulations. The absence of information about
554 scalloper behavior precluded a dynamic effort component of this model but revealed or stated
555 preference choice studies could address both these issues. Estimating a mechanistic and
556 predictive model of scallop effort would facilitate developing landscape models for testing how
557 population and regulatory changes in one region could affect others, per van Poorten and Camp
558 (2019). This is critical to avoid triggering cascading or unintended consequences for the regional
559 scallop population and fishery.

560

561 **5. Conclusions**

562 This work demonstrates that biologically-designed harvest regulations that consider the
563 overlap between harvest and spawning seasons are likely to provide ecological and
564 socioeconomic advantages over approaches currently employed for the bay scallop fishery in
565 Florida. Regulations such as later harvest seasons and rolling bag limits likely buffer against
566 uncertainty in the depletion level of the population. While many short-lived, annual species
567 exhibit harvest seasons presumably designed with respect to their spawning, this is one of the
568 first studies to quantitatively evaluate it. It provides a modeling framework that may be more
569 broadly applicable to other taxa. This template might be expanded via future research to allow

570 for more mechanistic descriptions of fisher utility, decision making, and implications for local
571 economic contribution.

572

573 **CRedit authorship contribution statement**

574 **Lisa Chong:** Methodology, Formal analysis, Writing – Investigation, Visualization, Review &
575 editing. **Nicholas Fisch:** Methodology, Formal analysis, Writing – Original draft, Investigation,
576 Review & editing. **John Scott Borsum:** Writing – Original draft, Review & editing. **Jennifer**
577 **Granneman:** Writing - Review & editing. **Diana Perry:** Writing - Original draft, Review &
578 editing. **Gabrielle Love:** Writing - Review & editing. **Brittany Hall-Scharf:** Writing - Review
579 & editing. **Robert Botta:** Writing - Review & editing. **Kai Lorenzen:** Writing - Review &
580 editing. **Edward Camp:** Supervision, Conceptualization, Methodology, Writing – Original draft,
581 Investigation, Review & editing. **Zachary Siders:** Supervision, Methodology, Writing –
582 Investigation, Visualization, Review & editing.

583

584 **Declaration of Competing Interest**

585 The authors report no declarations of interest.

586

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591

592 6. Supplementary information

593 **Table S1.** Management regulations tested. When bag limit is presented in parentheses, it refers
594 to the bag limit for each open month of the fishing season.

595 **Figure S1.** Results of generalized linear mixed model fit to the logarithm-transformed effort as a
596 function of day with a random effect for weekday. The observed data from Granneman et al.
597 (2021) is shown in black circles and the model-based predictions are shown in the red line.

598 **Figure S2.** Results of spawning output relative to unfished for the different management
599 regulations simulated in this study under different starting levels of population exploitation
600 (columns, only low and high depicted here) and different assumptions about the level of effort
601 expended between years (rows). The first row depicts a scenario with constant effort in each year
602 of the simulation, where the second row depicts a scenario with effort doubling over the course
603 of the 25-year simulation period. The horizontal lines depict the sensitivity analysis for natural
604 mortality ($M = 0.25$), where the red lines represent 25% decrease in natural mortality ($M = 0.19$)
605 and the orange lines represent 25% increase in natural mortality ($M = 0.32$).

606 **Figure S3.** Results of spawning output relative to unfished for the different management
607 regulations simulated in this study under different starting levels of population exploitation
608 (columns, only low and high depicted here) and different assumptions about the level of effort
609 expended between years (rows). The first row depicts a scenario with constant effort in each year
610 of the simulation, where the second row depicts a scenario with effort doubling over the course
611 of the 25-year simulation period. The horizontal lines depict the sensitivity analysis for steepness
612 ($h = 0.67$; $CR = 8$), where the red lines represent 25% decrease in steepness (50% decrease in

613 compensation ratio; $h = 0.5$ and $CR = 4$) and the orange lines represent 25% increase in
614 steepness (150% increase in compensation ratio; $h = 0.83$ and $CR = 20$).

615 **Figure S4.** Results of harvest per unit of effort for the different management regulations
616 simulated in this study under different starting levels of population exploitation (columns, only
617 low and high depicted here) and different assumptions about the level of effort expended
618 between years (rows). The first row depicts a scenario with constant effort in each year of the
619 simulation, where the second row depicts a scenario with effort doubling over the course of the
620 25-year simulation period. The horizontal lines depict the sensitivity analysis for natural
621 mortality ($M = 0.25$), where the red lines represent 25% decrease in natural mortality ($M = 0.19$)
622 and the orange lines represent 25% increase in natural mortality ($M = 0.32$).

623 **Figure S5.** Results of harvest per unit of effort for the different management regulations
624 simulated in this study under different starting levels of population exploitation (columns, only
625 low and high depicted here) and different assumptions about the level of effort expended
626 between years (rows). The first row depicts a scenario with constant effort in each year of the
627 simulation, where the second row depicts a scenario with effort doubling over the course of the
628 25-year simulation period. The horizontal lines depict the sensitivity analysis for steepness ($h =$
629 0.67 ; $CR = 8$), where the red lines represent 25% decrease in steepness (50% decrease in
630 compensation ratio; $h = 0.5$ and $CR = 4$) and the orange lines represent 25% increase in
631 steepness (150% increase in compensation ratio; $h = 0.83$ and $CR = 20$).

632 **Figure S6.** Results of catch per unit of effort for the different management regulations simulated
633 in this study under different starting levels of population exploitation (columns, only low and
634 high depicted here) and different assumptions about the level of effort expended between years
635 (rows). Catch per unit effort includes both scallops harvested and scallops caught and released in

636 order to comply with the bag limit. The first row depicts a scenario with constant effort in each
637 year of the simulation, where the second row depicts a scenario with effort doubling over the
638 course of the 25-year simulation period. The horizontal lines depict the sensitivity analysis for
639 natural mortality ($M = 0.25$), where the red lines represent 25% decrease in natural mortality (M
640 $= 0.19$) and the orange lines represent 25% increase in natural mortality ($M = 0.32$).

641 **Figure S7.** Results of catch per unit of effort for the different management regulations simulated
642 in this study under different starting levels of population exploitation (columns, only low and
643 high depicted here) and different assumptions about the level of effort expended between years
644 (rows). Catch per unit effort includes both scallops harvested and scallops caught and released in
645 order to comply with the bag limit. The first row depicts a scenario with constant effort in each
646 year of the simulation, where the second row depicts a scenario with effort doubling over the
647 course of the 25-year simulation period. The horizontal lines depict the sensitivity analysis for
648 steepness ($h = 0.67$; $CR = 8$), where the red lines represent 25% decrease in steepness (50%
649 decrease in compensation ratio; $h = 0.5$ and $CR = 4$) and the orange lines represent 25% increase
650 in steepness (150% increase in compensation ratio; $h = 0.83$ and $CR = 20$).

651 **7. References**

- 652 Abele, D., Brey, T., Philipp, E., 2009. Bivalve models of aging and the determination of
653 molluscan lifespans. *Exp. Gerontol.* 44, 307-315.
- 654 Aguilera, S., 2018. Measuring squid fishery governance efficacy: A social-ecological system
655 analysis. *Int. J. Commons.* 12.
- 656 Allen, M.S., Ahrens, R.N.M., Hansen, M.J., Arlinghaus, R., 2013. Dynamic angling effort
657 influences the value of minimum-length limits to prevent recruitment overfishing. *Fish.*
658 *Manag. Ecol.* 20, 247-257.
- 659 Arnold, W.S., Blake, N.J., Harrison, M.M., Marelli, D.C., Parker, M.L., Peters, S.C., Sweat,
660 D.E., 2005. Restoration of bay scallop (*Argopecten irradians* (Lamarck)) populations in
661 Florida coastal waters: planting techniques and the growth, mortality and reproductive
662 development of planted scallops. *J. Shellfish Res.* 24, 883-904.
- 663 Arkhipkin, A.I., Rodhouse, P.G., Pierce, G.J., Sauer, W., Sakai, M., Allcock, L., Zeidberg, L.D.,
664 2015. World squid fisheries. *Rev. Fish. Sci. Aquac.* 23, 92-252.
- 665 Arkhipkin, A.I., Hendrickson, L.C., Payá, I., Pierce, G.J., Roa-Ureta, R.H., Robin, J.P. and
666 Winter, A., 2021. Stock assessment and management of cephalopods: advances and
667 challenges for short-lived fishery resources. *ICES J. Mar. Sci.* 78, 714-730.
- 668 Arkhipkin, A.I., Winter, A.G. and Nigmatullin, C.M., 2022. Heavy fishery exploitation does not
669 affect sizes at recruitment and maturity of squid *Illex argentinus* and *Doryteuthis gahi*, in
670 the Southwest Atlantic. *ICES J. Mar. Sci.* 79, 182-192.
- 671 Baranov, F.I., 1918. On the question of the biological basis of fisheries. *Nauch. Issledov. Iktiolog.*
672 *Inst. Izv. I., Moscow*, pp. 81–128.

673 Barber, B.J., Blake, N.J., 1983. Growth and reproduction of the bay scallop, *Argopecten*
674 *irradians* (Lamarck) at its southern distributional limit. J. Exp. Mar. Biol. Ecol. 66, 247-
675 256.

676 Barber, B.J. and Blake, N.J., 1985. Substrate catabolism related to reproduction in the bay
677 scallop *Argopecten irradians concentricus*, as determined by O/N and RQ physiological
678 indexes. Mar. Biol. 87, 13-18.

679 Beard Jr, T.D., Cox, S.P., Carpenter, S.R., 2003. Impacts of daily bag limit reductions on angler
680 effort in Wisconsin walleye lakes. N. Am. J. Fish. Manag. 23, 1283-1293.

681 Ben-Hasan, A., Walters, C., Louton, R., Christensen, V., Sumaila, U.R., Al-Foudari, H., 2018.
682 Fishing-effort response dynamics in fisheries for short-lived invertebrates. Ocean Coast.
683 Manag. 165, 33-38.

684 Benoît, H.P., Capizzano, C.W., Knotek, R.J., Rudders, D.B., Sulikowski, J.A., Dean, M.J.,
685 Mandelman, J.W., 2015. A generalized model for longitudinal short-and long-term
686 mortality data for commercial fishery discards and recreational fishery catch-and-
687 releases. ICES J. Mar. Sci. 72, 1834-1847.

688 Bert, T.M., Arnold, W.S., McMillen-Jackson, A.L., Wilbur, A.E., Crawford, C., 2011. Natural
689 and anthropogenic forces shape the population genetics and recent evolutionary history of
690 eastern United States bay scallops (*Argopecten irradians*). J. Shellfish Res. 30, 583-608.

691 Bert, T.M., Arnold, W.S., Wilbur, A.E., Seyoum, S., McMillen-Jackson, A.L., Stephenson, S.P.,
692 Weisberg, R.H. and Yarbrow, L.A., 2014. Florida gulf bay scallop (*Argopecten irradians*
693 *concentricus*) population genetic structure: Form, variation, and influential factors. J.
694 Shellfish Res. 33, 99-136.

695 Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. U.K. Minist.
696 Agric. Fish. Fish. Invest. Ser. 2, 19.

697 Birdsong, M., Hunt, L.M., Arlinghaus, R., 2021. Recreational angler satisfaction: What drives
698 it?. Fish. 22, 682-706.

699 Blake, N.J., 1972. Environmental regulation of neurosecretion and reproductive activity in the
700 bay scallop, *Aequipecten irradians* (Lamarck). Ph.D. Thesis, University of Rhode Island,
701 Kingston. 161 p.

702 Brent, R., 1973. Algorithms for Minimization without Derivatives. Englewood Cliffs, NJ:
703 Prentice-Hall.

704 Bricelj, V.M., Krause, M.K., 1992. Resource allocation and population genetics of the bay
705 scallop, *Argopecten irradians*: effects of age and allozyme heterozygosity on
706 reproductive output. Mar. Biol. 113, 253-261.

707 Camp, E.V., Lorenzen, K., Taylor, M.D., 2019. Impacts of habitat repair on a spatially complex
708 fishery. Estuar. Coast. Shelf Sci. 244, 106102.

709 Eggers, D.M., 1993. Robust harvest policies for Pacific salmon fisheries. In Proceedings of the
710 International Symposium on Management Strategies for Exploited Fish Populations.
711 Alaska Sea Grant Report No. 93-02, pp 85-106.

712 Estabrooks, S.L., 2007. The possible role of telomeres in the short life span of the bay scallop,
713 *Argopecten irradians* (Lamarck 1819). J. Shellfish Res. 26, 307-313.

714 Forbes, J.P., Todd, C.R., Baumgartner, L.J., Watts, R.J., Robinson, W.A., Steffe, A.S., Thiem,
715 J.D., 2019. Simulation of different fishery regulations to prevent population decline in a
716 large freshwater invertebrate, the Murray crayfish (*Euastacus armatus*). Mar. Freshw.
717 Res. 71, 962-971.

718 Geiger, S.P., Cobb, J., Arnold, W.S., 2006. Variations in growth and reproduction of bay
719 scallops (*Argopecten irradians*) (Lamarck, 1819) from six subpopulations in the
720 northeastern Gulf of Mexico. *J. Shellfish Res.* 25, 491–501.

721 Geiger, S.P., Stephenson, S.P., Arnold, W.S., 2010. Protracted recruitment in the bay scallop
722 *Argopecten irradians* in a west Florida estuary. *J. Shellfish Res.* 29, 809–817.

723 Goodyear, C.P., 1980. Compensation in fish population, in: Hocutt C.H., Stauffer J.R. Jr, (Eds.).
724 Biological monitoring of fish. Lexington Books, DC Heath and Company, pp. 253–280.

725 Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: foundation
726 and current use. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 67-82.

727 Granneman, J., Baxley, C., Bollinger, M., Heil, A., LaGanke, M., Levine, E., Williams, K., 2021.
728 Evaluating the Impact of Recreational Harvest and Management Strategies for Bay
729 Scallops *Argopecten irradians concentricus* in a Florida Gulf Coast Management Zone.
730 *Mar. Coast. Fish.* 13, 413-432.

731 Hall-Scharf, B., Adams, C.M., Hodges, A.W., Geiger, S., 2018. Assessment of the Economic
732 Impact Associated with the Recreational Scallop Season in Hernando County, Florida,
733 TP-235/SG161, 8/2018. EDIS, 2018.

734 Hartill, B.W., Cryer, M., Morrison, M.A., 2005. Estimates of biomass, sustainable yield, and
735 harvest: neither necessary nor sufficient for the management of non-commercial urban
736 intertidal shellfish fisheries. *Fish. Res.* 71, 209-222.

737 Hoshino, E., Milner-Gulland, E.J., Hillary, R.M., 2012. Bioeconomic adaptive management
738 procedures for short-lived species: A case study of Pacific saury (*Cololabis saira*) and
739 Japanese common squid (*Todarodes pacificus*). *Fish. Res.* 121, 17-30.

740 Hunt, L.M., Arlinghaus, R., Lester, N., Kushneriuk, R., 2011. The effects of regional angling
741 effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing.
742 Ecol. Appl. 21, 2555-2575.

743 Hunt, L.M., Camp, E., van Poorten, B., Arlinghaus, R., 2019. Catch and non-catch-related
744 determinants of where anglers fish: a review of three decades of site choice research in
745 recreational fisheries. Rev. Fish. Sci. Aquac. 27, 261-286.

746 Hurley, K.L., Jackson, J. J., 2002. Evaluation of a 254-mm minimum length limit for crappies in
747 two southeast Nebraska reservoirs. N. Am. J. Fish. Manag. 22, 1369-1375.

748 Johnson, B.M., Carpenter, S.R., 1994. Functional and numerical responses: a framework for fish-
749 angler interactions?. Ecol. Appl. 4, 808-821.

750 Kellogg, R.L., Easley Jr, J.E., Johnson, T., 1988. Optimal timing of harvest for the North
751 Carolina bay scallop fishery. Am. J. Agric. Econ. 70, 50-62.

752 Lackey, R.T., 2005. Fisheries: history, science, and management. Water encyclopedia: surface
753 and agricultural water, 121-129.

754 Lellis-Dibble, K.A., McGlynn, K.E., Bigford, T.E., 2008. Estuarine fish and shellfish species in
755 US commercial and recreational fisheries: economic value as an incentive to protect and
756 restore estuarine habitat. U.S. Dep. Commerce, NOAA Tech. Memo. NMFSF/SPO-90,
757 94 p.

758 Leverone, J.R., 1992. Environmental requirements assessment of bay scallop *Argopecten*
759 *irradians concentricus*. Mote Marine Laboratory Technical Report, no 253.

760 Lorenzen, K., 2000. Allometry of natural mortality as a basis for assessing optimal release size in
761 fish-stocking programmes. Can. J. Fish. Aquat. 57, 2374-2381.

762 Lorenzen, K., 2022. Size- and age-dependent natural mortality in fish populations: Biology,
763 models, implications, and a generalized length-inverse mortality paradigm. *Fish. Res.*
764 255, 106454.

765 MacKenzie Jr, C.L., 2008. The bay scallop, *Argopecten irradians*, Massachusetts through North
766 Carolina: its biology and the history of its habitats and fisheries. *Mar. Fish. Rev.* 70, 6-79.

767 Martell, S.J., Pine, W.E., Walters, C.J., 2008. Parameterizing age-structured models from a
768 fisheries management perspective. *Can. J. Fish. Aquat.* 65, 1586-1600.

769 Melnychuk, M.C., Young, E.G., Anderson, L.E., Hilborn, R., 2021. Trading off retained daily
770 catch for longer seasons to maximize angler benefits in recreational fisheries
771 management. *ICES J. Mar. Sci.* 78, 1650-1662.

772 Myers, R.A., 2001. Stock and recruitment: generalizations about maximum reproductive rate,
773 density dependence, and variability using meta-analytic approaches. *ICES J. Mar. Sci.*,
774 58, 937-951.

775 Mullon, C., Fréon, P., Cury, P., 2005. The dynamics of collapse in world fisheries. *Fish.* 6, 111-
776 120.

777 Obregón, C., Tweedley, J.R., Loneragan, N.R., Hughes, M., 2020. Different but not opposed:
778 perceptions between fishing sectors on the status and management of a crab fishery. *ICES*
779 *J. Mar. Sci.* 77, 2354-2368.

780 Post, J.R., Parkinson, E.A., 2012. Temporal and spatial patterns of angler effort across lake
781 districts and policy options to sustain recreational fisheries. *Can. J. Fish. Aquat.* 69, 321-
782 329.

783 R Core Team, 2022. A language and environment for statistical computing. R Foundation for
784 Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

785 Reid, D.D., Montgomery, S.S., 2005. Creel survey based estimation of recreational harvest of
786 penaeid prawns in four southeastern Australian estuaries and comparison with
787 commercial catches. *Fish. Res.* 74, 169-185.

788 Robert, M., Faraj, A., McAllister, M.K., Rivot, E., 2010. Bayesian state-space modelling of the
789 De Lury depletion model: strengths and limitations of the method, and application
790 to the Moroccan octopus fishery. *ICES J Mar Sci.* 67, 1272–1290.

791 Rodhouse, P.G., 2001. Managing and forecasting squid fisheries in variable environments. *Fish.*
792 *Res.* 54, 3-8.

793 Rosenberg, A.A., Kirkwood, G.P., Crombie, J.A., Beddington, J.R., 1990. The assessment of
794 stocks of annual squid species. *Fish. Res.* 8, 335-350.

795 Sastry, A.N., 1963. Reproduction of the bay scallop, *Aequipecten irradians* Lamarck. Influence
796 of temperature on maturation and spawning. *Biol. Bull.* 125, 146-153.

797 Sauer, W.H., Gleadall, I.G., Downey-Breedt, N., Doubleday, Z., Gillespie, G., Haimovici, M.,
798 Ibáñez, C.M., Katugin, O.N., Leporati, S., Lipinski, M.R. and Markaida, U., 2021. World
799 octopus fisheries. *Rev. Fish. Sci. Aquac.* 29, 279-429.

800 Shumway, S.E., Parsons, G.J.G., (Eds.). 2016. *Scallops: biology, ecology, aquaculture, and*
801 *fisheries.* Elsevier, 1214 p.

802 Sydeman, W.J., Dedman, S., García-Reyes, M., Thompson, S.A., Thayer, J.A., Bakun, A.,
803 MacCall, A.D., 2020. Sixty-five years of northern anchovy population studies in the
804 southern California Current: a review and suggestion for sensible management. *ICES J.*
805 *Mar. Sci.* 77, 486-499.

806 Taylor, M.D., 2017. Preliminary evaluation of the costs and benefits of prawn stocking to
807 enhance recreational fisheries in recruitment limited estuaries. *Fish. Res.* 186, 478-487.

808 van Poorten, B.T., Camp, E.V., 2019. Addressing challenges common to modern recreational
809 fisheries with a buffet-style landscape management approach. *Rev. Fish. Sci. Aquac.* 27,
810 393-416.

811 Young, J.L., Bornik, Z.B., Marcotte, M.L., Charlie, K.N., Wagner, G.N., Hinch, S.G., Cooke,
812 S.J., 2006. Integrating physiology and life history to improve fisheries management and
813 conservation. *Fish.* 7, 262-283.

814 Žák, J., Vrtílek, M., Polačik, M., Blažek, R., Reichard, M., 2021. Short-lived fishes: Annual and
815 multivoltine strategies. *Fish Fish.* 22, 546-561.

816 **Figure captions**

817 **Figure 1.** Map of Big Bend region of Florida (red rectangle in inset) depicting the five scalloping
818 zones (A-E). Zone D (depicted in orange) was the area chosen for the baseline management
819 regulations in this study and spans Levy, Citrus, and Hernando counties. The per person bag
820 limit in gallons of whole scallops as well as the dates for the open and close of the scalloping
821 season are provided in the table by zone. Note that zone C has a rolling bag limit that is 50%
822 lower in the first 15 day of the season.

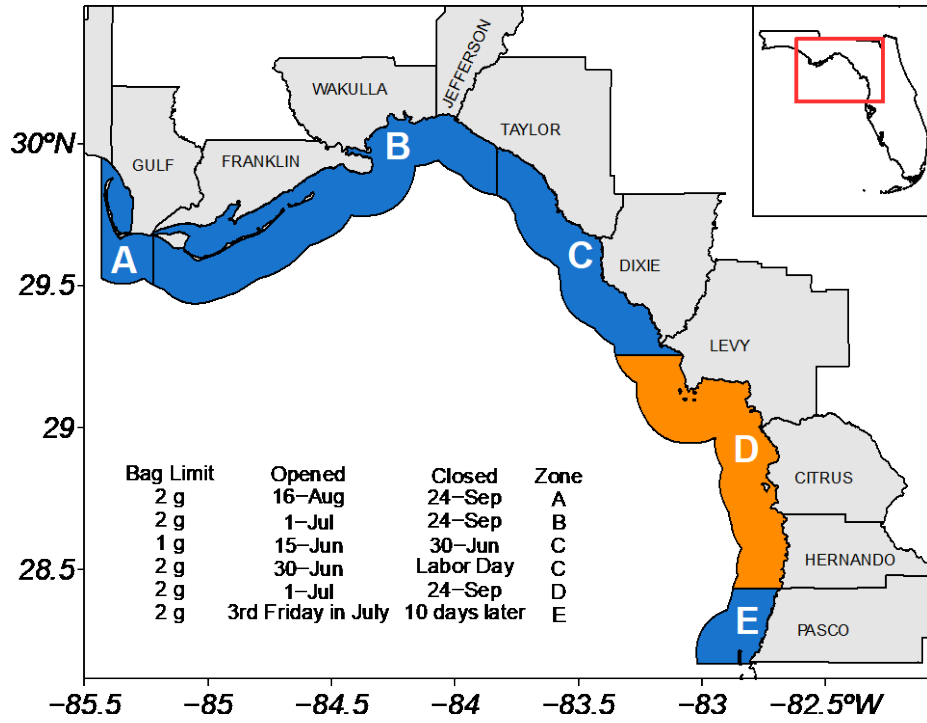
823
824 **Figure 2.** The shell height at age (A), weight at age (B), selectivity at age (C), proportion mature
825 at age (D), and natural mortality at age (E) for bay scallops calculated from the life history
826 parameters assumed in the simulation model.

827
828 **Figure 3.** Results of spawning output relative to unfished for the different management
829 regulations simulated in this study under different starting levels of population exploitation
830 (columns) and different assumptions about the level of effort expended between years (rows).
831 The first row depicts a scenario with constant effort in each year of the simulation, where the
832 second row depicts a scenario with effort doubling over the course of the 25-year simulation
833 period.

834
835 **Figure 4.** Results of harvest per unit of effort for the different management regulations simulated
836 in this study under different starting levels of population exploitation (columns) and different
837 assumptions about the level of effort expended between years (rows). The first row depicts a

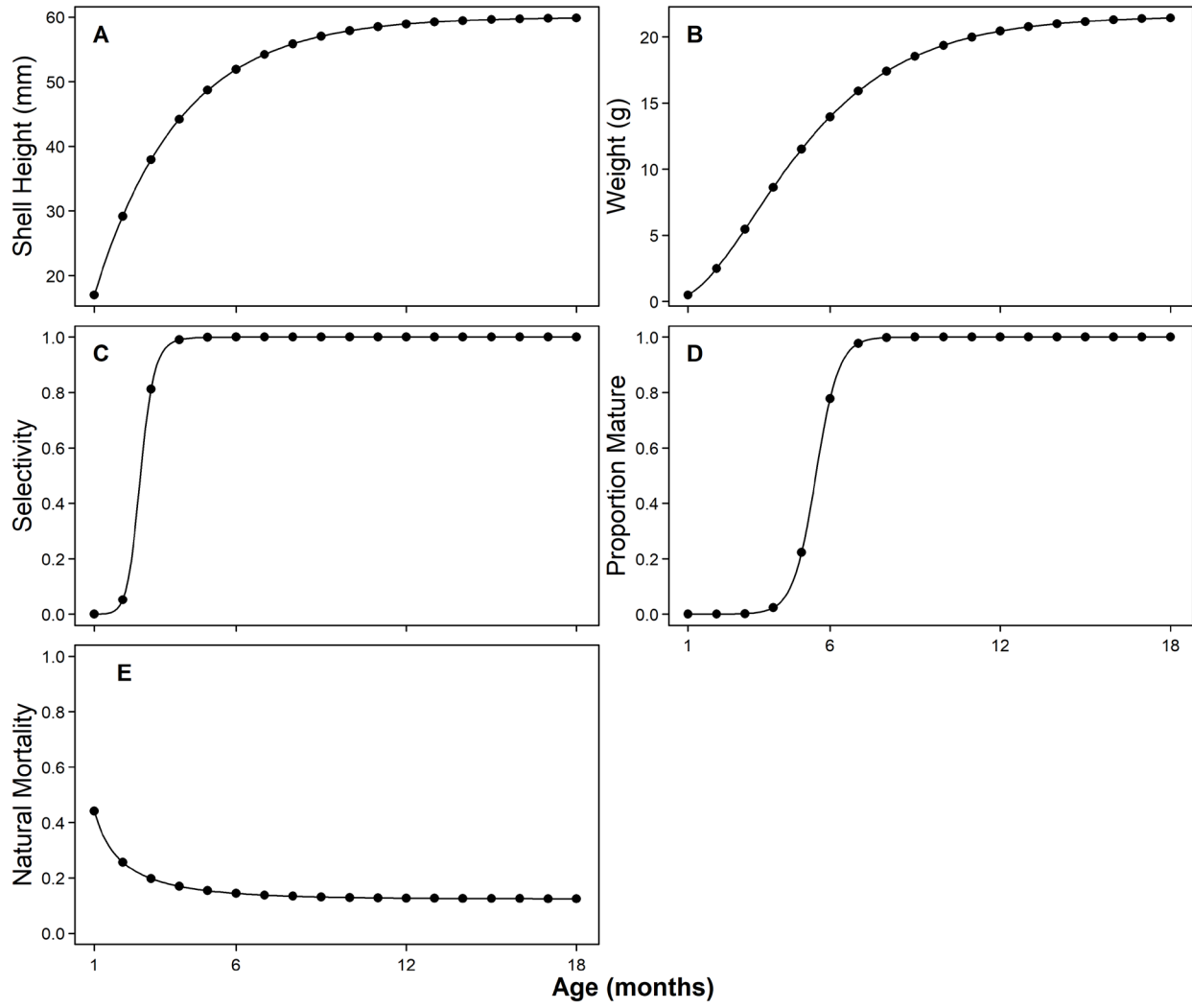
838 scenario with constant effort in each year of the simulation, where the second row depicts a
839 scenario with effort doubling over the course of the 25-year simulation period.

1 **Figures**



2

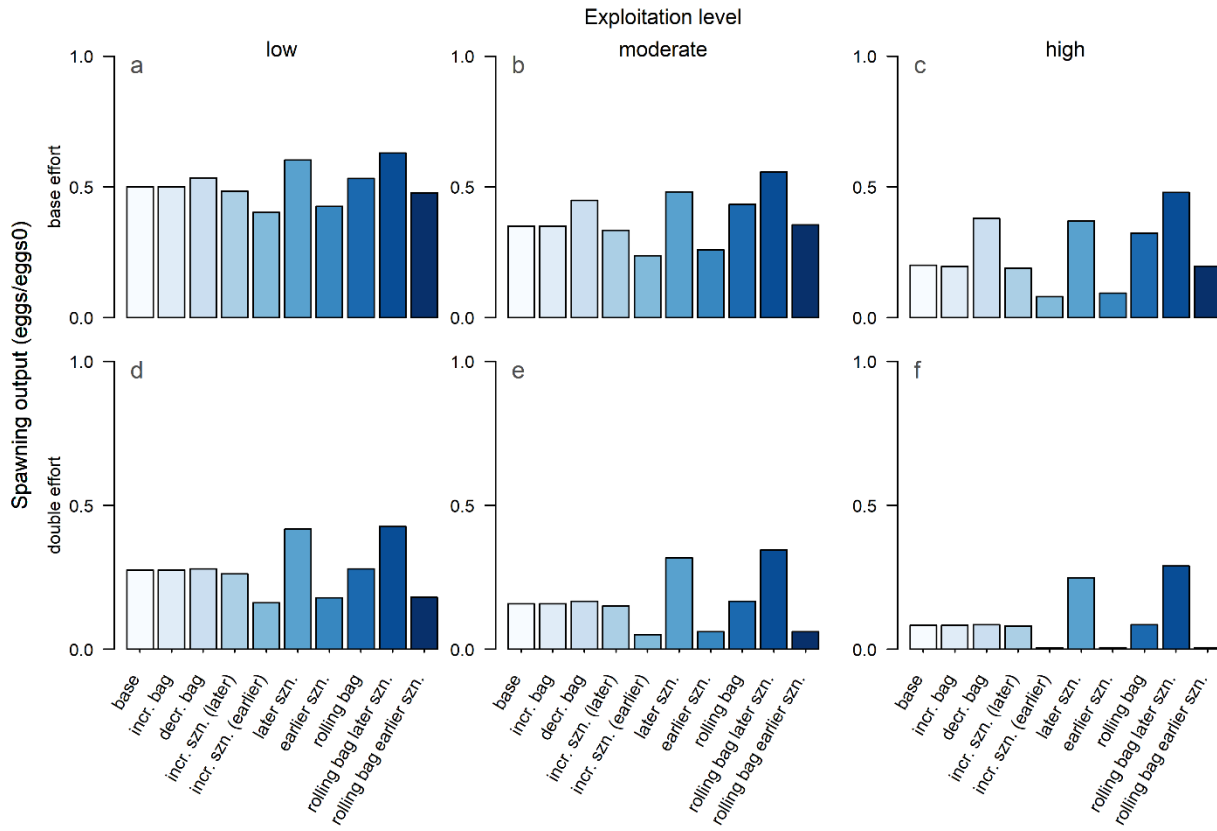
3 **Figure 1.**



4

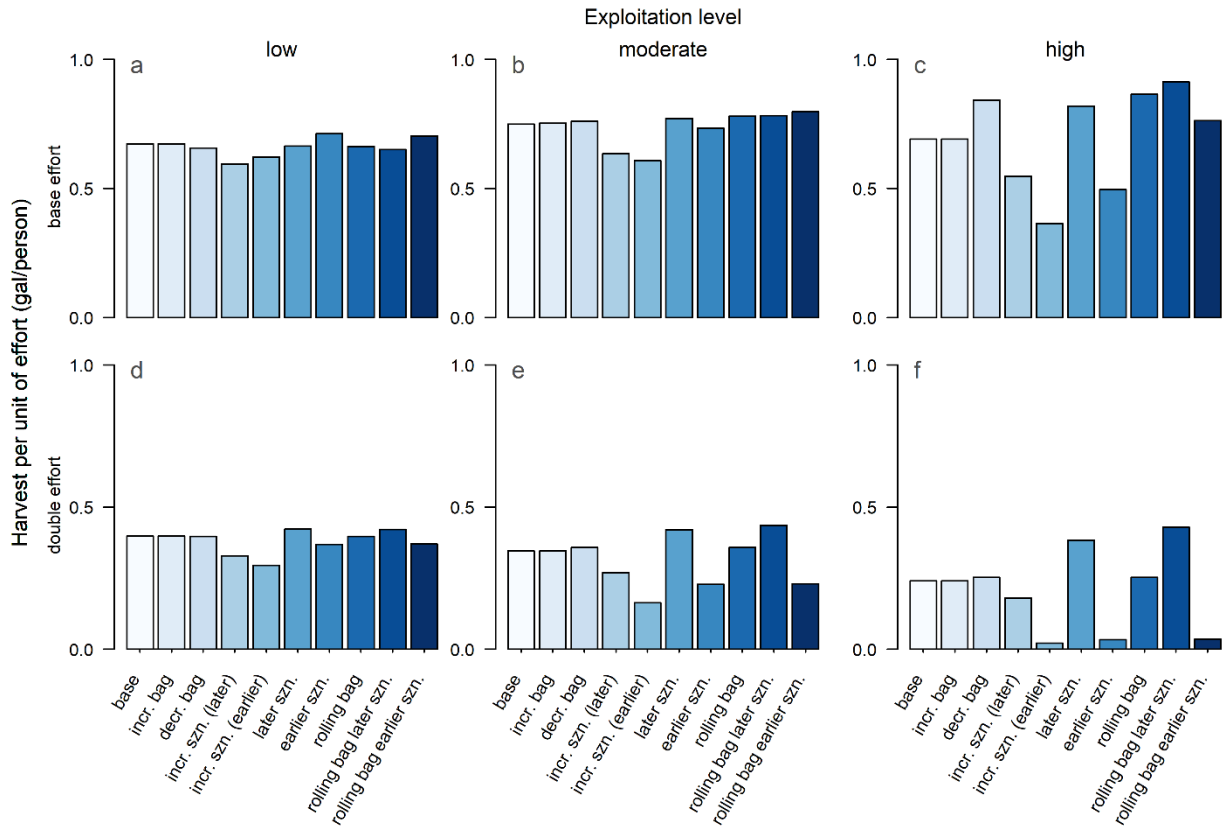
5 **Figure 2.**

6



7

8 **Figure 3.**



11 **Figure 4.**

Tables

Table 1. Parameters used in the bay scallop simulation model and their source. We provide more detail on how the source material led to the parameter values in the supplemental.

Description	Parameter	Value	Source
Life History			
Asymptotic length	L_∞	60	Barber and Blake (1983); Leverone et al. (1992); Geiger et al. (2006)
Brody growth coefficient	K	1/3	Barber and Blake (1983); Leverone et al. (1992); Geiger et al. (2006)
Theoretical age at size 0	t_0	0	Arbitrary
Length-weight a parameter	a	0.0001	Arbitrary
Length-weight b parameter	b	3	Standard cubic
Natural mortality at reference length	M_r	0.25	Granneman et al. (2021)
Allometric exponent	c	-1	Arbitrary (default)
Reference length	L_r	$L_\infty/2$	Arbitrary (default)
Unfished recruitment	R_0	Calibrated	Calibrated to achieve estimated average gallons of scallops per person similar to that found in Granneman et al. (2021)
Compensation ratio	CR	8	Arbitrary
Maturity parameter 1 (Age at 50% maturity)	ν	5.5	Blake (1972); Barber and Blake (1983); Shumway and Parsons (2016)
Maturity parameter 2 (Growth rate of logistic function)	ζ	2.5	Blake (1972); Barber and Blake (1983); Shumway and Parsons (2016)
Fecundity-weight scalar	η	0.1	Arbitrary

Gonadal-somatic index	GS_{month}	[0.05,0.05,0.05,0.05, 0.05,0.05,0.05,0.09, 0.125,0.09,0.07,0.05]	Fig 5. Geiger et al. (2006)
Probability of spawning in a given month	$\psi_{month} = GS_{month} / \sum_{month=Jan}^{Dec} GS_{month}$		GS_{month}
Management			
Selectivity			
Parameter 1 (length at 50% vulnerable)	κ	35	Arbitrary
Selectivity			
Parameter 2 (growth rate of logistic function)	τ	0.5	Arbitrary
Catchability*	q	0.0000319/3.8	Granneman et al. (2021)
Monthly Effort throughout the course of a year	E_{month}	[0,0,0,0,0,0,11415,6 929,4255,0,0,0]*3.8	Granneman et al. (2021)
Effort between years	$E_t = f(E_{month})$	Constant or linearly increasing to double the initial annual effort at the end of time series	Arbitrary, used as simulation treatment (see section 2.8 on uncertainty of starting conditions)

*Note that this is the catchability value which was used to estimate R_0 , three different values were used to project the population according to the population starting condition scenarios.

Table 2. Various equations used in the bay scallop simulation model.

Equation	Description	Equation
T2.1	Shell height at age	$L_a = L_\infty \left(1 - e^{(-K(a-t_0))}\right)$
T2.2	Weight at age	$W_a = aL_a^b$
T2.3	Natural mortality	$M_a = \begin{cases} M_r \left(\frac{L_a}{L_r}\right)^c & \text{for } 0 \leq a \leq 18 \\ \infty & \text{for } a > 18 \end{cases}$
T2.4	Maturity	$Mat_a = \frac{1}{1 + e^{-\zeta(a-v)}}$
T2.5	Fecundity	$Fec_a = \eta W_a$
T2.6	Fishery Selectivity	$s_a = \frac{1}{1 + e^{-\tau(L_a - \kappa)}}$
T2.7	Alpha Beverton-Holt	$\alpha = \frac{CR}{\Phi_0}$
T2.8	Beta Beverton-Holt	$\beta = \frac{CR - 1}{R_0 * \Phi_0}$
T2.9	Unfished eggs per recruit	$\Phi_0 = \sum_a l_a * Mat_a * \psi_a * \omega_a * Fec_a$
T2.10	Survivorship at age in unfished condition	$l_a = \begin{cases} 1 & \text{if } a = 1 \\ l_{a-1} e^{-(M_{a-1})} & \text{if } a > 1 \end{cases}$
T2.11	Baranov Catch Equation	$C_{a,t} = \frac{F_{a,t}}{F_{a,t} + M_a} N_{a,t} \left(1 - e^{-(F_{a,t} + M_a)}\right)$

Table 3. Management regulations tested in this study. When bag limit is presented in parentheses it refers to the bag limit for each open month of the fishing season. We defined a “rolling” bag limit as one in which the bag limit for the initial months of the season was lower than the limit in the final months. A “fixed” bag limit refers to a single bag limit that is set throughout the season per month.

Number	Name	Bag Limit (gallons)	Bag Type	Season Length (months)	Season Start	Season End
1	Base	2	Fixed	3	July	Sept
2	Increased bag	3	Fixed	3	July	Sept
3	Decreased bag	1	Fixed	3	July	Sept
4	Increased season (later)	2	Fixed	4	July	Oct
5	Increased season (earlier)	2	Fixed	4	June	Sept
6	Later season	2	Fixed	3	Aug	Oct
7	Earlier season	2	Fixed	3	June	Aug
8	Rolling bag limit	(1,2,2)	Rolling	3	July	Sept
9	Rolling bag limit and later season	(1,2,2)	Rolling	3	Aug	Oct
10	Rolling bag limit and earlier season	(1,2,2)	Rolling	3	June	Aug