

1 Optimal spatial management in a multi-use marine
2 habitat: Balancing fisheries and tourism

3 Carles Falcó^{1,2,†} and Holly V. Moeller^{3,‡}

4 ¹ Departament de Matemàtiques, Facultat de Ciències, Universitat Autònoma de Barcelona,
5 E-08193 Barcelona, Spain

6 ² Departament de Física, Facultat de Ciències, Universitat Autònoma de Barcelona, E-
7 08193 Barcelona, Spain

8 ³ Department of Ecology, Evolution, and Marine Biology, University of California-Santa
9 Barbara, Santa Barbara, CA, USA, 93106

10 [†] Co-Corresponding Author: C3/116 Departament de Física, Facultat de Ciències, Uni-
11 versitat Autònoma de Barcelona, E-08193 Barcelona, Spain, Carles.FalcoG@e-campus.uab.cat

12 [‡] Co-Corresponding Author: 1120 Noble Hall, UC Santa Barbara, Santa Barbara, Cali-
13 fornia, 93106-9120, hvmoeller@ucsb.edu

14 **Abstract**

15 Marine fisheries are an important source of food supply and play an important economic role
16 in many regions worldwide. However, due to aggressive fishing practices they are increasingly
17 overexploited. Marine reserves have the potential to alleviate this problem and moreover,
18 they also provide a physical area where an alternative economic activity can exist without
19 being in conflict with fishing gear. Here we explore the idea of combining multiple economic
20 activities in a marine ecosystem, namely: fishing and tourism. We use a model in which the
21 fish population evolves according to a reaction-diffusion partial differential equation, and we
22 consider the interactions between fishing and tourism. We use optimal control theory to find,
23 depending on the model parameters, the optimal management strategy. The results show
24 that, subject to certain conditions, it is possible to have two different revenue streams in the
25 same habitat in contrast with the classical view of competing uses. We also corroborate that
26 marine reserves emerge as the optimal strategy and that the presence of visitors in these
27 areas generates larger profits than if only fishing was considered.

28 **Recommendations for Resource Managers**

- 29 • Several economic activities in the same marine ecosystem can be more profitable than
30 single use habitats (e.g. fisheries), and appropriate management can have important
31 consequences for conservation.
- 32 • Marine reserves have the potential to solve the overexploitation problem in many fish-
33 eries, and they provide a physical area where tourism and fishing are not in direct
34 spatial conflict.
- 35 • Habitat economic and ecological features should be adequately examined when design-

36 ing a spatial management strategy.

37 *Keywords:* bioeconomics, fishing, habitat damage, optimal control theory, tourism

38 **Introduction**

39 For decades, humans have used the coastal environment for many things. In order to ensure
40 a sustainable coexistence of fishing and recreational activities and coastal industries (e.g.
41 mining, drilling, water control), the governance and legislation of such areas requires complex
42 management strategies [38, 31, 10]. These strategies also need to account for the prominent
43 role of coastal areas in global transportation and the increasing human demand for urban
44 settlements. Fisheries are significant for a number of reasons: They are an important source
45 of protein for humans, and they generate revenue and employment across the world [37].
46 In a changing climate scenario, ensuring fisheries efficiency and aquaculture sustainability
47 are the main challenges to meet global food demand [21, 32]. Similarly, coastal tourism is
48 one of the leading economic activities worldwide and it has become a major component of
49 some countries' GDP. Some regions of Central America and South Asia are clear examples
50 of marine ecosystems in which tourism plays a major economic role [12, 29]. Despite the
51 enormous logistic difficulties, marine spatial management strategies generating both food
52 supply and economic profits have been proven possible [19, 41]. For instance, Australia's
53 Great Barrier Reef has been protected by pioneering federal legislation for more than 40
54 years, which allows for fishing, marine tourism, and recreation, and assigns some areas to
55 preservation as well as scientific research [9].

56 A major challenge of multiple uses is potential conflict between them. Complex ownership
57 may also result in over-exploitation when competing users erode stock below the population
58 associated with maximum sustainable yield. While both fishing and tourism can be lucrative
59 activities, one might influence the other negatively by limiting its intrinsic value [20]. For

60 example, although there are no data relating fish biomass and visitor frequency, there is
61 strong evidence that divers tend to prefer environments with abundant and diverse marine
62 life [33]. Aggressive fishing practices can damage habitat and consequently diminish habitat
63 value and its tourism potential. Increasingly, fisheries are overexploited, which threatens not
64 only other habitat uses, but also food and economic security. Moreover, recent studies show
65 that even modern fishing gear might have a big impact on oceans [35].

66 Marine reserves have the potential to resolve this conflict between nearshore habitat uses.
67 Several studies concerning spatial management in marine reserve design have addressed this
68 issue [11, 34, 5]. One critique of marine reserves is that they remove fishable area from access,
69 potentially reducing employment and production. However, there is empirical evidence that
70 no-take areas are source populations and that their spillover effects can be commercially
71 feasible via techniques such as *fishing the line* [13, 16]. Theoretical studies also predict that
72 no-take areas emerge as the optimal management strategy when fishing damages the habitat
73 [24, 25], that the associated redistribution of fishing can actually increase employment [26],
74 and that they could be a solution for the bycatch problem [14]. Here, we study another
75 potential benefit: marine reserves could provide a physical area where tourism and fishing
76 are not in direct spatial conflict. More recent studies also point that the optimal reserve area
77 increases with tourism value [40], which suggests that accounting for tourism could have an
78 impact on ocean protection.

79 Here, we consider the interactions of some of these complexities with fisheries manage-
80 ment. Specifically, we model a system in which revenue may be generated through fishing
81 and through tourism, with varying degrees of conflict between these uses. We assume that
82 tourism generates profit which is strictly depending on the habitat biomass (e.g., total fish
83 stocks). In addition, in our model, population density follows a 1D reaction-diffusion partial
84 differential equation (PDE) and we use optimal control theory to compute the first-best sole
85 owner case, in which the system is optimally managed to yield the greatest profit across both

86 fishing and tourism industries. We also consider the impacts of habitat-damaging fishing on
 87 the optimal outcomes. We find that economic benefits from tourism can further incentivize
 88 the establishment of marine reserves, and that synergies (elevated profits in multiuse systems)
 89 rather than tradeoffs may emerge. These synergies are sensitive to the relative valuation of
 90 tourism and fishing, suggesting that with appropriate economic incentives, these two uses
 91 may coexist if managers can establish reserve networks.

92 **The Model**

93 In order to determine the optimal spatial management of a multi-use habitat, our model
 94 captures the ecological dynamics of fishing (including the direct effects of stock removal and
 95 the indirect effects of habitat damage), as well as the profit accrued from both fishing and
 96 tourism.

97 Following [24, 26] we model fish biomass density N as a continuous function of habitat
 98 space and of time. We assume that at every point fish population follows logistic growth at
 99 growth rate r and in a habitat with carrying capacity K . Spatial effects are introduced by
 100 allowing fish to move through a linear habitat of length L centered at $x = 0$. This happens
 101 via diffusion at a rate D . Moreover, we assume that fish cannot survive outside the habitat,
 102 so that fish biomass density vanishes at the habitat edges (Dirichlet boundary conditions;
 103 $N(-L/2) = N(L/2) = 0$). This leads to the known Fisher-KPP equation:

$$104 \quad \frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} + rN \left(1 - \frac{N}{K}\right). \quad (1)$$

105 When fishing occurs, there are two effects on the fish stock. First, fish are directly
 106 removed by harvest, at a rate qEN , where E is a measure of the local fishing effort at a
 107 certain time, and q is the catchability coefficient, which reflects the efficiency of a particular
 108 fishery. Second, fishing damages habitat, which reduces the maximum population that can

109 be locally supported. As in [23], we model this by assuming that fishing reduces the carrying
 110 capacity of the habitat, where the strength of habitat damage is governed by a habitat
 111 sensitivity coefficient g . Thus, we replace K with:

$$112 \quad K = \frac{K_0}{1 + gE}, \quad (2)$$

113 where K_0 is the carrying capacity of the habitat in the absence of fishing. In terms of pop-
 114 ulation growth rates, this assumption has a clear meaning. Growth rate at low population
 115 densities remains constant, even in the presence of fishing. However, habitat damage in-
 116 creases fish density-dependent mortality at a rate proportional to the fishing effort E . There
 117 are alternative ways to model habitat-fisheries interactions. For instance, in [3], it is assumed
 118 that the carrying capacity inside a marine protected area increases with the length of the
 119 protected area.

120 Adding the effects of habitat damage, we find that fish stock density changes over time
 121 according to:

$$122 \quad \frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} + rN \left(1 - \frac{1 + gE}{K_0} N \right) - qEN. \quad (3)$$

123 We look for solutions at equilibrium, where $\partial N / \partial t = 0$. Then Equation (3) becomes:

$$124 \quad D \frac{d^2 N}{dx^2} + rN \left(1 - \frac{1 + gE}{K_0} N \right) = qEN. \quad (4)$$

125 In other words, harvest is equal to the stock net growth, which is the result of both diffusion
 126 and local population growth.

127 In our model, income can be generated from two sources: fishing and tourism. As
 128 suggested in [33] marine life and diversity in an ecosystem can be a main attraction for
 129 divers and snorkelers. Although data relating tourist visits and biomass are not available, it
 130 is reasonable to assume that the frequency of these visitors will increase with fish density,

131 thus increasing the tourism profit. We model tourism profit per unit length at location x ,
 132 $\rho_t(x)$ by a logistic function with midpoint in N_0 . This parameter can be understood as a
 133 threshold value from which one can generate relevant profit. In the face of a fixed price per
 134 unit tourism a , tourism profit density follows:

$$135 \quad \rho_t = \frac{a}{1 + e^{-b(N-N_0)}}, \quad (5)$$

136 where b measures the steepness of the curve. Note that for large b , the logistic function
 137 converges pointwise to a step function with image $\{0, a\}$ and midpoint at N_0 . During our
 138 analysis, we will set b to be large enough for this approximation to be reasonable. This
 139 equation has a clear interpretation. Imagine that the geographic location of a particular
 140 ecosystem sets a fixed price a (e.g., due to willingness to pay). Also, no significant amount
 141 of tourists will visit the area unless there is abundant marine life. This determines the
 142 threshold value N_0 . Therefore, tourism profit will be negligible unless the stock density in
 143 the ecosystem is larger than N_0 . Further, reducing fishing (to allow $N > N_0$) will only
 144 be incentivized if a is sufficiently large to make tourism profit comparable to fishing profit.
 145 A similar function is used in [40] when trying to model the dependence between tourism
 146 density and biomass. Throughout the manuscript we will refer to N_0 and to a (or to their
 147 later dimensionless versions) as biomass/stock density threshold and tourism-fishing relative
 148 price respectively. In light of the above, total profit Π_t generated from tourism can be written
 149 as:

$$150 \quad \Pi_t = \int_{-L/2}^{L/2} \rho_t(x) dx. \quad (6)$$

151 We want to emphasize that Equation (6) represents total tourism profit, which means that
 152 it includes both revenue and tourism costs. While tourism can happen only above a certain
 153 threshold of stock density, its economic value a dictates how profitable it will be. When
 154 estimating this price, tourism costs should also be taken into account. Therefore, large

155 values of a denote scenarios in which tourism revenue is much larger than its costs, while
 156 smaller values of a indicate revenue which is comparable to the total tourism costs.

157 On the other hand, the profit coming from fishing generated at location x is the difference
 158 between the total fishing revenue and the cost of fishing. If harvested stock is sold at a price
 159 per unit biomass p , then fishing generates profit at a rate $pqEN$. If we assume that the first
 160 effort unit has a cost w_0 and that this cost increases linearly at a rate w_1 then fishing has a
 161 total cost: $(w_0 + w_1E)E$. Thus the fishing rent density can be written as:

$$162 \quad \rho_f = pqEN - (w_0 + w_1E)E. \quad (7)$$

163 And likewise, total fishing profit Π_f follows:

$$164 \quad \Pi_f = \int_{-L/2}^{L/2} \rho_f(x) dx. \quad (8)$$

165 We consider the case of a sole owner—a regulator with full control over the distribution
 166 of fishing within the habitat domain. We imagine that such a sole owner seeks a *first best*
 167 economic outcome of maximizing her or his profits. Such a regulator, taking into account the
 168 specifications of a particular ecosystem, might be interested in finding an optimal strategy
 169 either by combining these two income sources or by leaving one of them to dominate the
 170 other. Total profits Π are found by integrating the total rent density $\rho_t + \rho_f$ over the habitat
 171 domain. Then our problem consists of maximizing total profits subject to two constraints:
 172 stock density and fishing effort must be non-negative. In other words:

$$173 \quad \max_{E, N} \Pi = \Pi_t + \Pi_f, \quad (9)$$

$$174 \quad \text{subject to: } E, N \geq 0. \quad (10)$$

175

176 Model Analysis

177 Note that the presented model depends on twelve parameters – see Table 1. The first step
178 in our analysis is to introduce the following change of variables:

$$179 \quad \xi = x\sqrt{r/D}, \quad u = N/K_0, \quad f = qE/r, \quad \pi = \Pi/(pK_0\sqrt{rD}). \quad (11)$$

180

181 These new variables are, respectively, the dimensionless versions of the spatial position x ,
182 the stock density N , the fishing effort E and the total profit Π . With this transformation,
183 Equation (4) becomes:

$$184 \quad \frac{d^2u}{d\xi^2} = u(f - 1) + (1 + \gamma f)u^2, \quad (12)$$

185 with boundary conditions

$$186 \quad u(-\ell/2) = u(\ell/2) = 0. \quad (13)$$

187 After this change of variables (which can be found via standard dimensional analysis) Equa-
188 tion (4), which depended on six parameters (D, r, g, K_0, q, L) has transformed in Equation
189 (12) depending only on the two dimensionless parameters:

$$190 \quad \ell = L\sqrt{r/D}, \quad \gamma = gr/q. \quad (14)$$

191 Note that γ is a dimensionless version of the habitat sensitivity. This parameter will allow
192 us to distinguish between different types of habitat depending on their sensitivities. Observe
193 too that γ depends on how vulnerable the environment is (i.e. the habitat sensitivity g)
194 and on the efficiency of the fishery (i.e. the catchability coefficient q). On the other hand, ℓ
195 gives a typical length scale in our model, which of course depends on habitat length and fish
196 mobility and growth rate. Hence, a smaller dimensionless habitat could represent not only
197 smaller actual lengths but also, increased fish mobility or a slower growth rate.

198 With the change of variables (11), the dimensionless total profit arising from both tourism
 199 and fishing can be written as:

$$200 \quad \pi[u, f] = \int_{-\ell/2}^{\ell/2} [\alpha z(u) + uf - (c_0 + c_1 f)f] d\xi; \quad (15)$$

201 where $z(u) = [1 + \exp(-\beta(u - u_0))]^{-1}$. This expression, which depended before on seven
 202 parameters $(p, q, w_0, w_1, a, b, N_0)$ now depends on the five parameters:

$$203 \quad \beta = bK_0, \quad \alpha = a/(pK_0\sqrt{rD}) \quad u_0 = N_0/K_0, \quad (16)$$

$$204 \quad c_0 = w_0/(qpK_0), \quad c_1 = w_1r/(q^2pK_0).$$

205 Observe also that α represents a relative price between tourism and fishing. The larger the
 206 value of α , the more profitable tourism will be in comparison to fishing. This parameter
 207 should be understood as a weighting parameter – see [42] – which sets the management
 208 preferences regarding the two considered economic activities. Moreover, from now on, we
 209 will refer to u_0 as the biomass or stock density threshold, this is, the threshold density from
 210 which tourism becomes profitable.

211 We will determine the effort distribution and the stock density that maximize the total
 212 profits integral (15). Observe that although there is one control –the distribution of fishing
 213 effort $f(\xi)$ – this control directly affects both fishing and tourism profits. Recall that tourism
 214 will only be relevant if the local stock biomass exceeds a threshold value u_0 and α sets a
 215 high enough reward to incentivize foregoing fishing profits. Our goal then is to maximize
 216 profit subject to the biological constraint of non-negative stock and the economic constraint
 217 of non-negative fishing:

218
$$\max_{u, f} \pi[u, f], \tag{17}$$

219 subject to: $u, f \geq 0.$ (18)
 220

221 We introduce the new variable $v = du/d\xi$, which allows us to convert the state Eq. (12)
 222 into a system of two ordinary differential equations:

223
$$\frac{du}{d\xi} = v, \tag{19}$$

224
$$\frac{dv}{d\xi} = u(f^* - 1) + (1 + \gamma f^*)u^2. \tag{20}$$

226 with boundary conditions given by Eq (13).

227 In optimal control theory [18] the Hamiltonian for the maximization problem is

228
$$H[u, v, f, \lambda_1, \lambda_2] = uf - (c_0 + c_1f)f + \alpha z(u) \tag{21}$$

 229
$$+ \lambda_1 v + \lambda_2 [u(f - 1) - (1 + \gamma f)u^2].$$

230 Pontryagin's maximum principle tells us that the effort density that maximizes the rent
 231 integral also maximizes the Hamiltonian at every point. Observe that the Hamiltonian is a
 232 concave down parabola with respect to the variable f . Hence, its absolute maximum can be
 233 easily found by looking for its relative extrema. Denoting by f^* the optimal control – i.e.
 234 $\partial H/\partial f|_{f=f^*} = 0$ –, we obtain the following characterization:

235
$$f^* = \frac{u(1 + \lambda_2 - \gamma u) - c_0}{2c_1}. \tag{22}$$

236 The maximum principle also tells us that the adjoint variables $\lambda_1(\xi), \lambda_2(\xi)$ satisfy the

237 ordinary differential equations

$$238 \quad \frac{d\lambda_1}{d\xi} = -\frac{\partial H}{\partial u}, \quad (23)$$

$$239 \quad \frac{d\lambda_2}{d\xi} = -\frac{\partial H}{\partial v}, \quad (24)$$

241 alongside the transversality conditions $\lambda_2(\ell/2) = \lambda_2(-\ell/2) = 0$. Note that $\partial H/\partial v = \lambda_1$
242 and hence these two equations become:

$$243 \quad \frac{d^2\lambda_2}{d\xi^2} = f + \alpha z'(u) + \lambda_2(f - 1) - 2u\lambda_2(1 + \gamma f). \quad (25)$$

244 Equations (12) and (25), alongside zero Dirichlet boundary conditions and the characteri-
245 zation of the control f^* (22) constitute a two-point boundary value problem that we solve
246 numerically.

247 During our analysis we set $c_0 = 0.01$ and $c_1 = 0.001$. As reported in [24] changes of several
248 orders of magnitude of these parameters do not qualitatively affect the results. Based on
249 this previous work, in the simulations we choose a habitat length of $\ell = 15$ which allows the
250 formation of at least a single marine reserve. Moreover, this study found that habitat length
251 or slower fish mobility did not have a significant role in reserve networks patterns. We also
252 set $\beta = 15$, which causes tourism profit to approximate a step function between 0 (when
253 $u < u_0$) and α (when $u > u_0$). We chose different values of the habitat sensitivity in our
254 numerical analysis: First, we considered $\gamma = 0$, the case in which fishing does not damage
255 population. Then, we considered low ($\gamma = 0.5$) and high ($\gamma = 15$) sensitivity cases. The
256 choice of these particular values is based in [24] too. As reported by the authors, low and
257 high sensitivity ($\gamma < 1$ and $\gamma > 5$ respectively) produce different reserve network patterns
258 and in our simulations we treat these different regimes as an illustration of distinct real

259 scenarios. Also, a broad spectrum of values for u_0 and α have been examined. For a list of
260 model parameters, their meanings, and values used in analysis, see Table 1.

261 Results

262 The ideal case: fishing does not induce habitat damage

263 First, we examined the spatial tradeoff between fishing and tourism by varying the stock
264 threshold at which tourism is profitable, u_0 , in the absence of habitat damage (i.e. zero
265 habitat sensitivity, $\gamma = 0$). We began by choosing a tourism-fishing relative price (α) that
266 made its profit, Π_t , comparable to the total fishing profit Π_f . As u_0 increases, the tradeoff
267 between fishing and tourism intensifies because the minimum stock size necessary to accrue
268 tourism profit becomes larger and larger (Figure 1). This is reflected in the spatial distri-
269 bution of fishing. As reported in [24], marine reserves emerge as the optimal strategy at
270 the edges of the habitat, just inside of peaks in effort at the habitat edges (where fishing is
271 intensified to capture stock that might otherwise swim out of the habitat and be lost, Figure
272 1a). On the other hand, tourism happens at a large portion of the habitat even in the cases
273 where the needed biomass density for it to be profitable is relatively large. In these cases,
274 tourism is combined with fishing practice although at lower levels (Figure 1b-d). However,
275 once u_0 is close to the carrying capacity of the habitat, fishing (which reduces stock below
276 carrying capacity) and tourism are fundamentally incompatible, and the sole owner must
277 choose between these two uses (Figure 1e). As u_0 increases, the size of these edge reserves
278 also increases, leading to a reduction in overall fishing effort, an increase in stock size, and
279 a decrease in fishing profit (Figure 1, bottom bargraphs).

280 Under the hypothesis that fishing does not damage the habitat, we also explore scenarios
281 in which one of the two economic activities might be more profitable (Figure 2). We find
282 two qualitatively different behaviors. When fishing is more lucrative (lower values of the

283 tourism-fishing relative price α) the two uses are incompatible, and the optimal strategy is
284 essentially the same as in the no-tourism case ($\alpha = 0$, Figure 2a). Conversely, when tourism
285 is the most profitable activity, fishing becomes limited by the optimality requirement that
286 biomass density must be higher than a certain threshold in most of the habitat (Figure
287 2f-u). Hence, we find settings in which we have two important revenue streams (Figure 2,
288 panels l,m,q and r) and scenarios in which fishing becomes almost restricted to the edges
289 of the habitat (Figure 2, panels n,o,s and t). In this same situation, as u_0 increases, the
290 total reserve length of the habitat also increases monotonically until almost all the habitat
291 becomes a reserve. Note that at this point total biomass is close to the carrying capacity
292 of the habitat and total fishing effort reaches a minimum. In the limit $u_0 \rightarrow 1$ there is
293 an abrupt transition to the no-tourism case because meeting the economic requirement over
294 tourism is biologically impossible.

295 **The effects of habitat damage**

296 When habitat damages fishing (Figures 3 and 4), the optimal solutions become more com-
297 plex. Following [24], we observe the emergence of networks of marine reserves. In other
298 words, profit is maximized when fishing occurs in narrow bands that separate unfished ar-
299 eas. Tourism occurs within these reserves and in fished regions where the stock population
300 still exceeds the stock density threshold u_0 . However, when the tourism-fishing relative price
301 is non-zero ($\alpha \neq 0$) the geometry of these networks might change, sometimes by merging
302 two or more of these reserves into one, or by intensifying or diminishing the fishing activity
303 between them, which causes variations in the biomass density of each reserve. For example
304 panels c and d of Figure 3 show such a transition. In this case the number of reserves in the
305 habitat reduces from five to three achieving large enough biomass densities at some sites in
306 order to make tourism profitable.

307 When the tradeoff between tourism and fishing is acute (large biomass density threshold

308 u_0), the optimal solution depends upon the relative value between tourism and fishing (α). If
309 tourism provides a higher reward, then a sole owner would want to have enough population
310 to attract visitors. This can be achieved by reducing fishing yield in some regions so that
311 we ensure that population density is above u_0 . This is the case of panels h and j in Figures
312 3 and 4 for example. However, if u_0 is too close to the carrying capacity of the habitat we
313 need to choose one of the two uses (fourth column of panels in both Figures). At this point,
314 establishing the most profitable strategy depends entirely on α , namely the relative price
315 between the two economic activities.

316 As in the case where fishing does not impact the habitat, both Figures 3 and 4 show
317 two qualitatively behaviors, corresponding to the cases where one economic activity is much
318 more lucrative. However, when habitat damage is considered, we find that the compromise
319 between the two uses becomes more important since fishing has a higher impact on stock
320 density and therefore it restricts tourism. Note that many panels in both Figures show
321 elevated biomass densities which are the result of converting the whole habitat into one
322 reserve. In the case of low habitat sensitivity ($\gamma = 0.5$) and under certain conditions, fishing
323 is concentrated in small regions over the central area of the habitat although at lower levels.

324 The last columns of Figures 3 and 4 show that when fishing damages habitat, a larger
325 portion of the habitat becomes an unfished reserve and therefore the total fishing yield
326 becomes smaller. This behavior intensifies as the stock density threshold (u_0) increases,
327 leading to higher biomass densities than in the non-damaging fishing case. In such cases,
328 tourism happens in a large unique reserve in the habitat where biomass density is close to
329 the carrying capacity of the habitat. However they record lower total profits.

330 **Comparison of further scenarios**

331 In order to fully compare spatial management strategies depending on fishing impact on
332 habitat, we explore a larger spectrum of tourism-fishing relative prices (α). The results of

333 different strategies present variations in total biomass, total fishing effort, reserve length and
334 economic profits. We also pay attention to separate profits coming from fishing and tourism.
335 The presence of profitable tourism usually comes in conjunction with a higher density of fish
336 stocks (Figure 5a-c) which is caused by a decline in total fishing effort (Figure 5g-l). This is
337 intensified as tourism becomes valuable, fishing has a higher impact on habitat value, and the
338 two economic activities become incompatible. In other words, relative price (α) and habitat
339 sensitivity (γ) are relatively large and the stock density threshold u_0 increases. When fishing
340 does not damage habitat there is a strong correlation between biomass density, fishing effort
341 and the total reserve length of the habitat. However, as habitat sensitivity increases, a lower
342 fishing effort might not imply having a larger unfished portion of the habitat (Figures 5d-f).
343 This is because in some cases it is more profitable to fish at lower levels in highly populated
344 areas. In any case, when fishing damages habitat, above 70% of the habitat becomes a
345 reserve in contrast with the $\gamma = 0$ case.

346 When we look at fishing and tourism profits (Figure 5j-o), we find habitats which are
347 used almost exclusively as fisheries. These correspond to habitats where tourism might be
348 not profitable. Similarly we also find settings in which most of the profit comes from tourism,
349 when it is specially profitable. These are characterised by having a large population, close
350 to its carrying capacity in the central area, and being almost closed to fishing. Lastly we
351 find habitats where the two economic activities can coexist, becoming more profitable than
352 if only one of the two was considered. This does not only happen when there is almost
353 no threshold biomass for tourism to be profitable but also for a relatively large tourism-
354 fishing relative price (α). Remarkably as α increases the optimal strategy seems to include
355 significant contributions from tourism instead of converting the whole habitat into a fishery,
356 even in the cases where this threshold value is larger.

357 Last row in Figure 5 shows how total profit $\Pi_f + \Pi_t$ decreases monotonically as the stock
358 density threshold u_0 increases which is completely understandable since economic activity in

359 the habitat is becoming more and more limited. In other words, as u_0 increases, the intrinsic
360 value of the habitat decreases as well as the maximum profit that can be generated.

361 Discussion

362 Several points emerge from our analysis. Determining the optimal management strategy for
363 a habitat with two revenue streams is a clear example of a multi-optimization problem. Here,
364 we modeled the conflict between tourism and fishing, in which fishing reduces the viability
365 of tourism such that differences in valuation of the two industries impact their optimality.
366 This raises the question of whether fishing and tourism can coexist in a marine ecosystem to
367 generate a larger profit. Remarkably, our analysis revealed scenarios in which this could be
368 the case. Such settings not only produce larger profits but are also characterized by having
369 a larger portion of the habitat closed to fishing and hence higher population densities in
370 these reserve areas. This suggests that in contrast with the classical view of competing uses,
371 an appropriate management of different resources in a marine habitat could lead to both
372 economic and ecological benefits, agreeing with previous theoretical studies – see [42].

373 In conservation terms, these results suggest that accounting for tourism could mean not
374 only higher profits but also increased fish stocks, especially when habitat is more sensitive
375 to fishing. Moreover, reserve areas emerge as the optimal strategy even when there is a low
376 tourism value agreeing with [40]. However their pattern becomes somehow more complex
377 and sometimes unexpected, in contrast to the case with no tourism. Our analysis reveals
378 that under some conditions the optimal solution consists in opening a larger fraction of the
379 area to fishing although at lower levels. In all the cases that we studied, in the maximum
380 profit scenario 60% or more of the habitat is occupied by no-take areas. Note too that under
381 certain conditions, putting more habitat in reserve does not necessarily mean having more
382 fish in the entire habitat, which can be comprehended by accounting for the lower fishing

383 yield in those cases.

384 The synergies between tourism and fishing emerge as a result of the intrinsic habitat
385 value, which in our case is determined by the habitat sensitivity to fishing and the value of
386 tourism relative to fisheries. As one could expect when one of the revenue streams is much
387 more valuable, the optimal strategy consists of allocating almost all the available resources
388 in the interest of the most profitable economic activity. Note that in the case where tourism
389 activity is prominent, larger no-take optimal areas arise. This is consistent with the findings
390 of [40, 17], who found that the size of optimal reserves increases with habitat value. Our
391 results also suggest that accounting for tourism could alleviate overexploitation in specially
392 sensitive habitats, where one could expect a lower intrinsic habitat value for fishing.

393 If fishing is particularly destructive, the optimal management approach is generally a
394 single use habitat with tourism as the main activity. Because in these cases fishing and
395 tourism do not coexist, this could mean limited profit for habitats with lower intrinsic value.
396 Yet in presently managed systems, only 6% of marine protected areas prohibit fishing [6],
397 suggesting that coexistence between tourism and (especially recreational) fishing is possible.
398 Notably, in a scenario with high value of tourism relative to fisheries, by following the optimal
399 strategy one could achieve similar profit to the case where the habitat is less susceptible to
400 fishing induced damage. This suggests that, despite the loss of fishing revenue due to habitat
401 sensitivity [24], developing incentives for high-value tourism can maintain profit.

402 While our findings suggest the possibility for coexistence between extractive and non-
403 extractive uses of habitat, implementation of dual management strategies may be complex
404 in the real world. First, while there is strong evidence pointing to the efficiency of marine
405 protected areas in the ocean, there is also an open debate which questions its real potential
406 [30]. For example, in [15] the author argues that when a fishery has weak stocks, a heavy
407 no-catch strategy could induce very high mortality rates outside the protected area. Other
408 studies point that the discrepancy between predicted and realized profits in real scenarios

409 is due to deficient implementations [2]. There has also been recent work pointing out that
410 when fishing damages habitat and harvest can be allocated between different user groups,
411 the overall maximization of fishery profit consists in setting the catch share of one of the
412 groups to zero [27].

413 Our results also depend upon the relative value of tourism and fishing. If it is hard to
414 attract tourists (large biomass density threshold u_0) or one of the two revenue streams is much
415 more profitable (depending on the tourism-fishing relative price α), the two uses become
416 incompatible. Therefore a manager would like to be able to estimate the dependence between
417 tourism and biomass, which might seem unclear in a real scenario. For example, Cabo Pulmo,
418 Mexico is known to be a popular tourist destination due to its impressive recovery of fish
419 biomass [1]. The same user preference for marine wildlife over other environmental factors
420 is found in the Caribbean island of Bonaire. However in scenarios such Barbados, tourists
421 seem to prioritize terrestrial features [39]. Moreover, this also raises the question of how to
422 include the effects of other factors, such as fishing effort, on the value of tourism which is
423 not likely to be strictly dependent on fish stocks.

424 Note too that according to the definition of the dimensionless tourism-fishing relative
425 price (which depends on $1/\sqrt{D}$ where D is the diffusion constant) fish mobility can influence
426 the choice of management preferences for one of the economic activities. When fish are
427 highly mobile the tourism-fishing relative price decreases, which could result in reduced
428 stock densities at non-fished areas. On the other hand, a sessile population could facilitate
429 reaching appropriate tourism biomass densities and hence have benefits for conservation.

430 However, if diffusion is very low (i.e., a sessile fish population), marine reserve networks
431 become less economically effective as fisheries management tools. This is because in a network
432 design, catch, profit, and employment are supported by fish that *spill over*, crossing the
433 reserve boundary and entering fished waters where they are caught and brought to market [26,
434 24]. In our model, the effects of this spillover are reflected by the *fishing the line* phenomenon

435 we observe in which fishing effort piles up at the reserve boundaries [16]. Because we rescale
436 length by diffusion, considering a smaller habitat length is equivalent to considering a fish
437 stock with a faster diffusion rate (higher motility).

438 Additionally, habitat value could change with time as different uses can damage the
439 ecosystem and recent studies insist on the importance of stock recovery plans when fishing
440 damages the habitat [28]. In [17], the authors consider the impact that fishing has on
441 habitat quality over time, but there are several studies pointing that tourism could also
442 damage habitat value [8, 22, 7]. In our case that would mean lower tourism profits or even
443 higher u_0 for some cases. On the other hand, as ecotourism becomes popular, one could also
444 expect the opposite, with increases in tourism revenue creating incentives for conservation
445 and reserve establishment [4, 36].

446 Finally we emphasize the value of optimal control theory in similar problems, where
447 the functional to be maximized consists of several interacting terms which are weighted by
448 some parameters. Here, we have the two income streams, tourism and fisheries revenue, with
449 their relative price being the weight that decides which one plays a major role. As mentioned
450 before this is just an example of multi-optimization problems that commonly arise in ecology
451 and economics and we believe that optimal control theory might have a significant impact
452 on them.

453 **Acknowledgements**

454 The authors thank M.G. Neubert and the 2019 Nantucket Math Ecology (ACKME) Retreat
455 participants for helpful discussion. HVM acknowledges funding from a National Science
456 Foundation Postdoctoral Research Fellowship in Biology (DBI-401332).

457 **Author contributions**

458 CF and HVM conceived the ideas and designed the methodology. HVM supervised the
459 project. CF performed the simulations and led the writing of the manuscript. All authors
460 edited the manuscript and gave final approval for publication.

Table 1: Explanation of variables and parameters in the model, together with their typical units and the values used in numerical simulations.

Symbol	Meaning	Typical units	Rescaled version	Values
Variables				
x	space	km	ξ	
t	time	yr		
N	biomass density	$\text{kg}\cdot\text{km}^{-1}$	u	
E	fishing effort density	vessel $\text{day}\cdot\text{km}^{-1}\cdot\text{yr}^{-1}$	f	
Π	total profit	$\text{dollars}\cdot\text{yr}^{-1}$	π	
Parameters				
L	habitat length	km	ℓ	15
r	low-density growth rate	yr^{-1}		
K_0	carrying capacity in the absence of fishing	$\text{kg}\cdot\text{km}^{-1}$		
D	diffusion coefficient	$\text{km}^2\cdot\text{yr}^{-1}$		
g	habitat sensitivity	$\text{km}\cdot\text{yr}\cdot\text{vessel}\cdot\text{day}^{-1}$	γ	0,0.5,15
q	catchability coefficient	$\text{km}\cdot\text{vessel}\cdot\text{day}^{-1}$		
w_0	effort cost	$\text{dollars}\cdot\text{vessel}\cdot\text{day}^{-1}$	c_0	0.01
w_1	congestion cost	$\text{dollars}\cdot\text{km}\cdot\text{yr}\cdot\text{vessel}\cdot\text{day}^{-2}$	c_1	0.001
p	price per stock	$\text{dollars}\cdot\text{kg}^{-1}$		
a	tourism profit per unit length	$\text{dollars}\cdot\text{km}^{-1}$	α	0 – 1
N_0	biomass density threshold value	$\text{kg}\cdot\text{km}^{-1}$	u_0	0 – 1
b	logistic growth rate of tourism function	$\text{km}\cdot\text{kg}^{-1}$	β	15

462 Figure legends

Figure 1: Population density (solid line) and effort density (dashed line) when fishing does not damage habitat (i.e. zero habitat sensitivity, $\gamma = 0$) as the stock density threshold (u_0) increases from left to right. Red bands on x -axis mark regions where tourism is happening. Biomass, fishing effort and total profit integrated over the habitat together with total reserve length. Values are scaled according to maximum values found in analysis. Tourism profit for fixed tourism-fishing relative price (α) and fishing profit represented by Π_t and Π_f respectively for each case.

Figure 2: Population density (solid line) and effort density (dashed line) when fishing does not damage habitat (i.e. zero habitat sensitivity, $\gamma = 0$). Red bands on x -axis mark regions where tourism is happening. Last column includes biomass, fishing effort and total profit integrated over the habitat together with total reserve length for the non-tourism case first, and with varying stock density threshold (u_0) for fixed values of the tourism-fishing relative price (α). Tourism profit and fishing profit represented by Π_t and Π_f respectively for each case.

Figure 3: Population density (solid line) and effort density (dashed line) for the low-sensitivity case ($\gamma = 0.5$). Red bands on x -axis mark regions where tourism is happening. Last column includes biomass, fishing effort and total profit integrated over the habitat together with total reserve length for the non-tourism case first, and with varying stock density threshold (u_0) for fixed values of the tourism-fishing relative price (α). Tourism profit and fishing profit represented by Π_t and Π_f respectively for each case.

Figure 4: Population density (solid line) and effort density (dashed line) for the high-sensitivity case ($\gamma = 15$). Red bands on x -axis mark regions where tourism is happening. Last column includes biomass, fishing effort and total profit integrated over the habitat together with total reserve length for the non-tourism case first, and with varying stock density threshold (u_0) for fixed values of the tourism-fishing relative price (α). Tourism profit and fishing profit represented by Π_t and Π_f respectively for each case.

Figure 5: Biomass, reserve length, fishing effort integrated over the habitat and fishing, tourism and total profit as a function of the stock density threshold (u_0). Different values of the tourism-fishing relative price (α) represented with the heat map.

References

- [1] Octavio Aburto-Oropeza, Brad Erisman, Grantly Galland, Ismael Mascarenas, Enric Sala, and E. Ezcurra. Large recovery of fish biomass in a no-take marine reserve. *PloS one*, 6:e23601, 08 2011.
- [2] Tundi Agardy. Justified ambivalence about mpa effectiveness. *ICES Journal of Marine Science*, 75:1183–1185, 05 2018.
- [3] Claire W. Armstrong. A note on the ecological–economic modelling of marine reserves in fisheries. *Ecological Economics*, 62(2):242–250, 2007. Special Section: Ecological-economic modelling for designing and evaluating biodiversity conservation policies.
- [4] Donald Brightsmith, Amanda Stronza, and Kurt Holle. Ecotourism, conservation biology, and volunteer tourism: A mutually beneficial triumvirate. *Biological Conservation - BIOL CONSERV*, 141, 09 2008.
- [5] Mark Costello. Long live marine reserves: A review of experiences and benefits. *Biological Conservation*, 176, 08 2014.
- [6] Mark Costello and Bill Ballantine. Biodiversity conservation should focus on no-take marine reserves: 94 *Trends in ecology evolution*, 30:507–9, 09 2015.
- [7] Benjamin Cowburn, Charlotte Moritz, Chico Birrell, Gabriel Grimsditch, and Ameer Abdulla. Can luxury and environmental sustainability co-exist? assessing the environmental impact of resort tourism on coral reefs in the maldives. *Ocean Coastal Management*, 158, 03 2018.
- [8] Derrin Davis and Clement Tisdell. Recreational scuba-diving and carrying capacity in marine protected areas. *Ocean Coastal Management*, 26:19–40, 12 1995.

- 485 [9] Jon Day and Kirstin Dobbs. Effective governance of a large and complex cross-
486 jurisdictional marine protected area: Australia's great barrier reef. *Marine Policy*,
487 41:14–24, 09 2013.
- 488 [10] Elianny Domínguez-Tejo, Graciela Metternicht, Emma Johnston, and Luke Hedge. Ma-
489 rine spatial planning advancing the ecosystem-based approach to coastal zone manage-
490 ment: A review. *Marine Policy*, 72:115 – 130, 2016.
- 491 [11] Steven D. Gaines, Crow White, Mark H. Carr, and Stephen R. Palumbi. Designing
492 marine reserve networks for both conservation and fisheries management. *Proceedings*
493 *of the National Academy of Sciences*, 107(43):18286–18293, 2010.
- 494 [12] Edmund Green and Rachel Donnelly. Recreational scuba diving in caribbean marine
495 protected areas: Do the users pay? *Ambio*, 32:140–4, 04 2003.
- 496 [13] Benjamin Halpern, Sarah Lester, and Julie Kellner. Spillover from marine reserves and
497 replenishment of fished stocks. *Environmental Conservation*, 36, 12 2009.
- 498 [14] Alan Hastings, Steven D. Gaines, and Christopher Costello. Marine reserves solve
499 an important bycatch problem in fisheries. *Proceedings of the National Academy of*
500 *Sciences*, 114(34):8927–8934, 2017.
- 501 [15] Ray Hilborn. Traditional fisheries management is the best way to manage weak stocks.
502 *Proceedings of the National Academy of Sciences*, 114(50):E10610–E10610, 2017.
- 503 [16] Julie B. Kellner, Irene Tetreault, Steven D. Gaines, and Roger M. Nisbet. Fishing the
504 line near marine reserves in single and multispecies fisheries. *Ecological Applications*,
505 17(4):1039–1054, 2007.
- 506 [17] Michael Kelly, Michael Neubert, and Suzanne Lenhart. Marine reserves and optimal
507 dynamic harvesting when fishing damages habitat. *Theoretical Ecology*, 12, 11 2018.

- 508 [18] S. Lenhart and J. Workman. *Optimal Control Applied to Biological Models*. Chapman
509 and Hall/CRC, New York, 1 edition, 2007.
- 510 [19] S. Lester, J. Stevens, Rebecca Gentry, Carrie Kappel, Tom Bell, C. Costello, Steven
511 Gaines, D. Kiefer, C. Maue, J. Rensel, Rachel Simons, L. Washburn, and C. White.
512 Marine spatial planning makes room for offshore aquaculture in crowded coastal waters.
513 *Nature Communications*, 9:1–13, 03 2018.
- 514 [20] Priscila Lopes, Shirley Souza, Mariana Clauzet, Renato Silvano, and Alpina Begossi.
515 Fisheries, tourism, and marine protected areas: Conflicting or synergistic interactions?
516 *Ecosystem Services*, 16, 01 2015.
- 517 [21] Gorka Merino, Manuel Barange, Julia Blanchard, James Harle, Robert Holmes, Icarus
518 Allen, Edward Allison, M-C Badcheck, Nicholas Dulvy, Jason Holt, Simon Jennings,
519 Christian Mullon, and Lynda Rodwell. Can marine fisheries and aquaculture meet fish
520 demand from a growing human population in a changing climate? *Global Environmental*
521 *Change*, 22:795–806, 10 2012.
- 522 [22] Marco Milazzo, Renato Chemello, Fabio Badalamenti, Raffaele Camarda, and Silvano
523 Riggio. The impact of human recreational activities in marine protected areas: What
524 lessons should be learnt in the mediterranean sea? *Marine Ecology*, 23:280 – 290, 12
525 2002.
- 526 [23] Holly Moeller and Michael Neubert. Economically optimal marine reserves without
527 spatial heterogeneity in a simple two-patch model. *Natural Resource Modeling*, 06 2015.
- 528 [24] Holly V. Moeller and Michael G. Neubert. Habitat damage, marine reserves, and the
529 value of spatial management. *Ecological Applications*, 23(5):959–971, 2013.
- 530 [25] Michael Neubert. Marine reserves and optimal harvesting. *Ecology Letters*, 6:843 – 849,
531 09 2003.

- 532 [26] Michael G Neubert and Guillermo E Herrera. Triple benefits from spatial resource
533 management. *Theoretical Ecology*, 1(1):5–12, 2008.
- 534 [27] Rachel Nichols, Satoshi Yamazaki, and Sarah Jennings. Allocation of harvest between
535 user groups in a fishery with habitat effect. *Natural Resource Modeling*, 31(3):e12179,
536 2018.
- 537 [28] Rachel Nichols, Satoshi Yamazaki, and Sarah Jennings. The role of precaution in stock
538 recovery plans in a fishery with habitat effect. *Ecological Economics*, 146:359–369, 2018.
- 539 [29] Sean Pascoe, Amar Doshi, Olivier Thébaud, Colette Thomas, Heidi Schuttenberg, Scott
540 Heron, Naneng Setiasih, Chun Hong Tan, James True, Kristy Wallmo, Christy Loper,
541 and Emma Calgaro. Estimating the potential impact of entry fees for marine parks on
542 dive tourism in south east asia. *Marine Policy*, 47:147–152, 07 2014.
- 543 [30] Linwood Pendleton, Gabby Ahmadia, Howard Browman, Ruth Thurstan, David Ka-
544 plan, and Valerio Bartolino. Debating the effectiveness of marine protected areas. *ICES*
545 *Journal of Marine Science*, 75:1156–1159, 05 2018.
- 546 [31] M.R. Phillips and A.L. Jones. Erosion and tourism infrastructure in the coastal zone:
547 Problems, consequences and management. *Tourism Management*, 27(3):517 – 524, 2006.
- 548 [32] Jake C. Rice and Serge M. Garcia. Fisheries, food security, climate change, and biodi-
549 versity: characteristics of the sector and perspectives on emerging issues. *ICES Journal*
550 *of Marine Science*, 68(6):1343–1353, 04 2011.
- 551 [33] Enric Sala, Christopher Costello, Dawn Dougherty, Geoffrey Heal, Kieran Kelleher,
552 Jason H. Murray, Andrew A. Rosenberg, and Rashid Sumaila. A general business
553 model for marine reserves. *PLOS ONE*, 8(4):1–9, 04 2013.

- 554 [34] Enric Sala and Sylvaine Giakoumi. No-take marine reserves are the most effective
555 protected areas in the ocean. *ICES Journal of Marine Science*, 75(3):1166–1168, 08
556 2017.
- 557 [35] Jennifer C. Selgrath, Sarah E. Gergel, and Amanda C. J. Vincent. Shifting gears:
558 Diversification, intensification, and effort increases in small-scale fisheries (1950-2010).
559 *PLOS ONE*, 13(3):1–24, 03 2018.
- 560 [36] Amanda Stronza, Carter Hunt, and Lee Fitzgerald. Ecotourism for conservation? *An-*
561 *annual Review of Environment and Resources*, 44, 10 2019.
- 562 [37] Lydia Teh and Rashid Sumaila. Contribution of marine fisheries to worldwide employ-
563 ment. *Fish and Fisheries*, 14, 12 2011.
- 564 [38] Chua Thia-Eng. Essential elements of integrated coastal zone management. *Ocean*
565 *Coastal Management*, 21(1):81 – 108, 1993. Integrated Coastal Management.
- 566 [39] Maria C. Uyarra, Isabelle M. Côté, Jennifer A. Gill, Rob R.T. Tinch, David Viner,
567 and Andrew R. Watkinson. Island-specific preferences of tourists for environmental
568 features: implications of climate change for tourism-dependent states. *Environmental*
569 *Conservation*, 32(1):11–19, 2005.
- 570 [40] Daniel F. Viana, Benjamin S. Halpern, and Steven D. Gaines. Accounting for tourism
571 benefits in marine reserve design. *PLOS ONE*, 12(12):1–18, 12 2017.
- 572 [41] Godwin K. Vondolia, Wenting Chen, Claire W. Armstrong, and Magnus D. Norling.
573 Bioeconomic Modelling of Coastal Cod and Kelp Forest Interactions: Co-benefits of
574 Habitat Services, Fisheries and Carbon Sinks. *Environmental & Resource Economics*,
575 75(1):25–48, January 2020.

576 [42] Bui Bich Xuan and Claire W. Armstrong. Trading Off Tourism for Fisheries. *Environ-*
577 *mental and Resource Economics*, 73(2):697–716, June 2019.