

1 **Title: Life histories decide reserve benefits in transient yields and bycatch**
2 **persistence**

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22 **Abstract**

23 Recent research indicates that marine reserves can both improve fisheries yields of
24 target species and maintain the persistence of bycatch species. However, the prevalent
25 equilibrium analyses prevent our understandings in transient behavior at short-time
26 scales. Here, we develop high dimensional theoretical frameworks by considering age
27 structure to assess the relative advantages between reserve-only and no-reserve
28 fisheries management strategies. Our results show that whether strategies with only
29 reserves can achieve higher fisheries yields (measured by both weight and number)
30 and maintain bycatch persistence depends on the life histories of both target and
31 bycatch species through perspectives of transient oscillations. Our research has
32 important practical applications especially for the West Coast groundfish fishery in
33 the USA, as it suggests that reserves can perform benefits in both fisheries and
34 conservation goals for target species with older ages at maturity and lower adult
35 survivorship.

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37 **Keywords:** Marine reserves, bycatch persistence, transients, life histories, fisheries
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45 **Introduction**

46 A central problem in marine ecology is improving harvested yields in fisheries and
47 maintaining species persistence and biodiversity in conservation. To meet these goals
48 simultaneously, different fisheries strategic managements have been proposed (Game
49 *et al.* 2009; Gaines *et al.* 2010; Cohen & Foale 2013; Chen *et al.* 2020). Among which
50 the most influenced methods are traditional fixed/limitation harvesting strategies and
51 relatively new proposed ones by designing marine reserves (Hastings & Botsford
52 1999; Hastings *et al.* 2017; Hilborn 2017). The inevitable problem deserving attention
53 is that which method can perform better to achieve higher fisheries yields, but without
54 facing the risk of species extinction because of overfishing. A theoretical framework
55 suggests that establishing marine reserves is a better choice by achieving equivalent
56 fisheries yields with advantages in maintaining species persistence in comparison with
57 traditional fisheries management by harvesting effort control each year (Hastings &
58 Botsford 1999). However, the single species assumption prevents more general
59 predictions in biodiversity such as considering the effect of some more easily extinct
60 species relative to the target species in fisheries.

61

62 The incidental catch of unwanted species (i.e. the so-called "bycatch species") is
63 ubiquitous and has been a great threat to fisheries sustainability (Aalto & Baskett
64 2013; Komoroske & Lewison 2015; Scales *et al.* 2018; Welch *et al.* 2018). Therefore,
65 exploring strategies to improve the harvested yields of the target species but keeping

66 the persistence of the bycatch species have great meanings in the practical
67 applications. To date, protecting the bycatch species and simultaneously optimizing
68 the target fisheries yields are still a challenge due to different sustainable catch rates
69 among species (Hastings *et al.* 2017). Nevertheless, an extended two-species model
70 predicts that establishing marine reserve can achieve conservation and fisheries
71 benefits simultaneously, especially when the bycatch species are long-lived with low
72 fecundity (Hastings *et al.* 2017). Although existing multispecies with mixed life
73 histories demonstrates the important role that marine reserve played in
74 ecosystem-based fisheries management, more specific information about how life
75 histories affect the relative advantages between different fisheries management
76 methods (e.g. traditional fishing effort control vs. establishing marine reserves) still
77 needs further answers. Besides, previous researches suggest that a model with age
78 structure plays an important and non-negligible role in deciding which fisheries
79 management method is better (Hilborn 2017). Moreover, the limitations of implicit
80 equilibrium conditions prevent barriers to investigate how the advantages of marine
81 reserves in improving fisheries yields and maintaining bycatch persistence vary in
82 relatively short time scales before the ecosystem achieves stable equilibrium states;
83 that is the insight into the ecosystem with transient dynamics (Hopf *et al.* 2016;
84 Hastings *et al.* 2018; Morozov *et al.* 2019).

85

86 Understanding how transient dynamics of fisheries yields response to different
87 management strategies is essential for monitoring fisheries and making the right

88 decisions in adaptive management. Adaptive management is a widely accepted
89 iterative approach to frequently regulate fisheries policy implementation based on the
90 difference between empirical monitoring data and theoretical expectations (Kaplan *et*
91 *al.* 2019; Nickols *et al.* 2019). It has been suggested that setting an expected timeline
92 is necessary for adaptive management during the recovery of harvested populations
93 (Kaplan *et al.* 2019). This derives from the fact that, once marine reserves are
94 established, the abundance of fish populations may vary greatly and lead to
95 undetectability in fisheries caused by a variety of factors including life histories
96 (White *et al.* 2013; Kaplan *et al.* 2019; Nickols *et al.* 2019). These findings provide
97 important inspirations to compare the relative yields advantages between fisheries
98 management strategies of traditional effort control and the implementation of marine
99 reserves. If the transient oscillations are too strong and the amplitude is big enough,
100 fisheries yields under reserve implementation policy can probably be higher at one
101 moment but lower at the other moment relative to the yields using nonspatial
102 approaches, which increases the difficulty to decide between different fisheries
103 management strategies. It has been demonstrated that life histories can greatly
104 regulate transients in population abundance, and fish individuals with old ages at
105 maturity and low natural mortality rates will increase transient dynamics (White *et al.*
106 2013).

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108 To explore the transient phenomena in fisheries management as well as the intrinsic
109 mechanism, we develop theoretical frameworks consist of reserve-only and

110 no-reserve models which are derived from the two extreme cases in previous models
111 (Hastings *et al.* 2017). We further extend the models to high dimensions by adding
112 age structure to investigate the transient behavior of the target fish species (who are
113 easily persistent even under the stress of fishing) under the persistence of the bycatch
114 species (who have a high risk of going extinct) based on several assumptions. First,
115 we assume that the transient dynamics of the target fish species are independent of the
116 dynamics of the bycatch species (i.e. no ecological connections between two species)
117 (Chen 2020). Second, we assume that the movement abilities are different between
118 fish adults and larvae. Adults tend to be sedentary while larvae can disperse
119 everywhere. Third, we assume that the proportions of fish individuals that are subject
120 to reserve protection (i.e. marine reserve size) in the reserve-only model are the same
121 for both target and bycatch species, and the fractions of fish stocks that left
122 unharvested (i.e. escapement rate) in the no-reserve model are the same for two
123 species. This assumption is possible in the real world when the costs of making
124 fishing gear selective are relatively high. With these assumptions, we compare the
125 fisheries yields measured by both number and weight under two different fisheries
126 management strategies and explore the mechanism that causes the variations of the
127 relative fisheries yields advantages. We investigate the effect of life histories on
128 transient metrics through sensitive analysis, and wavelet analysis (which is an
129 accepted method in transient analyses in ecology; see (Torrence & Compo 1998;
130 Cazelles *et al.* 2008; Cazelles *et al.* 2014)) is used to observe the periodicity of the
131 transient dynamics of the target fished species. With these analyses, we aim to answer

132 three questions: i) In transient time scales, whether and when the reserve-only policy
133 can achieve advantages of fisheries yields under bycatch species persistence relative
134 to no-reserve policy in fisheries management? ii) Whether transient fisheries
135 management strategies depend on different fisheries yields measurements (i.e. number
136 vs. weight)? iii) How life histories of both target fish species and bycatch species
137 regulate the relative fisheries yields advantages between two fisheries management
138 strategies during transient dynamics?

139 **Model**

140 **Model overview**

141 We study two-species systems with both the reserve-only model and the no-reserve
142 model, which can achieve equivalent fisheries yields based on previous conclusions
143 (Hastings & Botsford 1999; Hastings *et al.* 2017). The two species are the target
144 species with strong stock in fisheries whose life histories such as high fecundity, early
145 maturity make it easy to persist and the bycatch weak stock species which has reverse
146 life histories and easier to reach an unacceptably low level. We consider the age
147 structure (results without age structure are shown in Fig. S1) of the target species
148 while ignoring the age structure of the weak stock species so that to simplify and
149 focus on the central issue in this study. In addition to increasing age for all adults each
150 year, the age structure of the target species is featured with two points: i) all the
151 youngest adults come from the larvae recruitment in one year; ii) all the oldest adults
152 (i.e. reach the maximum age) will die next year. Among different age classes, we
153 assume that older mature individuals have higher fecundity. See schematic in Fig. 1.

154 The per-capita fecundity in each age class is expressed as $\mathbf{m} = (m_1, m_2, \dots, m_n)^T$,
155 and the corresponding weight per individual is $\mathbf{B} = (B_1, B_2, \dots, B_n)^T$. We denote a_M
156 as the age at maturity, then fecundity is zero when fish individual age is smaller than
157 the threshold a_M and the fecundity (expressed as a function of length) is $m_a =$
158 $q[L_M(1 - e^{-k(a-a_0)})]^d$ when fish individual age surpasses the threshold of maturity
159 (White *et al.* 2013; Kaplan *et al.* 2019), where a is fish individual age, L_M is the
160 fish individual asymptotic maximum length, k is the growth rate, q and d are
161 constants, and a_0 is the age at length zero. Similarly, fish individual weight at age a
162 is expressed as $B_a = p[L_M(1 - e^{-k(a-a_0)})]^w$, where p and w are constants
163 (Kaplan *et al.* 2019).

164 **Part 1 reserve-only model**

165 When only using marine reserves rather than fixed harvesting rates as fisheries
166 management methods, an implicit assumption is that all adult fish are harvested
167 outside marine reserves. To maintain the persistence of weak stock species (i.e.
168 non-target fish species), the reserve size c should be no smaller than a critical value.
169 According to previous research (Hastings *et al.* 2017), the critical value is

$$170 \quad c^* = (1-s_w)/(\alpha_w m_w), \quad (1)$$

171 where s_w , α_w , and m_w are survival rate, proliferation rate per generation, and
172 per-capita fecundity for the weak stock species, respectively.

173

174 The adult density with age structure at time t inside the marine reserve is defined as

175 $\mathbf{N}_t^R = (N_{1,t}^R, N_{2,t}^R, \dots, N_{n,t}^R)^T$. Thus, the total number of larvae produced inside the

176 marine reserve is the dot product of adult density and fecundity multiplied by the
177 reserve size. Based on the “well-mixed” assumption as suggested in previous research
178 (Hastings & Botsford 1999; Hart 2006; Hopf *et al.* 2019), the larvae density both
179 inside and outside the marine reserve is $c\mathbf{m}^T \cdot \mathbf{N}_t^R$ which equals the total number
180 because the total marine system size is scaled as 1. Therefore, the density of larvae
181 that survive to adults will be

$$182 \quad A_{t+1} = f(c\mathbf{m}^T \cdot \mathbf{N}_t^R), \quad (2)$$

183 where $f(\cdot)$ is the Beverton–Holt growth function. We further define the adult natural
184 survival rate each year as a fixed value s ; note that all fish individuals will die next
185 year once they achieve the maximum age (See Fig. 1a). According to simple
186 derivations (see Section one in appendix), the age-structured adult density inside
187 reserve at time t is

$$188 \quad \mathbf{N}_t^R = (A_t, sA_{t-1}, s^2A_{t-2}, \dots, s^{n-1}A_{t-n+1})^T. \quad (3)$$

189 The fisheries yields measured by number can be expressed as

$$190 \quad Y_t^{nR} = A_t(1 - c), \quad (4)$$

191 and the fisheries yields measured by weight can be expressed as

$$192 \quad Y_t^{wR} = B_1A_t(1 - c). \quad (5)$$

193 **Part 2 no-reserve model**

194 When using traditional ways of fixed harvesting rate without marine reserves (See Fig.
195 1b), the escapement rate E should be no smaller than the critical value E^* to maintain
196 the persistence of the weak stock species. Based on previous research (Hastings *et al.*
197 2017), we have

198
$$E^* = \frac{1}{s_w + \alpha_w \cdot m_w}. \quad (6)$$

199 Defining a_E as the critical age that fish individuals are harvested, the escapement
 200 rate is 1 when fish individual age is smaller than a_E , and the escapement rate is E^*
 201 when fish individual age is larger than a_E . With a general form, we denote the
 202 escapement rate for the age-structured strong stock species as $\mathbf{E} = (E_1, E_2, \dots, E_n)^T$,
 203 and the population density at time t is $\mathbf{N}_t^O = (N_1, {}_tO, N_{2,t}^O, \dots, {}_o_{Nn,t})^T$. Similar to the
 204 reserve-only model, the total larvae produced by all the adults are the dot product of
 205 adult density and fecundity. Thus, the density of larvae that survive to adults will be

206
$$A'_{t+1} = f(\mathbf{m}^T \cdot \mathbf{N}_t^O). \quad (7)$$

207 The age-structured adult density at time t is

208
$$\mathbf{N}_t^O = (A'_t E_1, s E_2 A'_{t-1} E_1, \dots, s^{n-1} \prod_{j=1}^n E_j A'_{t-n+1})^T, \quad (8)$$

209 and the specific derivation can be seen in Section one in the appendix. To exhibit
 210 fisheries yields with concise form in the next step, we show the density at time t
 211 before harvesting as

212
$$\mathbf{N}_t^{OT} = (A'_t, s E_1 A'_{t-1}, \dots, s^{n-1} A'_{t-n+1} \prod_{j=1}^{n-1} E_j)^T, \quad (9)$$

213 and thus, the fisheries yields in number can be expressed as

214
$$Y_t^{nO} = (\mathbf{N}_t^{OT})^T \cdot (1 - \mathbf{E}), \quad (10)$$

215 and the fisheries yields in weight can be expressed as

216
$$Y_t^{wO} = \text{sum}[\mathbf{B} \circ \mathbf{N}_t^{OT} \circ (1 - \mathbf{E})]. \quad (11)$$

217 **Results**

218 Our results have shown the transient oscillations can occur for the dynamics of
 219 population densities (Fig. 2a₁-a₇), fisheries yields measured by number (Fig. 2b₁-b₇)

220 and fisheries yields measured by weight (Fig. 2c_{1-c7}), and the periodicity is exhibited
221 with wavelet analyses (Fig. 3). Moreover, regardless of the measurement methods (i.e.
222 measured by weight or measured by number), the fisheries yields produced by the
223 reserve-only model can always be higher (red) or lower (yellow) than the yields
224 produced by the no-reserve model with appropriate hypothetical parameter settings
225 during the whole transient period (Fig. 2b₁; Fig. 2c₁). In other cases, it would be
226 difficult to judge which model can achieve higher fisheries yields as the transient
227 oscillations lead to higher fisheries yields with the reserve-only model at one moment
228 while lower ones at another moment and this is true for both kinds of yields measured
229 by weight and by number (blue lines in Fig. 2b₁ and Fig. 2c₁). The parameter values
230 are arbitrary. However, the yield comparison conclusion that three situations (i.e.
231 fisheries yields with the reserve-only model is higher, lower, or difficult to judge
232 relative to yields with no-reserve model) can happen is robust with other parameters
233 values and with different bycatch species for all the hypothetical cases (Fig. 2b_{1-b3};
234 Fig. 2c_{1-c3}). For the empirical cases, the results about the relative advantages of
235 fisheries yields between two fisheries management methods (i.e. methods with
236 reserve-only model vs. no-reserve model) are consistent with that for the hypothetical
237 cases (i.e. all three situations can occur) if fisheries yields are measured by weight
238 (Fig. 2c_{4-c7}). However, if fisheries yields are measured by the number, fisheries
239 yields with the reserve-only model are always higher relative to that with the
240 no-reserve model (Fig. 2b_{4-b7}).

241 The effect of life histories for target species on fisheries yields shows that, with

242 empirical parameter settings, fisheries management methods with the reserve-only
243 model can always lead to higher fisheries yields relative to the no-reserve model no
244 matter how influencing factors (age at maturity, age at fishing and adult survivorship
245 for the target species) varies among the suitable parameter value ranges (Fig. 4a-c).
246 However, the relative advantages in fisheries yields change with influencing factors if
247 fisheries yields are measured by weight (Fig. 4e-g). Specifically, the target species
248 with life histories of younger age at maturity, younger age at fishing, and higher adult
249 survivorship can achieve higher fisheries yields with no-reserve fisheries management
250 method relative to the reserve-only method. On the contrary, the target species with
251 reversed life histories can lead to higher fisheries yields with the reserve-only method
252 relative to the no-reserve method. The robust results still hold among different weak
253 species (shown in different colors in Fig. 4) and among different time steps (Fig. S2,
254 S3). For the hypothetical cases, the effects of adult survivorship on fisheries yields
255 measured by weight (i.e. higher adult survivorship benefits for methods with
256 no-reserve model) are similar to the results for the empirical cases (Fig. 4g; Fig. S4g,
257 S5g, S6g), while the effects of other factors (age at maturity and age at fishing) on
258 both kinds of fisheries yields as well as the effects of adult survivorship on fisheries
259 yields measured by number are different from that for the empirical cases (Fig. 4; Fig.
260 S4, S5, S6).

261

262 For the empirical cases, fisheries yields measured by both number and weight are
263 always higher with the no-reserve fisheries management method than that with the

264 reserve-only method if the critical values of reserve size for the weak species
265 persistence in the reserve-only model are identical to the critical values of escapement
266 rate in the no-reserve model (Fig. 4d, h). However, fisheries management with the
267 reserve-only method can achieve higher fisheries yields relative to the no-reserve
268 method if the critical reserve size is small while the critical escapement rate is very
269 large. On the contrary, for the hypothetical cases, fisheries yields with the no-reserve
270 method are always lower than that with the reserve-only method when the critical
271 reserve size and escapement rate are equal, and could be higher when the critical
272 escapement rate is mediate and the critical reserve size is too big or too small (Fig.
273 S4d, h; Fig. S5d, h; Fig. S6d, h). This suggests that the critical reserve size in the
274 reserve-only model and the critical escapement rate in the no-reserve model can
275 greatly regulate the relative yield advantages between two fisheries management
276 methods (i.e. which method can achieve higher fisheries yields), which is important as
277 the critical values of both reserve size and escapement rate are linked to the life
278 histories of the bycatch weak stock species to meet the persistence condition.

279

280 Sensitive analyses show that the transient metric θ oscillates and has strong
281 periodicity with the variations of influencing factors (i.e. age at maturity, age at
282 fishing, and adult survivorship) (Fig. 5, Fig. S7, Fig. S8). It suggests that the initial
283 trajectories of the system periodically close to or leave the stable level, and thus the
284 amplitude of the oscillations of the population dynamics decrease or increase
285 periodically by regulating the life histories of the target species such as age at maturity,

286 age at fishing as well as adult survivorship.

287 **Discussion**

288 Marine reserves are important in fisheries management (Mangel 2000; Edgar *et al.*
289 2014; Herrera *et al.* 2016). Our results have shown that fisheries management
290 strategies by only establishing marine reserves without fishing effort control cannot
291 always be the optimal method to improve the fisheries yields as well as maintain
292 species persistence if the dynamics of the two-species system is investigated from the
293 transient short time scale rather than the asymptotic equilibrium state. When fisheries
294 management with marine reserves can achieve higher fisheries yields relative to
295 traditional management with fishing effort control depends on the measurement
296 methods of fisheries yields and the life histories of both the target species and the
297 bycatch species. If fisheries yields are measured by fish individual numbers,
298 establishing a marine reserve could be the primary fisheries management strategies,
299 especially for the US West Coast groundfish fishery (Hastings *et al.* 2017; Nickols *et*
300 *al.* 2019; Chen 2020). If fisheries yields are measured by weight which can make the
301 theoretical frameworks include the difference of both fecundity and biomass for fish
302 individuals of different ages (Kaplan *et al.* 2019), traditional fishing effort control will
303 not be the obvious disadvantage strategies in both improving fisheries yields and
304 maintaining species persistence. The effect of fisheries yields measurement on
305 fisheries management strategies derives from the fact that fisheries management by
306 establishing marine reserves only harvest relatively young adults each year because
307 all the adult fish individuals in the harvested area come from the larvae dispersal from

308 the marine reserves, while fisheries management by fishing effort control can harvest
309 relatively old adult which have relatively large biomass (or weight). Thus, the
310 measurement with weight benefits for the traditional fisheries management in
311 evaluating its advantage of improving fisheries yields.

312

313 Further mechanisms show that whether the fisheries management strategies of
314 no-reserve can improve fisheries yields under bycatch persistence depends on the life
315 histories of both target and bycatch species. If the target species are younger at
316 maturity or have higher adult survivorship, strategies with no-reserve can achieve
317 higher fisheries yields relative to the target species with older age at maturity or with
318 lower adult survivorship (Fig. 4). Nevertheless, for the hypothetical cases, the effect
319 of age at maturity and age at fishing on both kinds of fisheries yields are complex
320 among different weak species relative to empirical cases; that is fisheries yields with
321 the reserve-only model are higher relative to yields with the no-reserve model for one
322 weak species while it is lower for another weak species (Fig. 4; Fig. S4, S5, S6). The
323 differences between the hypothetical and the empirical cases derive from the fact that
324 adult survivorship in the hypothetical cases is very low while it is very high in the
325 empirical cases (Hastings *et al.* 2017; Chen 2020). Thus, both the age at maturity and
326 at fishing cannot be too old in hypothetical cases. Otherwise, the target strong stock
327 species cannot persist.

328

329 The life histories of the bycatch species can regulate the relative yield advantages

330 between two fisheries management strategies through deciding the critical reserve size
331 and escapement rate to maintain persistence according to the weak stock persistence
332 conditions shown in Eq. 1 and Eq. 6. For example, if the critical reserve size is 0.1
333 and the critical escapement rate is 0.95 so that fisheries management with
334 reserve-only strategies can achieve higher fisheries yields relative to no-reserve
335 strategies (Fig. 4), the corresponding life histories of the bycatch species can be
336 predicted by the combination of Eq. 1 and Eq. 6 through controlling one life-history
337 parameter (e.g. achieve adult survivorship and fecundity by controlling proliferation
338 rate per generation). On the contrary, solving equations 1 and 6 with the assumption
339 that the critical reserve size equals the critical escapement rate can achieve life
340 histories of bycatch under which strategies with no-reserve produce higher fisheries
341 yields relative to strategies with only reserves. In such a case, even if the bycatch
342 species are long-lived with low fecundity which is important based on the previous
343 model (Hastings *et al.* 2017), reserves cannot make sure benefits simultaneously in
344 fisheries and conservation.

345

346 The life histories can regulate the relative fisheries yields advantages between two
347 fisheries management strategies through the other perspective by regulating the
348 amplitude of the transient oscillations. To make the relative yield advantages
349 predictable, the amplitude of the transient oscillations of the system should not be too
350 big. Otherwise, the “up and down” of the fisheries yields with time will make it
351 complex to predict which fisheries management strategy (no-reserve vs. reserve-only)

352 is more suitable for both conservation and fisheries goals. To achieve small amplitude
353 of the transient oscillations, the life histories of both the target and bycatch species
354 can be regulated because of the periodical relationships between the transient metric
355 θ (which decides the amplitude of transient oscillations (White *et al.* 2013; Kaplan *et*
356 *al.* 2019; Chen 2020)) and life history parameters of both the target and bycatch
357 species (Fig.5).

358

359 We consider the effect of age structure in the main research. If there is no age
360 structure as shown in Hastings *et al.* (2017) (fisheries yields measured by weight are
361 identical to that measured by number), the transient analysis suggests that traditional
362 fisheries management methods can achieve higher fisheries yields relative to
363 strategies with marine reserves, but it cannot maintain the persistence of the bycatch
364 species (yellow color in Fig. S1). When bycatch species is persistent, strategies with
365 marine reserves can achieve higher fisheries yields (Fig. S1), which is consistent with
366 previous equilibrium research that strategies with marine reserves can perform an
367 important role in fisheries management by solving bycatch problems (Hastings *et al.*
368 2017). However, when the adult survivorship is very high as shown in the empirical
369 cases, traditional strategies without reserves can achieve higher fisheries yields
370 relative to strategies with marine reserves and maintain bycatch species persistence at
371 the beginning of the transient time scales, which is consistent with our results with
372 age structure regardless of the results without age structure at the equilibrium state
373 still show the advantage of strategies with marine reserves (Fig. 2; Fig. S1h, j, l, n).

374 Besides, relative to our theoretical frameworks, models developed by Hastings et al.
375 (2017) do not show obvious transient phenomena (Fig. S1), which are consistent with
376 previous conclusions that transients are difficult to observe in models without age
377 structure (White *et al.* 2013; Chen 2020). This derives from the fact that age structure
378 often leads to high dimensions which have been suggested to be the main mechanism
379 to cause transients (Hastings *et al.* 2018; Morozov *et al.* 2019).

380

381 Previous investigations in the transient dynamics of fish abundance after establishing
382 marine reserves indicate that the transient metric θ (which determines the amplitude
383 of the transient oscillations) becomes, in general, large with the increasing of age at
384 maturity and small with the increasing of natural mortality (White *et al.* 2013).
385 However, our sensitivity analyses indicate that the transient metric θ increases and
386 decreases periodically with the variation of both ages at maturity and adult
387 survivorship (Fig. 5). The difference between our research and previous ones (White
388 *et al.* 2013) derives from the fact that previous research considers the transient
389 response of linear models with Leslie matrices while we consider the non-linear ones
390 and thus the eigenvalues of matrix A and A' vary with population density (Section
391 two in appendix). These results suggest that considering the non-linear effect of larval
392 survival to adult will increase the difficulty of investigating the transient dynamics as
393 the predictability periodically varies with life histories, and thus increase the difficulty
394 to judge which fisheries management strategies (reserve-only vs. no-reserve) perform
395 better. Further insight into the periodicity of the transient dynamics of the system with

396 time is helpful for predictability, and our wavelet analyses provide answers for this
397 (Fig. 3; Fig. S9-S14).

398

399 Our researches are based on the “scorched earth” assumption (Malvadkar & Hastings
400 2008; Edwards *et al.* 2010) for the fisheries management with reserve-only strategies,
401 which does not consider the effect of economic costs in fisheries(Sanchirico *et al.*
402 2006; White *et al.* 2008). If the effect of economic costs is considered, harvesting all
403 adults in the harvested area (i.e. the scorched earth assumption) can lead to high
404 harvesting costs in fisheries as the catchability decreases with the decreasing of
405 population density in the natural system. In that case, costs with reserve-only
406 strategies are higher and may not be a better choice for fisheries management relative
407 to traditional methods without reserves.

408

409 We ignore the age structure of the bycatch species so that the persistence conditions
410 are easy to achieve although the conditions are necessary but not sufficient (Chen
411 2020). By considering the age structure of the bycatch species, high dimensions lead
412 to much complex persistence conditions, which deserves developing new analytical
413 and simulation approaches. However, similar conclusions may be achieved even if we
414 consider the effect of the age structure of the bycatch species if new theoretical
415 frameworks are still based on the assumption that there are no ecological connections
416 between the target and the bycatch species. Future works can explore the
417 predator-prey or competition connections between the target and the bycatch species,

418 which can greatly regulate the population density of both species (Frid & Marliave
419 2010; Aalto & Baskett 2013) and thus further play a role in predicting relatively
420 higher fisheries yields between different fisheries management strategies under
421 bycatch persistence in transient time scales (specific information is shown in another
422 manuscript).

423

424 **Materials and methods**

425 With both reserve-only and no-reserve models, we first simulate the transient
426 dynamics of the population density and fisheries yields of the target species. The
427 system starts with the initial condition at a stable age distribution. To make a
428 comparison, the initial conditions are the same for both reserve-only and no-reserve
429 models. The parameter values for simulations come from previous researches
430 (Hagerman 1952; Hunter *et al.* 1990; White *et al.* 2013; Hastings *et al.* 2017; Kaplan
431 *et al.* 2019; Chen 2020) and can be seen in Table S1. We use the average values if
432 these parameters are different between male and female individuals. Specifically,
433 $\alpha_0 = -5.10$, $d = 2.96$, $p = 2.41 \times 10^{-4}$, $w = 2.96$, $k = 0.087$, $L_M = 45.55$, and
434 the maximum age is 50. Coefficient q is regulated to maintain a positive growth rate.
435 The Beverton–Holt functional form is $f(n) = \frac{\alpha\beta n}{\beta+n}$ (Chen 2020), where α and β
436 denote the proliferation rate per generation and carrying capacity, respectively. We
437 explore the effect of life histories on transient metric θ which determines the
438 amplitude of transient oscillations and measures how close the initial system state is
439 to the final equilibrium state (White *et al.* 2013; Kaplan *et al.* 2019). To calculate

440 transient metric θ , we transform both reserve-only and no-reserve models into
441 identical cases (see details in Section two in appendix).

442

443 **Ethics.** This article has no ethical problems.

444 **Data accessibility.** This article has no additional data and there is no need to deposit
445 data to a public repository.

446 **Author contributions.** Renfei Chen designed research, performed research, and
447 wrote the paper; Chengyi Tu performed the wavelet analyses; Quan-Xing Liu edited
448 and wrote the paper.

449 **Competing interests.** There are no competing interests.

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453

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565 **Figure legend**

566 **Figure 1. Schematic of the theoretical frameworks.** (a) fisheries strategies by only
567 using reserves. (b) traditional fisheries strategies by fishing effort control without
568 reserves. The life histories of both target and bycatch species do not change between
569 different fisheries strategies.

570 **Figure 2. Transient dynamics of population density and fisheries yields for target**
571 **species under the persistence of different bycatch species.** Solid lines denote
572 reserve-only strategies, and dashed lines denote no-reserve strategies. Different colors
573 represent different parameter settings to perform sensitivity analyses. (a₁-a₇) Transient
574 dynamics of population density. Note that population density with reserve-only
575 strategies denotes density inside marine reserves. (b₁-b₇) transient dynamics of
576 fisheries yields measured by number. (c₁-c₇) transient dynamics of fisheries yields
577 measured by weight. a₁-a₇, b₁-b₇, and c₁-c₇ correspond to situations 1-7, and specific
578 definitions and differences among different situations can be seen in (Chen 2020).

579

580 **Figure 3. Wavelet analyses of the transient dynamics in an empirical case.**
581 (Corresponding to the last line in figure 2, i.e. situation 7). It denotes the wavelet
582 power spectrum of the raw series, and the power values increase from white (low
583 values) to dark red (high values).

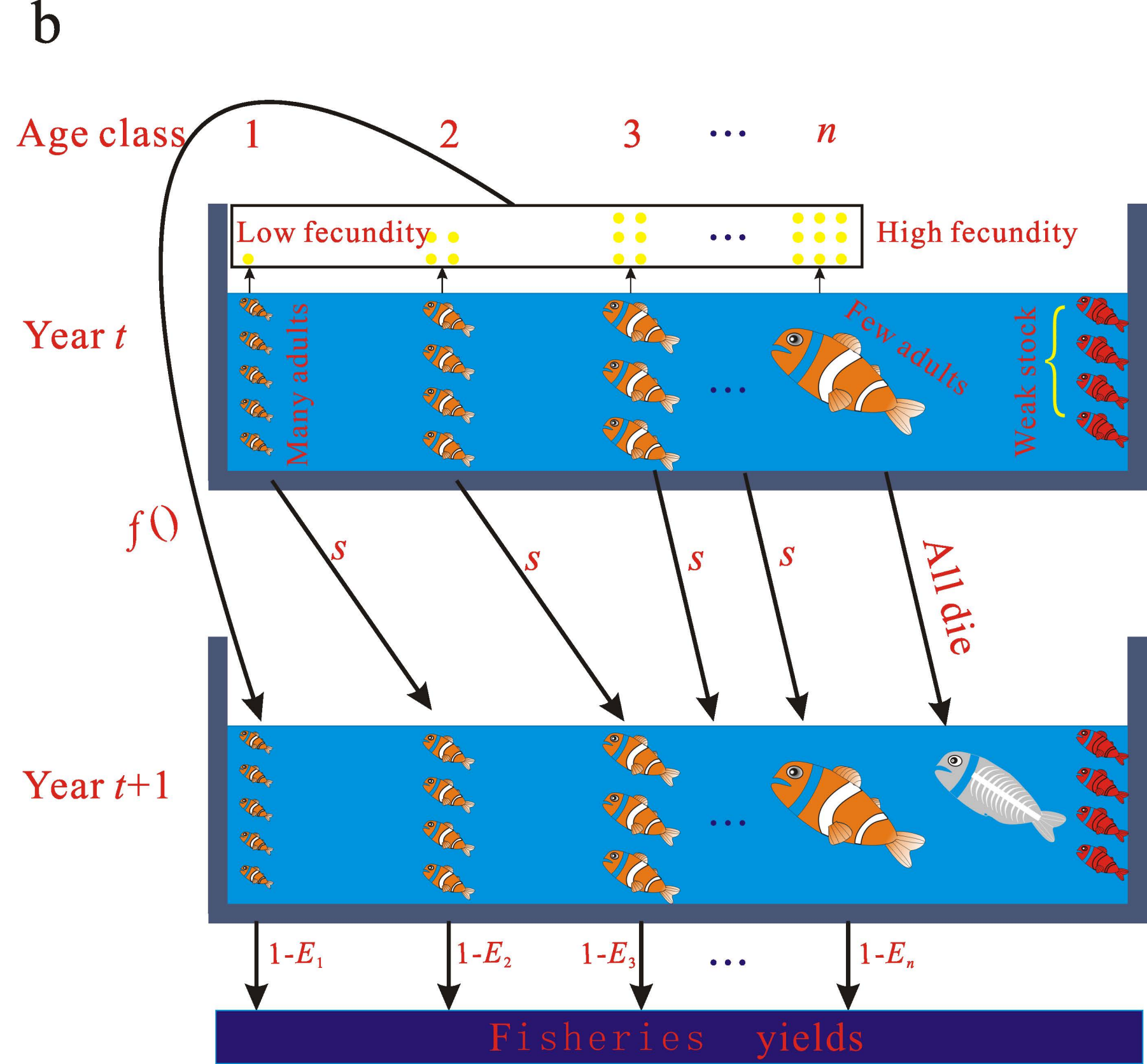
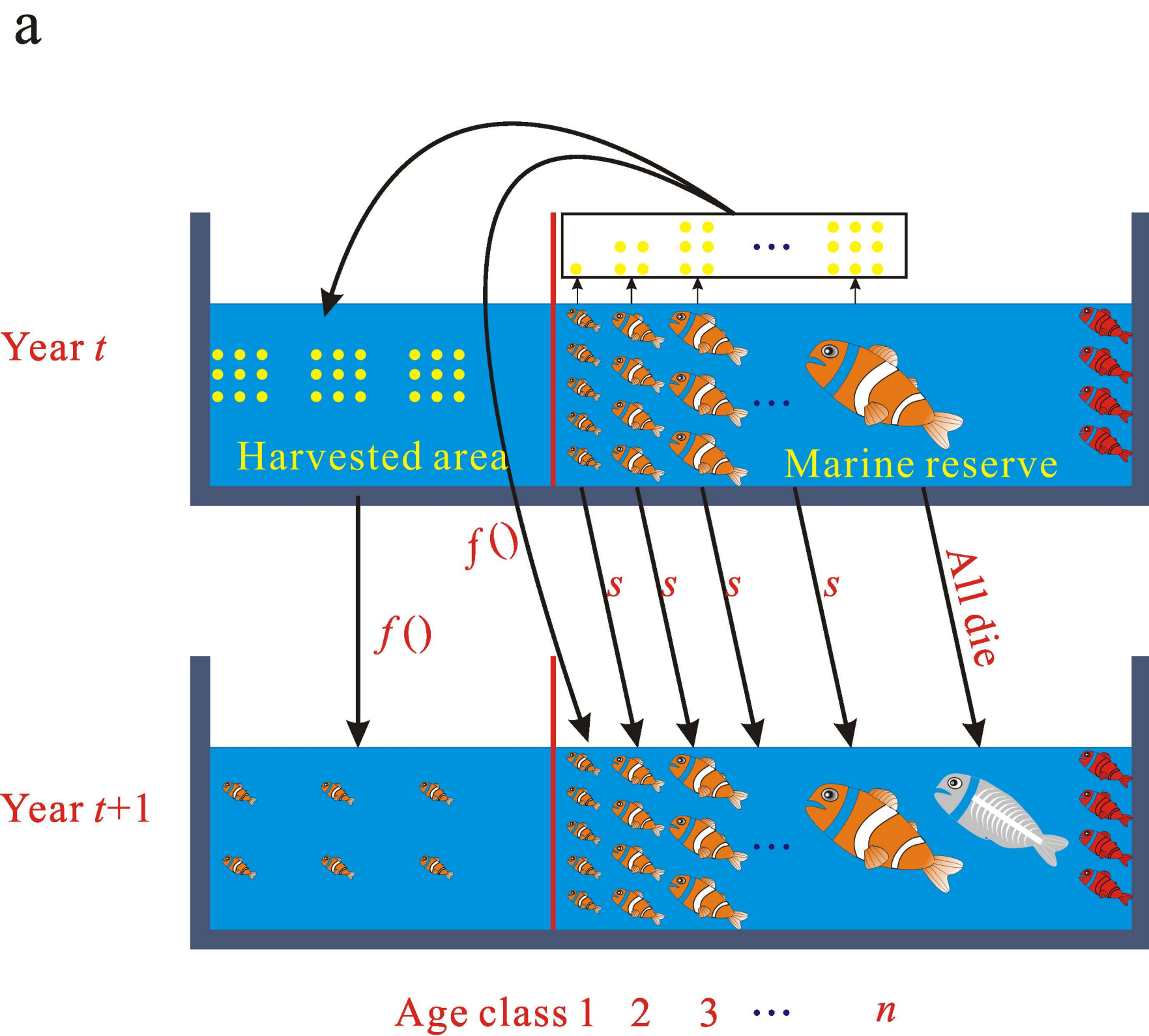
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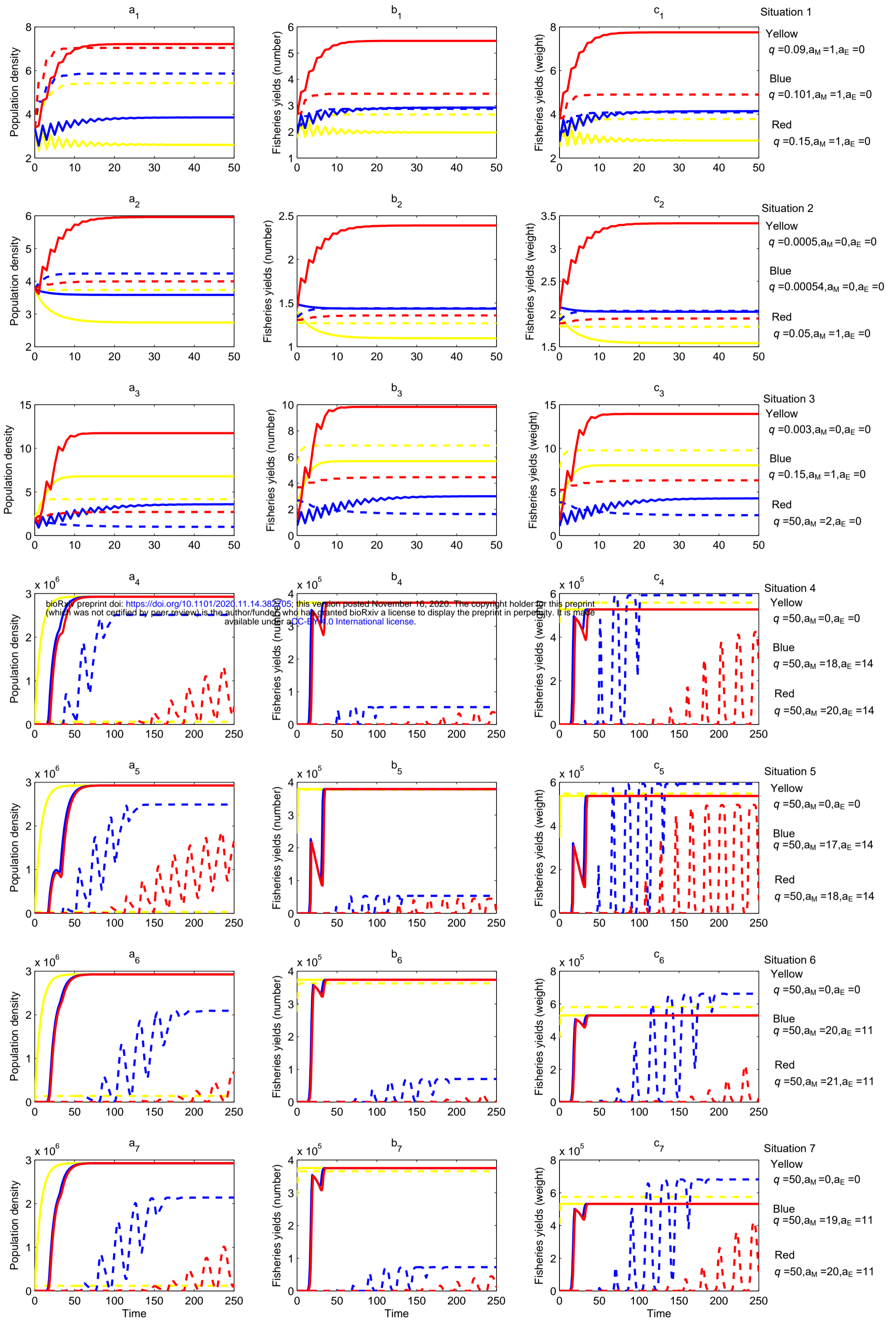
585 **Figure 4. Effects of life histories and harvesting management on fisheries yields**
586 **with both reserve-only and no-reserve strategies for empirical cases (situations**

587 **4-7).** (a-c) Fisheries yields measured by number response to age at maturity, age at
588 fishing, adult survivorship, respectively for target species. (d) Fisheries yields
589 measured by number response to the critical reserve size and the critical escapement
590 rate. (e-g) Fisheries yields measured by weight response to age at maturity, age at
591 fishing, adult survivorship, respectively for target species. (h) Fisheries yields
592 measured by weight response to the critical reserve size and the critical escapement
593 rate. In a-c and e-g, solid lines denote reserve-only strategies, and dashed lines denote
594 no-reserve strategies. Different colors represent different bycatch species. In d and h,
595 yellow colors denote critical reserve size with reserve-only strategies, and red colors
596 denote critical escapement rate with no-reserve strategies. All subplots denote the time
597 step at 50. Parameter settings: (a, e) $q = 50$, $a_E = 0$; (b, f) $q = 50$, $a_M = 1$; (c, d, g, h) q
598 $= 50$, $a_M = 1$, $a_E = 0$; see Table S1 and Materials and methods for other parameters.

599

600 **Figure 5. Sensitive analyses of transient metric θ in response to different**
601 **parameters for empirical case (situation 7) with different fisheries management**
602 **strategies.** (a) age at maturity, (b) age at fishing, (c) adult survivorship, (d) critical
603 reserve size (yellow) and critical escapement rate (red). In a and c, yellow color
604 denotes reserve-only strategies, and red colors denote no-reserve strategies. Parameter
605 settings: (a) $q = 50$, $a_E = 0$; (b) $q = 50$, $a_M = 1$; (c, d) $q = 50$, $a_M = 1$, $a_E = 0$; see Table
606 S1 and Materials and methods for other parameters.





$q = 50$
 $a_M = 0$
 $a_E = 0$

$q = 50$
 $a_M = 19$
 $a_E = 11$

$q = 50$
 $a_M = 20$
 $a_E = 11$

