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

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Abstract

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

Recommendations for Resource Managers

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

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

**Introduction**

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

A major challenge of multiple uses is potential conflict between them. Complex ownership may also result in over-exploitation when competing users erode stock below the population associated with maximum sustainable yield. While both fishing and tourism can be lucrative activities, one might influence the other negatively by limiting its intrinsic value [20]. For
example, although there are no data relating fish biomass and visitor frequency, there is strong evidence that divers tend to prefer environments with abundant and diverse marine life [33]. Aggressive fishing practices can damage habitat and consequently diminish habitat value and its tourism potential. Increasingly, fisheries are overexploited, which threatens not only other habitat uses, but also food and economic security. Moreover, recent studies show that even modern fishing gear might have a big impact on oceans [35].

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

Here, we consider the interactions of some of these complexities with fisheries management. Specifically, we model a system in which revenue may be generated through fishing and through tourism, with varying degrees of conflict between these uses. We assume that tourism generates profit which is strictly depending on the habitat biomass (e.g., total fish stocks). In addition, in our model, population density follows a 1D reaction-diffusion partial differential equation (PDE) and we use optimal control theory to compute the first-best sole owner case, in which the system is optimally managed to yield the greatest profit across both
fishing and tourism industries. We also consider the impacts of habitat-damaging fishing on the optimal outcomes. We find that economic benefits from tourism can further incentivize the establishment of marine reserves, and that synergies (elevated profits in multiuse systems) rather than tradeoffs may emerge. These synergies are sensitive to the relative valuation of tourism and fishing, suggesting that with appropriate economic incentives, these two uses may coexist if managers can establish reserve networks.

The Model

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

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

\[
\frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} + r N \left( 1 - \frac{N}{K} \right). \tag{1}
\]

When fishing occurs, there are two effects on the fish stock. First, fish are directly removed by harvest, at a rate \( qEN \), where \( E \) is a measure of the local fishing effort at a certain time, and \( q \) is the catchability coefficient, which reflects the efficiency of a particular fishery. Second, fishing damages habitat, which reduces the maximum population that can
be locally supported. As in [23], we model this by assuming that fishing reduces the carrying
capacity of the habitat, where the strength of habitat damage is governed by a habitat
sensitivity coefficient $g$. Thus, we replace $K$ with:

$$K = \frac{K_0}{1 + gE},$$  \hspace{1cm} (2)

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

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

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

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

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

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

In our model, income can be generated from two sources: fishing and tourism. As
suggested in [33] marine life and diversity in an ecosystem can be a main attraction for
divers and snorkelers. Although data relating tourist visits and biomass are not available, it
is reasonable to assume that the frequency of these visitors will increase with fish density,
thus increasing the tourism profit. We model tourism profit per unit length at location $x$, $\rho_t(x)$ by a logistic function with midpoint in $N_0$. This parameter can be understood as a threshold value from which one can generate relevant profit. In the face of a fixed price per unit tourism $a$, tourism profit density follows:

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

(5)

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

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

(6)

We want to emphasize that Equation (6) represents total tourism profit, which means that it includes both revenue and tourism costs. While tourism can happen only above a certain threshold of stock density, its economic value $a$ dictates how profitable it will be. When estimating this price, tourism costs should also be taken into account. Therefore, large
values of $a$ denote scenarios in which tourism revenue is much larger than its costs, while smaller values of $a$ indicate revenue which is comparable to the total tourism costs.

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

$$\rho_f = pqEN - (w_0 + w_1E)E. \tag{7}$$

And likewise, total fishing profit $\Pi_f$ follows:

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

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

$$\max_{E,N} \Pi = \Pi_t + \Pi_f; \tag{9}$$

subject to: $E, N \geq 0. \tag{10}$
Model Analysis

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

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

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

\[ \frac{d^2u}{d\xi^2} = u(f - 1) + (1 + \gamma f)u^2, \] (12)

with boundary conditions

\[ u(-\ell/2) = u(\ell/2) = 0. \] (13)

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

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

Note that \( \gamma \) is a dimensionless version of the habitat sensitivity. This parameter will allow us to distinguish between different types of habitat depending on their sensitivities. Observe too that \( \gamma \) depends on how vulnerable the environment is (i.e. the habitat sensitivity \( g \)) and on the efficiency of the fishery (i.e. the catchability coefficient \( q \)). On the other hand, \( \ell \) gives a typical length scale in our model, which of course depends on habitat length and fish mobility and growth rate. Hence, a smaller dimensionless habitat could represent not only smaller actual lengths but also, increased fish mobility or a slower growth rate.
With the change of variables (11), the dimensionless total profit arising from both tourism and fishing can be written as:

\[
\pi[u, f] = \int_{-\xi/2}^{\xi/2} \left[ \alpha z(u) + uf - (c_0 + c_1 f)f \right] d\xi; \tag{15}
\]

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

\[
\beta = bK_0, \quad \alpha = a/(pK_0\sqrt{rD}) \quad u_0 = N_0/K_0, \quad c_0 = w_0/(qpK_0), \quad c_1 = w_1r/(q^2pK_0). \tag{16}
\]

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

We will determine the effort distribution and the stock density that maximize the total profits integral (15). Observe that although there is one control – the distribution of fishing effort \( f(\xi) \) – this control directly affects both fishing and tourism profits. Recall that tourism will only be relevant if the local stock biomass exceeds a threshold value \( u_0 \) and \( \alpha \) sets a high enough reward to incentivize foregoing fishing profits. Our goal then is to maximize profit subject to the biological constraint of non-negative stock and the economic constraint of non-negative fishing:
\[
\max_{u, f} \pi[u, f],
\]
subject to: \( u, f \geq 0. \) \hspace{1cm} (17) \hspace{1cm} (18)

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

\[
\frac{du}{d\xi} = v, \hspace{1cm} (19)
\]

\[
\frac{dv}{d\xi} = u\left(f^* - 1\right) + (1 + \gamma f^*)u^2. \hspace{1cm} (20)
\]

with boundary conditions given by Eq (13).

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

\[
H[u, v, f, \lambda_1, \lambda_2] = uf - (c_0 + c_1 f)f + \alpha \pi(u)
+ \lambda_1 v + \lambda_2 \left[u(f - 1) - (1 + \gamma f)u^2\right]. \hspace{1cm} (21)
\]

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

\[
f^* = \frac{u(1 + \lambda_2 - \gamma u) - c_0}{2c_1}. \hspace{1cm} (22)
\]

The maximum principle also tells us that the adjoint variables \( \lambda_1(\xi), \lambda_2(\xi) \) satisfy the
ordinary differential equations

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

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

alongside the transversality conditions
\[
\lambda_2(\ell/2) = \lambda_2(-\ell/2) = 0.
\]

Note that \(\partial H/\partial v = \lambda_1\) and hence these two equations become:

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

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

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

Results

The ideal case: fishing does not induce habitat damage

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

Under the hypothesis that fishing does not damage the habitat, we also explore scenarios in which one of the two economic activities might be more profitable (Figure 2). We find two qualitatively different behaviors. When fishing is more lucrative (lower values of the
tourism-fishing relative price \( \alpha \) the two uses are incompatible, and the optimal strategy is essentially the same as in the no-tourism case (\( \alpha = 0 \), Figure 2a). Conversely, when tourism is the most profitable activity, fishing becomes limited by the optimality requirement that biomass density must be higher than a certain threshold in most of the habitat (Figure 2-u). Hence, we find settings in which we have two important revenue streams (Figure 2 panels l,m,q and r) and scenarios in which fishing becomes almost restricted to the edges of the habitat (Figure 2 panels n,o,s and t). In this same situation, as \( u_0 \) increases, the total reserve length of the habitat also increases monotonically until almost all the habitat becomes a reserve. Note that at this point total biomass is close to the carrying capacity of the habitat and total fishing effort reaches a minimum. In the limit \( u_0 \rightarrow 1 \) there is an abrupt transition to the no-tourism case because meeting the economic requirement over tourism is biologically impossible.

The effects of habitat damage

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

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

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

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

**Comparison of further scenarios**

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

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

Last row in Figure 5 shows how total profit $\Pi_f + \Pi_t$ decreases monotonically as the stock density threshold $u_0$ increases which is completely understandable since economic activity in
the habitat is becoming more and more limited. In other words, as $u_0$ increases, the intrinsic value of the habitat decreases as well as the maximum profit that can be generated.

Discussion

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

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

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

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

While our findings suggest the possibility for coexistence between extractive and non-extractive uses of habitat, implementation of dual management strategies may be complex in the real world. First, while there is strong evidence pointing to the efficiency of marine protected areas in the ocean, there is also an open debate which questions its real potential [30]. For example, in [15] the author argues that when a fishery has weak stocks, a heavy no-catch strategy could induce very high mortality rates outside the protected area. Other studies point that the discrepancy between predicted and realized profits in real scenarios
is due to deficient implementations [2]. There has also been recent work pointing out that when fishing damages habitat and harvest can be allocated between different user groups, the overall maximization of fishery profit consists in setting the catch share of one of the groups to zero [27].

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

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

However, if diffusion is very low (i.e., a sessile fish population), marine reserve networks become less economically effective as fisheries management tools. This is because in a network design, catch, profit, and employment are supported by fish that spill over, crossing the reserve boundary and entering fished waters where they are caught and brought to market [26]. In our model, the effects of this spillover are reflected by the fishing the line phenomenon.
we observe in which fishing effort piles up at the reserve boundaries [16]. Because we rescale length by diffusion, considering a smaller habitat length is equivalent to considering a fish stock with a faster diffusion rate (higher motility).

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

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

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Author contributions

CF and HVM conceived the ideas and designed the methodology. HVM supervised the project. CF performed the simulations and led the writing of the manuscript. All authors edited the manuscript and gave final approval for publication.
Tables
Table 1: Explanation of variables and parameters in the model, together with their typical units and the values used in numerical simulations.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Meaning</th>
<th>Typical units</th>
<th>Rescaled version</th>
<th>Values</th>
</tr>
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<tbody>
<tr>
<td><strong>Variables</strong></td>
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<td></td>
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</tr>
<tr>
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<td>space</td>
<td>km</td>
<td>$\xi$</td>
<td></td>
</tr>
<tr>
<td>$t$</td>
<td>time</td>
<td>yr</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$N$</td>
<td>biomass density</td>
<td>kg·km$^{-1}$</td>
<td>$u$</td>
<td></td>
</tr>
<tr>
<td>$E$</td>
<td>fishing effort density</td>
<td>vessel day$^{-1}$·km$^{-1}$·yr$^{-1}$</td>
<td>$f$</td>
<td></td>
</tr>
<tr>
<td>$\Pi$</td>
<td>total profit</td>
<td>dollars·yr$^{-1}$</td>
<td>$\pi$</td>
<td></td>
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<tr>
<td><strong>Parameters</strong></td>
<td></td>
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<td>habitat length</td>
<td>km</td>
<td>$\ell$</td>
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<tr>
<td>$r$</td>
<td>low-density growth rate</td>
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<td>carrying capacity in the absence of fishing</td>
<td>kg·km$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$D$</td>
<td>diffusion coefficient</td>
<td>km$^2$·yr$^{-1}$</td>
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<td></td>
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<td>$g$</td>
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<td>km·kg$^{-1}$</td>
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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 ($\alpha$) and fishing profit represented by $\Pi_t$ and $\Pi_f$ 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 ($\alpha$). Tourism profit and fishing profit represented by $\Pi_t$ and $\Pi_f$ 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 ($\alpha$). Tourism profit and fishing profit represented by $\Pi_t$ and $\Pi_f$ 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 ($\alpha$). Tourism profit and fishing profit represented by $\Pi_t$ and $\Pi_f$ 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 ($\alpha$) represented with the heat map.
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