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RESEARCH

Social-ecological models with social hierarchy and spatial structure applied to small-scale fisheries

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Abstract

Socio-ecological models combine ecological systems with human social dynamics in order to better understand human interactions with the environment. To model human behavior, replicator dynamics can be used to model how societal influence and financial costs can change opinions about resource extraction. Previous research on replicator dynamics has shown how evolving opinions on conservation can change how humans interact with their environment and therefore change population dynamics of the harvested species. However, social-ecological models often assume that human societies are homogeneous with no social structure. Building on previous work on social-ecological models, we develop a two-patch socio-ecological model with social hierarchy in order to study the interactions between spatial dynamics and social inequity. We found that fish movement between patches is a major driver of model dynamics, especially when the two patches exhibit different social equality and fishing practices. Further, we found that the societal influence between groups of harvesters was essential to ensuring stable fishery dynamics. Next, we developed a case study of two independently managed fisheries that were connected by fish movement where one human group fishes sustainably while another was over-harvests, resulting in a fishery collapse of both patches. We also found that because in this model, the influence of one human patch on another only communicates the amount of each catch and no fishing strategies were employed, increased social influence decreased the sustainability of the fishery. The findings of this study indicate the importance of including spatial components to socio-ecological models and highlights the importance of understanding species' movements when making conservation decisions. Further, we demonstrate how incorporating fishing methods from outside sources can result in higher stability of the harvested population, demonstrating the need for effective communication across management regimes.

Keywords Two-patch model · Replicator dynamics · Social hierarchy · Socio-ecological model · Species movement

Introduction

Social-ecological models treat human behavior as a variable as opposed to a set parameter. Allowing human behavior to be dynamic allows for the study of how decision-making can change in response to environmental factors and, in turn, alter how humans interact with resources and profits (Bauch 2005; Ostrom 2009; Innes et al. 2013; Oraby et al. 2014; Bauch et al. 2016; Sigdel et al. 2017; Thampi et al. 2018). As human societies grow increasingly intricate and interconnected, these models can help us to analyze how our social structures can influence the environment around us (Liu et al. 2007). Social-ecological modeling provides important insight not only into how human decision-making can influence ecological patterns but can also show hidden processes, reveal regime shifts, and identify vulnerabilities of systems that do not exist within the purely social or ecological models (Liu et al. 2007; Young et al. 2007; Ostrom 2009; Lade et al. 2013). Socio-ecological models can also be used in systems where data are difficult to collect, as parameters can be changed in order to analyze different hypothetical scenarios. As social-ecological models are simulations of human and environmental interactions, they allow flexibility and can

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be adapted to fit the specific system of study and improve place-based management practices (Young et al. 2007; Liu et al. 2007; Felipe-Lucia et al. 2022)

Due to their adaptability, socio-ecological models can use a wide range of strategies to represent human decision-making. One such method is replicator dynamics, which model human decision-making where an individual makes conservation choices based on weighing the perceived benefits of conservation with the costs, as well as the social pressure to conform to the group's stance on conservation (Bauch 2005). Individuals will therefore "replicate" the behavior of their peers by changing their harvest practices based on the opinion of the majority (Bauch and Bhattacharyya 2012). Models that employ replicator dynamics have been used to show how this social learning is a key component to vaccination uptake in public health, and preexisting social norms can actually suppress vaccine uptake despite frequent disease outbreaks (Bauch and Bhattacharyya 2012; Oraby et al. 2014). Replicator dynamics can also have conservation applications as pest invasion models have shown ways to simultaneously mitigate pest outbreaks and the cost to address them in the timber industry (Barlow et al. 2014). Further, land use changes have been modeled to have completely different dynamics when human decision-making was added to replicator dynamic models (Innes et al. 2013). However, past work on human behavior has generally assumed that human societies are homogeneous, and all people are subject to the same social influence and ecological dynamics.

Understanding effective conservation strategies can be especially difficult if the organism being protected has a migratory pattern that crosses over multiple management jurisdictions such as country borders (Ogburn et al. 2017; Garrone-Neto et al. 2018; Ramírez-Valdez et al. 2021). Borders can also create challenges when gathering population data that require extensive fieldwork (Cozzi et al. 2020; Hebblewhite and Whittington 2020). The fragmentation of management can also result in a mismatch of conservation strategies that become ineffective when the distinct management bodies do not coordinate efforts (Siddons et al. 2017). Research on the importance of coordinated research efforts has been conducted on many terrestrial species with large migratory ranges and has consistently shown that cooperation among government bodies is essential to protecting the health of highly migratory species or species whose native ranges expand across multiple countries (Plumptre et al. 2007; Gervasi et al. 2015; Meisingset et al. 2018). Because fish are generally migratory, management cooperation is especially relevant in international waters or waters where different government bodies share jurisdiction (Mchich et al. 2000). Previous research on two-patch fishing models has shown that fish movement rates between patches can affect population stability when there are different fishing pressures in each patch (Mchich et al. 2000; Cai et al. 2008). Economic output can also be maximized in multi-patch fishing models as high dispersal can result in a higher overall yield of the system than the yield of each patch combined (Auger et al. 2022). High dispersal across patches is commonly found to be an essential component to maximizing population health and economic gain from fishing (Freedman and Waltman 1977; Moeller and Neubert 2015; Auger et al. 2022). Two-patch models help us to understand the population dynamics of fish species better that face different pressures in each patch and have even resolved conflicts between fishing groups (Mchich et al. 2000).

Homophily is a concept from sociology where humans tend to take information and the opinions from subgroups similar to them before listening to subgroups of different social standing (Brechwald and Prinstein 2011). Contrary to the assumption made by previous models that human groups are homogeneous, the vast majority of real-world societies exhibit some form of hierarchy or inequality. Societies with different social subgroups can often exhibit an "us vs. them" mentality and compete for resources (Borgatti 2003). Barnes-Mauthe (2013) showed that fishing communities can exhibit homophily, which is the tendency for people to obtain information and opinions from those who are similar to themselves before seeking views from those who are perceived as different. Therefore, people in different social groups may be receiving different information and opinions about conservation and acting accordingly (McPherson et al. 2001). For example, in Kenya, communication among fishers has been shown to stay within groups using the same gear type which has inhibited successful regulation of the whole fishery (Crona and Bodin 2006). Further, in the southwest Madagascar octopus fishery, fishing method and location typically falls along gendered lines. When fishing restrictions were imposed on tidal flats, women's access to octopus harvest was restricted, while men, who were generally in charge of fishery management typically fished in deeper waters, were able to maintain their livelihood (Baker-Médard 2017). In Thailand, ethnicity has been shown to be a source of fishing conflict which has exacerbated resource depletion (Pomeroy et al. 2007). The existence of social structures is extremely prevalent in human societies which can affect how people interact with the environment. However, there is little existing research that uses replicator dynamics study to study how social hierarchies alter harvest practices. People's relationship with the environment has been shown to be influenced by many factors such as social status, wealth, gender, education, and even notions of self-importance (Baker-Médard et al. 2021b; Sari et al. 2021). Competition over resources has been shown to be exacerbated by social hierarchies and "top-down" regulation whereas when social connectivity is considered in management plans, management outcomes are not only improved, but costs are reduced as well (Krackhardt and Stern 1988; Grafton 2005; Bodin and Crona 2009).

Research on small-scale fisheries is a growing and essential field as they are drastically understudied yet are relied on by many people around the globe (FAO 2022; FAO et al. 2023). Due to tight social structures, community decision-making, and strong reliance on the environment, small-scale fisheries are systems that are well represented by socio-ecological models and replicator dynamics (Grafton 2005; Thampi et al. 2018; Barnes et al. 2019). Successful management of small-scale fisheries has shown to be contingent upon the careful consideration of social dynamics and power structures within the fishery (Alexander et al. 2015; Defeo et al. 2016; Nyikahadzoi et al. 2017). Further, the specific dynamics of the fishery in question have been shown to be important components to models, as models with multiple patches can actually mitigate overfishing if there is high movement of the harvested species between patches (Cressman et al. 2004). No previous research has combined two-patch fishing models with a hierarchical human decision-making model in order to study how space and social dynamics affect fishery dynamics.

In this study, we couple a human-decision replicator dynamics model with social hierarchies with a two-patch resource model in order to understand how decision-making is affected by spatial and hierarchical factors. This model reflects two fisheries are connected by the stray rate of two subpopulations of fish, where each subpopulation is independently managed. The two management regimes influence one another based on how many people are fishing in the other group. The objectives of this study were (1) to compare the output of previous replicator dynamics studies with the new two-patch model to understand the effect of fish movement on harvesting decisions, (2) understand the effect of social hierarchy and communication across groups on the dynamics of this model, and (3) use a two-patch small-scale fishery as a case study to understand how fishery dynamics are driven when one group fishes sustainably while the other over-harvests. We hypothesized that higher cooperation between groups would benefit fish stocks overall and that increased fish movement would increase the health of fish populations.

Methods

Model construction

We build on the work of Bauch et al. (2016) by extending their old-growth forest model to a two-patch model (Fig. 1). The resource population models adapted from Bauch et al. (2016) are as follows:

$$\frac{dF_i}{dt} = r_i F_i(1 - F_i) - \frac{h_i * F_i}{F_i + s_i} - m_j F_i + m_i F_j \qquad (1)$$

where the change in resource populations F_i is dependent on r_i, the net population growth of each patch i, and both populations follow logistic growth. The second term, $\frac{h_i * F_i}{F_i + s_i}$, denotes population lost to human activity. h_i is the harvesting efficiency of the respective human population, and s_i controls the supply and demand of the system. Because we extend this to a two-patch model, the m_i parameter denotes the stray rate between each of the subpopulations of fish out of patch i and into patch j. In this study, we assume a closed population between the two patches. Therefore, individual fish move directly from patch to patch and do not disperse elsewhere, nor are individual fish immigrating from outside areas.

For the model of human activity and opinion, we use replicator dynamics from evolutionary game theory to simulate societal influence on an individual's opinion. Humans in this population can either be harvesters (therefore participating

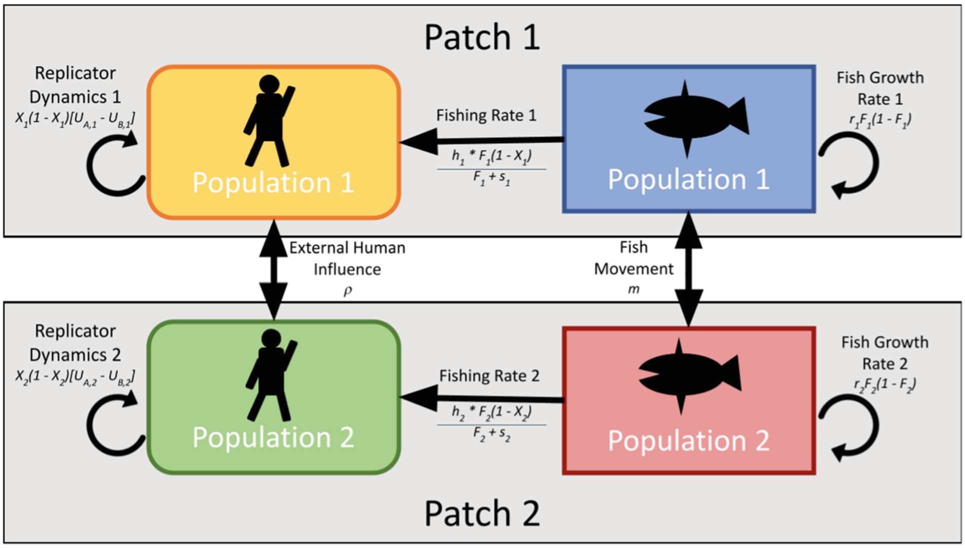

Fig. 1 A conceptual representation of our model as a two-patch extension of Bauch et al. (2016). Here, each fish population (F_i) in each patch i increases through natural growth and movement of fish into the patch. Fish populations are decreased through emigration out of the patch and fishing mortality. The number of fishers (X_i) in each patch i changes in response to fish population levels, the cost of stopping fishing activity, and the opinions of those in the patch and those in the other patch

in harvesting activity) or conservationists (who do not partake in resource extraction) in their respective patch, but can change from their current opinion to the other based on the perceived values and costs of each stance. Social dynamics are represented by the proportion of conservationists in a population (X) and the proportion of harvesters ($1 - X$). These two groups of conservationists and harvesters interact with one another using the term $(X)(1-X)$ which simulates individuals "sampling" the opinions of other individuals in the population. If one opinion dominates in the population (i.e., $X \gg (1 - X)$ or $(1 - X) \gg X$), the rate of changing opinions will be slow as the power of societal pressure makes it challenging for the other opinion to gain traction. However, if X and $(1 - X)$ are close, the rate of change in opinion will be fast as society has a split opinion on conservation versus harvest, so individuals will be quick to take up the opinions of others. In this model, each person holds an opinion (conservation or harvest) by weighing the benefits of conservation (U_A) against the benefits of harvest (U_B), resulting in the replicator equation:

$$\frac{dX_i}{dt} = k_i X_i(1 - X_i)[U_{A,i} - U_{B,i}] \tag{2}$$

$$\frac{dX_i}{dt} = k_i X_i(1 - X_i)[\Delta U_i] \tag{3}$$

where k_i refers to the rate of interaction within a group. As individuals "sample" the opinions of others in their group, they can switch from A to B if $U_B > U_A$ and vice versa. In our model, we adapted U_A, the perceived benefit of conservation, from Bauch et al. (2016) with the added influence of the other population's opinion. U_A is therefore given by the following:

$$U_{A,i} = \frac{1}{(F_i + c_i)} + d_i X_i + \rho_i X_j \tag{4}$$

where $\frac{1}{(F_i+c_i)}$ represents the perceived rarity of the harvested population within a patch. As F_i and c_i (the rarity valuation parameter) decrease, perceived rarity will increase, therefore adding to the perceived benefit of protecting resources. d_i refers to the social influence that each population has on itself, and as an individual encounters a conservationist in their own population (X_i), the social benefit of also being a conservationist is shown in d_i. ρ_i has this similar effect of social influence, but denotes the social effect of the opposite population on decision-making (X_j). Individuals in each population i are receiving information about the conservation practices of the other population j, and the influence that this has on each population is encapsulated by ρ_i. In other words, higher values of ρ indicate higher homophily between the groups, and lower values of ρ indicate these groups only adopting fishing practices from within their patch. Also, the only information that is being communicated to human patch i is how many people from human patch j are fishing $(1-X_j)$. Human patch i is not receiving any information on fishing practices or changes in the opposite patch fish population. Fishers are only fishing in their respective patches and do not move to the other. Instead, they influence fishing in the opposite patch through the outside social influence of ρ_i.

U_B (the perceived benefits of harvest) is as follows:

$$U_{B,i} = \omega_i + d_i(1 - X_i) + \rho_i(1 - X_j) \tag{5}$$

where ω_i is the cost of conservation (i.e., revenue lost by not harvesting) where now, d_i is the within-population social benefit of switching to harvesting $(1 - X_i)$ and ρ_i is the other population's $(1 - X_j)$ ability to change the opinion of an individual to be a harvester.

Plugging (4) and (5) into Eq. 2 gives the following:

$$\frac{dX_1}{dt} = k_1 X_1(1-X_1)[\frac{1}{F_1 + c_1} - \omega_1 + d_1(2X_1-1) + \rho_1(2X_2-1)] \tag{6}$$

$$\frac{dX_2}{dt} = k_2 X_2(1-X_2)[\frac{1}{F_2 + c_2} - \omega_2 + d_2(2X_2-1) + \rho_2(2X_1-1)] \tag{7}$$

where specifics of the derivation are outlined in the supplementary material. Coupling the resource population and human opinion models gives the following:

$$\frac{dF_1}{dt} = r_1 F_1(1-F_1) - \frac{h_1 * F_1(1 - X_1)}{F_1 + s_1} - m_2 F_1 + m_1 F_2 \tag{8}$$

$$\frac{dF_2}{dt} = r_2 F_2(1-F_2) - \frac{h_2 * F_2(1 - X_2)}{F_2 + s_2} - m_1 F_2 + m_2 F_1 \tag{9}$$

$$\frac{dX_1}{dt} = k_1 X_1(1-X_1)[\frac{1}{F_1 + c_1} - \omega_1 + d_1(2X_1-1) + \rho_1(2X_2-1)] \tag{10}$$

$$\frac{dX_2}{dt} = k_2 X_2(1-X_2)[\frac{1}{F_2 + c_2} - \omega_2 + d_2(2X_2-1) + \rho_2(2X_1-1)] \tag{11}$$

where the harvesting pressure is now a function of the number of harvesters in a population ($\frac{h_i F_i(1-X_i)}{F_i+s_i}$). Further, the opinion of each population will shift based on the perceived population health of their respective patch weighed against the costs and benefits of conservation. As resources decrease, individuals will sway more toward conservation, thereby relieving harvest pressure. However, we now have an external influence in this model: the opinions of people in population j. Therefore, if human population j is continuing to fish, humans in population i will be more influenced to do so as well. The strength of this external influence is ρ, and in this study, we plan to simulate inequalities in human societies with this parameter.

The default parameters used to analyze the fish movement and human hierarchy parameters were taken from analyses done in Bauch et al. (2016) and are given in Table 1. Here, Bauch et al. (2016) found an oscillatory behavior where decreased forest cover resulted in decreased harvest due to

Table 1 Default parameter values used in this analysis taken from Bauch et al. (2016) where oscillations are observed

Parameter	Population 1	Population 2	Definition
r	0.16	0.16	Fish net growth
s	0.8	0.8	Supply and demand
h	0.25	0.25	Harvesting efficiency
k	0.17	0.17	Rate of sampling opinions or social interaction
ω	1.44	1.44	Conservation cost
c	0.5	0.5	Rarity valuation
d	0.3	0.3	Strength of social influence (within population)
m	0.01	0.01	Fish movement (from opposite patch)
ρ	0.01	0.01	Strength of social influence (from opposite population)

the replicator dynamics of the human system which allowed for forest recovery and humans to begin high harvest once again.

Parameter analyses

In order to understand how fish movement (m_1 and m_2) affects dynamics, we first compare how the system will change when both patches are equal (i.e., all of the parameters in each patch are the same) by increasing both m_1 and m_2 incrementally and running the model for 1000 years. We then compare this to the asymmetrical case, where we just increase the m_1 parameter and see the effect on the model for the next 1000 years. Further, to analyze the human hierarchy parameters ρ_1 and ρ_2, we constructed the same analyses of increasing ρ_2, or the amount of influence of human population 1 (X_1) has on the dynamics of human population 2 (X_2). We also compared this to the effect on incrementally increasing d_1.

Two-patch small-scale fishery case study

For a small-scale fishery, we choose to model a two-patch fishery where patch 1 is fishing sustainably while patch 2 is over-harvesting. The harvested fish species has a mid-range growth rate and regularly diffuses across the two patches, such as the parrot fish modeled in Thampi et al. (2018), which uses a fish growth rate of 0.35 fish per year, but alters patch 1's growth rate to be 0.4 fish per year. For the harvesting efficiency, we choose a maximal fishing rate of 0.5. These parameters were adapted from a coral reef fishing model (Thampi et al. 2018) where $r = 0.35$ and $h = 0.5$ are the mid-level growth rate and max fishing rates analyzed by this paper. For the fish movement parameters m, we chose 0.2 for each as these are the values used in the two-patch fishing model described in Cai et al. (2008). We used the s parameter described in the Bauch et al. (2016) model of $s = 0.8$. For the purposes of our study, we are assuming a constant net growth rate of fish populations and that reproduction happens locally within each patch. The rate at which humans interact with one another is described by the parameter k. In our default model, we use $k = 1.014$ as adapted from the Thampi et al. (2018) default model. Thampi et al. (2018) calculated this parameter by fitting conservation opinion data in the United States from 1965 to 1990 to coral health data at that time (Thampi et al. 2018). We used the default rarity valuation parameter c from Thampi et al. (2018) where $c = 1.68$. The cost of conservation default parameter is $\omega = 0.35$ from Bauch et al. (2016). Further, as our default model has no human social hierarchy, we set $d = \rho = 0.5$ for our social norm strengths as adapted from Bauch et al. (2016) which models social decision-making regarding deforestation.

Table 2 Parameter values used to simulate sustainable fishing practices in patch 1 and overfishing in patch 2

Parameter	Population 1	Population 2	Definition
r	0.4	0.35	Fish net growth
s	0.8	0.8	Supply and demand
h	0.25	0.5	Harvesting efficiency
k	1.014	1.014	Rate of sampling opinions or social interaction
ω	0.2	0.35	Conservation cost
c	1.5	1.5	Rarity valuation
d	0.5	0.5	Strength of social influence (within population)
m	0.2	0.2	Fish movement (from opposite patch)
ρ	0.5	0.1	Strength of social influence (from opposite population)

Based on the default model described above, we then change parameters such that patch 1 is fished sustainably, meaning the fish population in patch 1 is able to persist regardless of the fishing pressure from the human population 1. We then set patch 2 to be over-fished, meaning human patch 2 is fishing at too high a rate for the fish population to survive over time (Table 2). Further, we add a socially hierarchical component where patch 2 has a higher social influence on patch 1. To analyze the overfishing scenario, we incrementally increased the parameters m and ρ and simulated this system for 100 years in order to assess how increasing each new parameter would affect the overall dynamics of the system.

Results

Fish movement parameter

To analyze the result of space on socio-ecological models, we observed the effects of increasing both m_1 and m_2 simultaneously (the symmetrical case) and compared this to the effects of only increasing m_1, or the fish movement from patch 2 to patch 1 (Fig. 2). Here, we find that fish movement does not change dynamics in the symmetrical case (Fig. 2a, b, and c), showing that if all parameters are the same in each patch, the fish movement between them does not change dynamics. However, if there are differences between patches (Fig. 2d, e, and f), fish movement will greatly alter dynamics, and if the model is undergoing oscillations, the linear aspects of the fish movement parameters will eventually overcome the non-linear dynamics of oscillations if the fish movement parameter is sufficiently high.

Social hierarchy parameter

In Fig. 3, we can see that increases in d_1 result in higher amplitude oscillations, where F_1 will dip to almost 0 for many years and then recover back to 1. Increases in d_1 affect the model differently than increases in ρ_2, the influence of the other human population. Here, the population dynamics of F_1 stay relatively constant around 0.2 and only have very small oscillations around this number; therefore, increases in d_1 can result in extreme booms and busts of resource populations while increases in ρ_2 results in limited populations, but the resulting dynamics oscillate less, which indicates more stable dynamics. Increases in either d_1 or ρ_2 result in less frequent

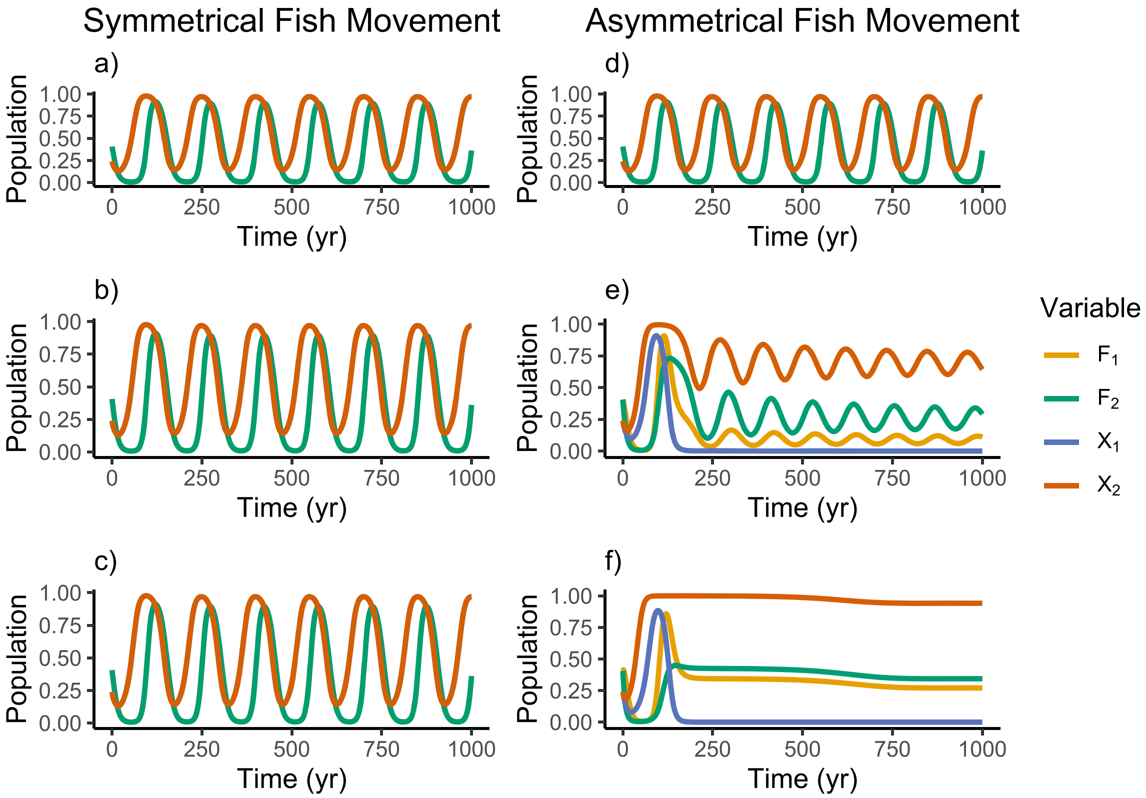

Fig. 2 **a**, **b**, and **c** Both m_1 and m_2 were set to 0.01, 0.05, and 0.1, respectively. The corresponding graphs show the dynamics of these models with the new parameterizations. **d**, **e**, and **f** The changes in model dynamics when m_2 is held at 0 and only m_1 (the fish movement from patch 2 to patch 1) is increased by 0.01, 0.05, and 0.1, respectively. All other parameters were held at the values given in Table 2

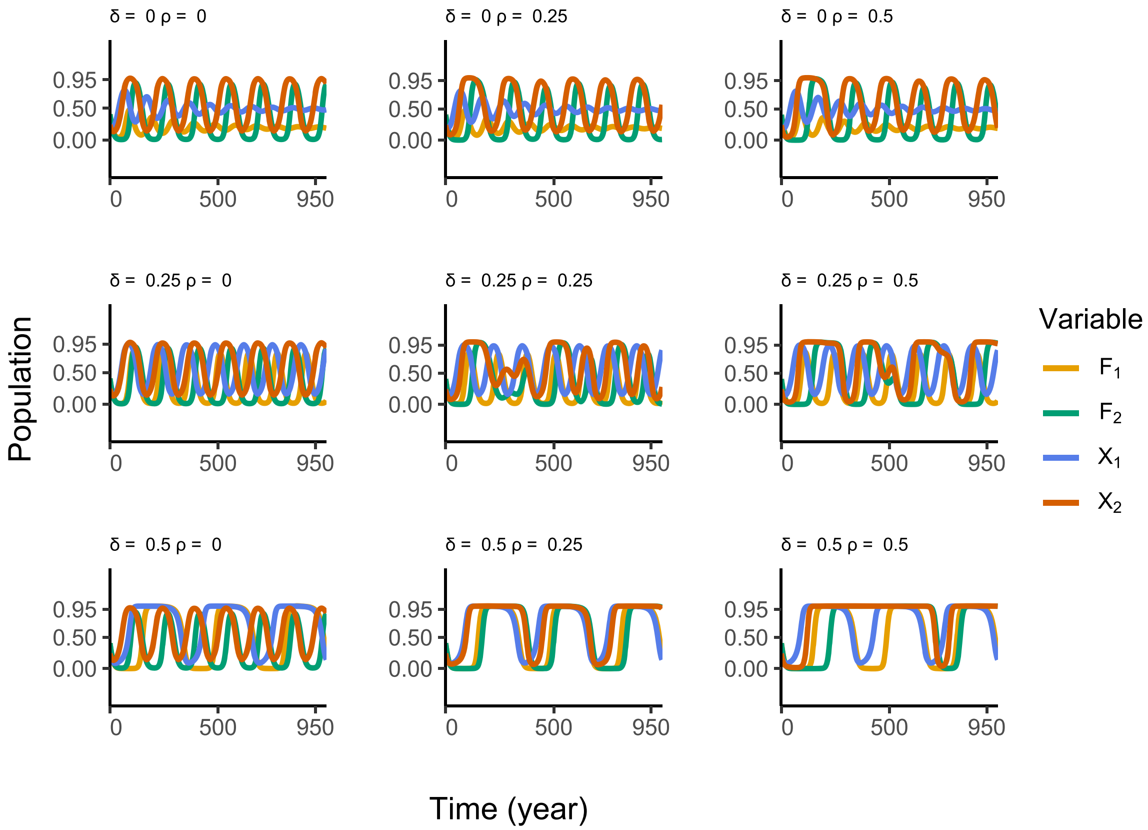

Fig. 3 The difference in increasing social pressure within population 1 (the d_1 parameter is increased down the columns of graphs) versus increasing social pressure from population 1 onto population 2 (the ρ_2 parameter is increased across rows of graphs) which models increasing the social pressure of the

oscillations, meaning humans are slower to change population levels and that plot 1's resource populations spend more time at the peaks of their oscillations before either recovering from 0 or decreasing from 1.

Scenario analysis

We then modeled a hypothetical scenario where patch 1 is fished sustainably whereas patch 2 is experiencing overfishing and has a higher social sway than patch 1. We modeled

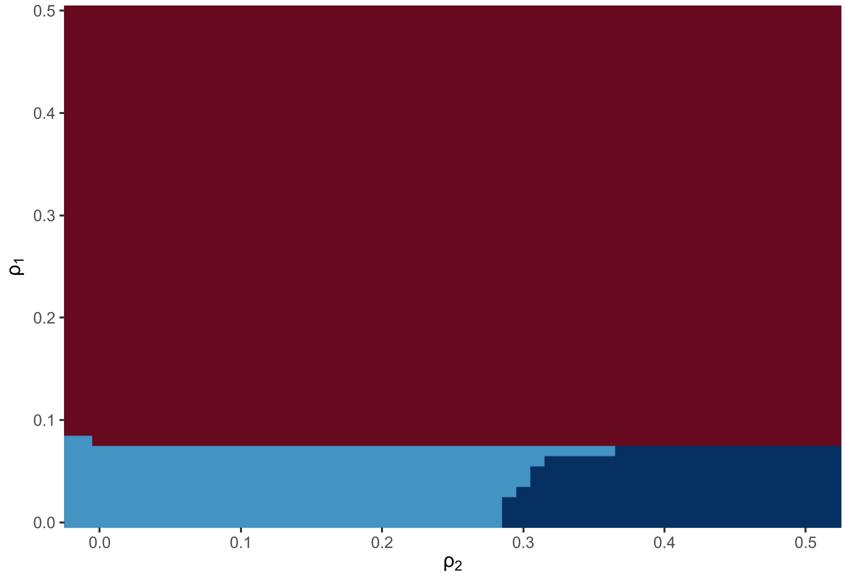

Fig. 4 ρ_1 and ρ_2 were incrementally increased and the model was run for 200 years. This graph shows the final dynamics of the system after those 200 years where the red area indicates a fishery collapse, where both patches fish at full capacity until stocks go to 0. The light blue area shows where some fish populations stay at a constant level, and only X_2 continues to fish whereas X_1 ceases fishing all together. The darker blue patch shows where both patches stop fishing all together and fish stocks in both patches remain at full capacity

overfishing by altering fish new growth rates (r), harvesting efficiencies (h), costs of conservation (ω), and external social norm strengths (ρ) (Table 2). Here, the unsustainable practices of human population 2 are so exploitative, that both fish populations eventually collapse. We used this overfishing parameterization for the rest of the analysis of a two-patch small-scale fishery.

Next, we ran our model with the parameterization outlined in Table 2 with incrementally higher external social influence values (ρ) in each population and observed how this affected the final population of each fish patch (Fig. 4). We found that higher values of ρ_1 actually resulted in fish stocks collapsing in both patches whereas increases of ρ_2 maintained fish populations. At low values of ρ_2, X_2 continued fishing but X_1 stopped fishing all together, resulting in stable fish populations. As ρ_2 increased, fishing eventually stopped in both patches and fish populations remained at 1.

We then ran a similar analysis with the fish dispersal parameter, m, by changing m_1 and m_2 individually. Contrary to the effect external social influence (ρ) had on the model, dispersal had a more direct and continuous effect on the final population of fish in each patch. For example, as fish movement from patch 2 to patch 1 increased (i.e., from the unsustainable patch to the sustainable patch), this actually maintained low fish populations in the sustainable patch, but resulted in crashed populations in the unsustainable (Fig. 5a). However, if the fish movement was increased from patch 1 to patch 2 (from the sustainable fishing to unsustainable), both patches eventually collapsed to zero (Fig. 5b).

Discussion

Instead of just social norms controlling the dynamics of our model, we found that the fish movement between patches (m) was a major driver of population sustainability or collapse (Fig. 5). As we increased the movement of fish into the sustainable patch in the fishery scenario (Fig. 5a), populations in that respective patch also increased because humans in population 1 continued to fish sustainably. Further, as those in population 2 decreased fishing rates, this influenced population 1 to also decrease their number of fishers. As a result, population 1 maintained high fish stocks while population 2 had low stocks. On the contrary, as fish moved from the sustainable patch 1 to the unsustainable patch 2 (Fig. 5b), both fish populations collapsed as m_2 increased because fish movement away from patch 1 eventually grew to be too great for human population 1 to fish sustainably and human population 2 continued to over-fish in their own patch. When both patches are subject to the same conditions (Fig. 2a, b, and c), fish movement does not affect the dynamics at all. It is only when each patch is subject to different conditions, in the case of Fig. 2d, e, and f, where only the fish movement between patches is asymmetrical, does the movement of fish become extremely important in dynamics. This finding is especially relevant to fisheries where different areas where a particular species is fished may be subject to different regulations, environmental conditions, or opinions about conservation. High fish migration has been shown to be an essential part of maximizing economic benefits from fishing in multi-patch models (Moeller and Neubert 2015). Because fish are generally migratory and therefore can be difficult to track, constraining fishing to one group of people is more challenging (Grafton 2005), especially for fish species that exhibit different movement patterns based on life stage, and requires more management coordination (Siddons et al. 2017).

Increases in d_1 and ρ_2 model how dynamics will change if human patch 1 is more influenced by themselves (d_1) or if they have more influence on the other patch (ρ_2) (Fig. 3). This

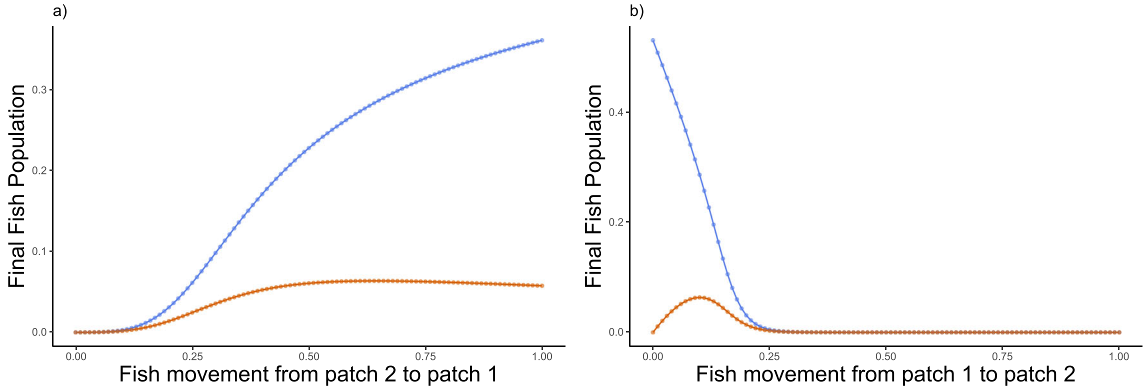

Fig. 5 Final fish populations after 100 years in the two-patch fishing model where patch 1 (F_1) is fished sustainably but human population 1 has a lower social influence than patch 2, where F_2 is being fished unsustainably. **a** shows how increases in fish movement into patch 1 (m_1) affect final populations and **b** shows how increases in fish movement into patch 2 (m_2) affect final populations

analysis showed that increasing either parameter maintained the oscillatory behavior of the model, however as either d_1 or ρ_2 increased, the frequency of these oscillations decreased. In other words, as a human population began to incorporate influence more, this resulted in similar dynamics, but over longer timescales. This is an example of how as humans begin to coordinate with the actions of their peers, changes to fishing pressures can also actually be delayed. The dynamics of the model change from individual decisions, which happen almost instantly, to coordinated efforts, which can take longer to implement.

Increases in the ρ_1 (the human influence of the sustainable patch on the non-sustainable fishers) parameter in the non-symmetric case, contrary to our hypothesis, actually resulted in a collapse of both fisheries because the only information being passed on to the other human population is the number of fishers in the sustainable patch as opposed to what sustainable fishing practices were used in order to maintain fishing yields (Fig. 4). As a result, when patch 2 is over-fished and the other patch 1 is fished sustainably, the human population 2 will continue to over-fish their own resources because the patch 1 is influencing this group to continue fishing through the high external social influence (ρ). Instead of modeling a cohesive system where communication fostered effective conservation, we created a scenario where each community raced to fish each patch as opposed to coming to a common understanding of sustainable fishing practices, further highlighting that the content of the information being disseminated matters in successful conservation (Gray et al. 2012). The importance of information can be reflected in real-world fisheries such as in Lake Kariba between Zambia and Zimbabwe. Here, small-scale fishers are reluctant to participate in the co-management of this shared resource and have been found to resort to illegal fishing practices in order to maximize fish catch (Nyikahadzoi et al. 2017). Clear communication is essential across management regimes. Co-management is an increasingly used strategy in fisheries regulation because it balances power structures with social and environmental needs. However, clear and open communication has been shown to be an essential component to successful co-management (Ratner et al. 2012; Alexander et al. 2015; Defeo et al. 2016; Nyikahadzoi et al. 2017; Doria et al. 2020).

Further, because of the outside human influence term, ρ_i, people are not responding directly to their respective fishing patch, but also to the conservation opinion of the other group. The inclusion of the fish movement term from each patch overcame the oscillations from the non-linear components of the model because fish movement is a linear term in this model. Adding a spatial component to socio-ecological models can greatly change their dynamics and therefore how people are expected to act in these models. The dispersion of fish populations must be well understood in order to institute effective conservation practices because any decision made by one group of people to conserve resources may be rendered ineffective if this fished species is highly migratory and the other group of harvesters is using unsustainable conservation practices. Further, because of the outside influences from the other human patch, fishers are no longer responding directly to fish levels in their respective patch, i, but are also influenced by the proportion of fishers in the other patch, j. In a scenario where fish is abundant in one patch, this will also encourage fishing in the other patch because incentive to fish will increase from the outside influence parameter. Past research has exemplified how multi-patch models and the addition of spatial components change the dynamics of systems, especially in fisheries (Mchich et al. 2000; Cai et al. 2008; Moeller and Neubert 2015; Auger et al. 2022).

The decision to include the external social influence term in our model within the injunctive social norms $X(1-X)$ implies that external influence can still change an opinion for or against conservation. However, an individual's willingness to take up a new opinion is still dictated by the overall opinion of their own population exemplifies homophily. Social network–based conservation can replace "top-down" regulation which can exclude stakeholders but has been shown to be susceptible to homophily (Newman and Dale 2007). Conservation has been shown to be more effective when human populations are more cohesive and that those with subgroups experience more barriers to effective conservation (Bodin and Crona 2009).

Here, we model individual decisions to fish based on the perceived benefits and costs of fishing activity. It does not account for organized decision-making on fishing practices or co-management, and there is no mechanism for dispute resolution and regulation enforcement. Co-management is the organized collaboration between stakeholders to regulate ecological extraction while resolving societal conflicts and is one such way management can incorporate complex social-ecological structures (Armitage et al. 2009). Fisheries are increasingly applying principles of co-management as it creates cooperation and conflict resolution between different stakeholders while focusing on ecological sustainability (Butler et al. 2015; Trimble and Berkes 2015; Murunga et al. 2021). Co-management can also be a mechanism for addressing social inequalities in fisheries (Goetze 2005; Freitas et al. 2020; Haque et al. 2022). However, they can also fail if social structures are ignored when making conservation decisions (Cumming et al. 2017; Baker-Médard et al. 2021a). A limitation of this model is that it does not account for this organized decision-making and only represents fisheries that have not yet instituted these governing mechanisms.

This model does not account for the movement of fishers between patches, which could be a possible extension of this model to represent a fishery where there is an overlap between the fishing grounds of the two human groups. Further research on the model could also be used in this study and could consider an open system, where fish diffusion does not necessarily have to pass between patches and could diffuse into non-fished areas. Further, extensions of this work could observe model dynamics with fish species with a long lifespan or fast reproduction rates. Also, stronger social ties have been shown to be more adaptable to environmental change (Grafton 2005); therefore, further studies could evaluate the effect of climate change or extreme events on this social system (White and Wulfing 2024). The specific way we chose to incorporate social hierarchy into the model could be changed. There are many ways to model social systems, so another application of this study would be to compare its results to models that incorporate social hierarchy differently. Next, further work on parameterizing our model to a real-world system could help understand if our model is properly capturing the underlying dynamics of two-patch fishing systems with social hierarchy. Our model only incorporates public opinion, fishing rates, and financial gains from fisheries as aspects that could cause fishery failure. In practice, other issues such as non-compliance to fishing regulations, hyper-stability, and regulation lag time could all be additional factors that result in fishery collapse but are not incorporated in this model (Erisman et al. 2011; Pinsky and Fogarty 2012; Belhabib et al. 2014). Further, this study does not consider Allee effects in the fish populations, which may alter how spatial dynamics interacts with management practices (White et al. 2021). Finally, our model assumed that the uptake of opinions happens solely through social networks and weighing costs of conservation against the benefits. In reality, there may be more factors that influence one's harvesting decisions such as governing bodies or media consumption.

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Data availability All supplemental material and code for this project are available at https://github.com/swulfing/SocEco.

Declarations

Competing Interests The authors declare no competing interests.

References

Alexander SM, Armitage D, Charles A (2015) Social networks and transitions to co-management in Jamaican marine reserves and small-scale fisheries. Glob Environ Chang 35:213–225. https://doi.org/10.1016/j.gloenvcha.2015.09.001

Armitage DR, Plummer R, Berkes F, Arthur RI, Charles AT, Davidson-Hunt IJ, Diduck AP, Doubleday NC, Johnson DS, Marschke M, McConney P, Pinkerton EW, Wollenberg EK (2009) Adaptive co-management for social-ecological complexity. Front Ecol Environ 7(2):95–102. https://doi.org/10.1890/070089

Auger P, Kooi B, Moussaoui A (2022) Increase of maximum sustainable yield for fishery in two patches with fast migration. Ecol Model 467:109898. https://doi.org/10.1016/j.ecolmodel.2022.109898

Baker-Médard M (2017) Gendering marine conservation: the politics of marine protected areas and fisheries access. Soc Nat Resour 30(6):723–737. https://doi.org/10.1080/08941920.2016.1257078

Baker-Médard M, Concannon K, Gantt C, Moen S, White ER (2021a) Socialscape ecology: integrating social factors into spatially-explicit marine conservation planning. SocArXiv. https://doi.org/10.31235/osf.io/m2kqa

Baker-Médard M, Gantt C, White ER (2021b) Classed conservation: socio-economic drivers of participation in marine resource management. Environ Sci Policy 124:156–162. https://doi.org/10.1016/j.envsci.2021.06.007

Barlow L-A, Cecile J, Bauch CT, Anand M (2014) Modelling interactions between forest pest invasions and human decisions regarding firewood transport restrictions. PLoS ONE 9(4):e90511. https://doi.org/10.1371/journal.pone.0090511

Barnes ML, Bodin Ö, McClanahan TR, Kittinger JN, Hoey AS, Gaoue OG, Graham NAJ (2019) Social-ecological alignment and ecological conditions in coral reefs. Nat Commun 10(1):2039. https://doi.org/10.1038/s41467-019-09994-1

Barnes-Mauthe M (2013) The total economic value of small-scale fisheries with a characterization of post-landing trends: an application in Madagascar with global relevance. Fisheries Res 11

Bauch CT (2005) Imitation dynamics predict vaccinating behaviour. Proc R Soc B: Biol Sci 272(1573):1669–1675. https://doi.org/10.1098/rspb.2005.3153

Bauch CT, Bhattacharyya S (2012) Evolutionary game theory and social learning can determine how vaccine scares unfold. PLoS Comput Biol 8(4):e1002452. https://doi.org/10.1371/journal.pcbi.1002452

Bauch CT, Sigdel R, Pharaon J, Anand M (2016) Early warning signals of regime shifts in coupled human-environment systems. Proc Natl Acad Sci 113(51):14560–14567. https://doi.org/10.1073/pnas.1604978113

Belhabib D, Koutob V, Sall A, Lam VWY, Pauly D (2014) Fisheries catch misreporting and its implications: the case of Senegal. Fish Res 151:1–11. https://doi.org/10.1016/j.fishres.2013.12.006

Bodin Ö, Crona BI (2009) The role of social networks in natural resource governance: what relational patterns make a difference? Glob Environ Chang 19(3):366–374. https://doi.org/10.1016/j.gloenvcha.2009.05.002

Borgatti S (2003) The network paradigm in organizational research: a review and typology. J Manag 29(6):991–1013. https://doi.org/10.1016/S0149-2063(03)00087-4

Brechwald WA, Prinstein MJ (2011) Beyond homophily: a decade of advances in understanding peer influence processes: beyond homophily. J Res Adolesc 21(1):166–179. https://doi.org/10.1111/j.1532-7795.2010.00721.x

Butler JRA, Young JC, McMyn IAG, Leyshon B, Graham IM, Walker I, Baxter JM, Dodd J, Warburton C (2015) Evaluating adaptive co-management as conservation conflict resolution: learning from seals and salmon. J Environ Manage 160:212–225. https://doi.org/10.1016/j.jenvman.2015.06.019

Cai L, Li X, Song X (2008) Modeling and analysis of a harvesting fishery model in a two-patch environment. Int J Biomath 01(03):287–298. https://doi.org/10.1142/S1793524508000242

Cozzi G, Behr DM, Webster HS, Claase M, Bryce CM, Modise B, Mcnutt JW, Ozgul A (2020) African wild dog dispersal and implications for management. J Wildl Manag 84(4):614–621. https://doi.org/10.1002/jwmg.21841

Cressman R, Křivan V, Garay J (2004) Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments

Crona B, Bodin Ö (2006) What you know is who you know? Communication patterns among resource users as a prerequisite for co-management. Ecol Soc 11(2):art7. https://doi.org/10.5751/ES-01793-110207

Cumming GS, Morrison TH, Hughes TP (2017) New directions for understanding the spatial resilience of social-ecological systems. Ecosystems 20(4):649–664. https://doi.org/10.1007/s10021-016-0089-5

Defeo O, Castrejón M, Pérez-Castañeda R, Castilla JC, Gutiérrez NL, Essington TE, Folke C (2016) Co-management in Latin American small-scale shellfisheries: assessment from long-term case studies. Fish Fish 17(1):176–192. https://doi.org/10.1111/faf.12101

Doria CRC, Athayde S, Lima HMD, Carvajal-Vallejos FM, Dutka-Gianelli J (2020) Challenges for the governance of small-scale fisheries on the Brazil-Bolivia transboundary region. Society & Natural Resources 33(10):1213–1231. https://doi.org/10.1080/08941920.2020.1771492

Erisman BE, Allen LG, Claisse JT, Pondella DJ, Miller EF, Murray JH (2011) The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Can J Fish Aquat Sci 68(10):1705–1716. https://doi.org/10.1139/f2011-090

FAO (2022) The state of world fisheries and aquaculture 2022. Towards blue transformation. FAO. https://doi.org/10.4060/cc0461en

FAO, Duke University, & WorldFish (2023) Illuminating hidden harvests: the contributions of small-scale fisheries to sustainable developmentt - executive summary. FAO. https://doi.org/10.4060/cc6062en

Felipe-Lucia MR, Guerrero AM, Alexander SM, Ashander J, Baggio JA, Barnes ML, Bodin Ö, Bonn A, Fortin M-J, Friedman RS, Gephart JA, Helmstedt KJ, Keyes AA, Kroetz K, Massol F, Pocock MJO, Sayles J, Thompson RM, Wood SA, Dee LE (2022) Conceptualizing ecosystem services using social-ecological networks. Trends in Ecology & Evolution 37(3):211–222. https://doi.org/10.1016/j.tree.2021.11.012

Freedman HI, Waltman P (1977) Mathematical models of population interactions with dispersal. I: stability of two habitats with and without a predator. SIAM J Appl Math 32(3):631–648. https://doi.org/10.1137/0132052

Freitas CT, Espírito-Santo HMV, Campos-Silva JV, Peres CA, Lopes PFM (2020) Resource co-management as a step towards gender equity in fisheries. Ecol Econ 176:106709. https://doi.org/10.1016/j.ecolecon.2020.106709

Garrone-Neto D, Sanches EA, de Daros FAL de M, Imanobu CMR, Moro PS (2018) Using the same fish with different rules: a science-based approach for improving management of recreational fisheries in a biodiversity hotspot of the Western South Atlantic. Fish Manage Ecol 25(4):253–260. https://doi.org/10.1111/fme.12288

Gervasi V, Brøseth H, Nilsen EB, Ellegren H, Flagstad Ø, Linnell JDC (2015) Compensatory immigration counteracts contrasting conservation strategies of wolverines (Gulo gulo) within Scandinavia. Biol Cons 191:632–639. https://doi.org/10.1016/j.biocon.2015.07.024

Goetze TC (2005) Empowered co-management: towards power-sharing and indigenous rights in Clayoquot Sound, BC. Anthropologica 47(2):247–265. https://www.jstor.org/stable/25606239

Grafton RQ (2005) Social capital and fisheries governance. Ocean & Coastal Management 48(9–10):753–766. https://doi.org/10.1016/j.ocecoaman.2005.08.003

Gray S, Chan A, Clark D, Jordan R (2012) Modeling the integration of stakeholder knowledge in social-ecological decision-making: benefits and limitations to knowledge diversity. Ecol Model 229:88–96. https://doi.org/10.1016/j.ecolmodel.2011.09.011

Haque ABMM, Nahiduzzaman Md, Saha SM (2022) Can adaptive co-management reduce poverty and inequality in the coastal fishing community? An impact evaluation in the riverine system in Bangladesh. Regional Studies in Marine Science 56. https://doi.org/10.1016/j.rsma.2022.102721

Hebblewhite M, Whittington J (2020) Wolves without borders: transboundary survival of wolves in Banff National Park over three decades. Global Ecology and Conservation 24:e01293. https://doi.org/10.1016/j.gecco.2020.e01293

Innes C, Anand M, Bauch CT (2013) The impact of human-environment interactions on the stability of forest-grassland mosaic ecosystems. Sci Rep 3(1):2689. https://doi.org/10.1038/srep02689

Krackhardt D, Stern RN (1988) Informal networks and organizational crises: an experimental simulation. Social Psychology Quarterly 51(2):123. https://doi.org/10.2307/2786835

Lade SJ, Tavoni A, Levin SA, Schlüter M (2013) Regime shifts in a social-ecological system. Thyroid Res 6(3):359–372. https://doi.org/10.1007/s12080-013-0187-3

Liu J, Redman CL, Schneider SH, Ostrom E, Pell AN, Lubchenco J, Taylor WW, Ouyang Z, Deadman P, Kratz T, Provencher W (2007) Coupled human and natural systems

Mchich R, Auger P, Raïssi N (2000) The dynamics of a fish stock exploited in two fishing zones. Acta Biotheor 48:201–218

McPherson M, Smith-Lovin L, Cook JM (2001) Birds of a feather: homophily in social networks. Ann Rev Sociol 27(1):415–444. https://doi.org/10.1146/annurev.soc.27.1.415

Meisingset EL, Loe LE, Brekkum Ø, Bischof R, Rivrud IM, Lande US, Zimmermann B, Veiberg V, Mysterud A (2018) Spatial mismatch between management units and movement ecology of a partially migratory ungulate. J Appl Ecol 55(2):745–753. https://doi.org/10.1111/1365-2664.13003

Moeller HV, Neubert MG (2015) Economically optimal marine reserves without spatial heterogeneity in a simple two-patch model: economically optimal marine reserves. Nat Resour Model 28(3):244–255. https://doi.org/10.1111/nrm.12066

Murunga M, Partelow S, Breckwoldt A (2021) Drivers of collective action and role of conflict in Kenyan fisheries co-management. World Dev 141:105413. https://doi.org/10.1016/j.worlddev.2021.105413

Newman L, Dale A (2007) Homophily and agency: creating effective sustainable development networks. Environ Dev Sustain 9(1):79–90. https://doi.org/10.1007/s10668-005-9004-5

Nyikahadzoi K, Mhlanga W, Madzudzo E, Tendaupenyu I, Silwimba E (2017) Dynamics of transboundary governance and management of small scale fisheries on Lake Kariba: implications for sustainable use. Int J Environ Stud 74(3):458–470. https://doi.org/10.1080/00207233.2017.1308159

Ogburn MB, Harrison A-L, Whoriskey FG, Cooke SJ, Mills Flemming JE, Torres LG (2017) Addressing challenges in the application of animal movement ecology to aquatic conservation and management. Front Mar Sci 4. https://doi.org/10.3389/fmars.2017.00070

Oraby T, Thampi V, Bauch CT (2014) The influence of social norms on the dynamics of vaccinating behaviour for paediatric infectious diseases. Proceedings of the Royal Society B: Biological Sciences 281(1780):20133172. https://doi.org/10.1098/rspb.2013.3172

Ostrom E (2009) A general framework for analyzing sustainability of social-ecological systems. Science 325(5939):419–422. https://doi.org/10.1126/science.1172133

Pinsky ML, Fogarty M (2012) Lagged social-ecological responses to climate and range shifts in fisheries. Clim Change 115(3–4):883–891. https://doi.org/10.1007/s10584-012-0599-x

Plumptre AJ, Kujirakwinja D, Treves A, Owiunji I, Rainer H (2007) Transboundary conservation in the greater Virunga landscape: its importance for landscape species. Biol Cons 134(2):279–287. https://doi.org/10.1016/j.biocon.2006.08.012

Pomeroy R, Parks J, Pollnac R, Campson T, Genio E, Marlessy C, Holle E, Pido M, Nissapa A, Boromthanarat S, Thu Hue N (2007) Fish wars: conflict and collaboration in fisheries management in Southeast Asia. Mar Policy 31(6):645–656. https://doi.org/10.1016/j.marpol.2007.03.012

Ramírez-Valdez A, Rowell TJ, Dale KE, Craig MT, Allen LG, Villaseñor-Derbez JC, Cisneros-Montemayor AM, Hernández-Velasco A, Torre J, Hofmeister J, Erisman BE (2021) Asymmetry across international borders: research, fishery and management trends and economic value of the giant sea bass (*Stereolepis Gigas*). Fish Fish 22(6):1392–1411. https://doi.org/10.1111/faf.12594

Ratner BD, Oh EJV, Pomeroy RS (2012) Navigating change: second-generation challenges of small-scale fisheries co-management in the Philippines and Vietnam. J Environ Manage 107:131–139. https://doi.org/10.1016/j.jenvman.2012.04.014

Sari I, Ichsan M, White A, Raup SA, Wisudo SH (2021) Monitoring small-scale fisheries catches in Indonesia through a fishing logbook system: challenges and strategies. Mar Policy 134:104770. https://doi.org/10.1016/j.marpol.2021.104770

Siddons SF, Pegg MA, Klein GM (2017) Borders and barriers: challenges of fisheries management and conservation in open systems: challenges of fisheries management and conservation in open systems. River Res Appl 33(4):578–585. https://doi.org/10.1002/rra.3118

Sigdel RP, Anand M, Bauch CT (2017) Competition between injunctive social norms and conservation priorities gives rise to complex dynamics in a model of forest growth and opinion dynamics. J Theor Biol 432:132–140. https://doi.org/10.1016/j.jtbi.2017.07.029

Thampi VA, Anand M, Bauch CT (2018) Socio-ecological dynamics of Caribbean coral reef ecosystems and conservation opinion propagation. Sci Rep 8(1):2597. https://doi.org/10.1038/s41598-018-20341-0

Trimble M, Berkes F (2015) Towards adaptive co-management of small-scale fisheries in Uruguay and Brazil: lessons from using Ostrom's design principles. Maritime Studies 14(1):14. https://doi.org/10.1186/s40152-015-0032-y

White ER, Wulfing S (2024) Extreme events and coupled socio-ecological systems. Ecol Model 495:110786. https://doi.org/10.1016/j.ecolmodel.2024.110786

White ER, Baskett ML, Hastings A (2021) Catastrophes, connectivity and Allee effects in the design of marine reserve networks. Oikos 130(3):366–376. https://doi.org/10.1111/oik.07770

Young OR, Osherenko G, Ekstrom J, Crowder LB, Ogden J, Wilson JA, Day JC, Douvere F, Ehler CN, McLeod KL, Halpren BS, Peach R (2007) Solving the crisis in ocean governance: place-based management of marine ecosystems. Environment: Science and Policy for Sustainable Development 49(4):20–32. https://doi.org/10.3200/ENVT.49.4.20-33

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