Abstract: In spite of wide spread use of territorial use rights fisheries (TURFs) as a management tool, efficient design of spatial property rights, particularly in context of communal ownership, remains poorly understood. We develop a spatially explicit game-theoretic model of a two-patch communally exploited TURF network to investigate spatial scale, species dispersal, and fisher interactions. We characterize biological networks and patch sizes conducive to fostering internally cooperative harvesting behaviors. We also characterize the magnitude and spatial distribution of cost of any defection from cooperative harvesting behaviors. We find when neighboring patches are each independently cooperative, profitability in presence of high larval-stage dispersal is higher than when species are immobile. Mutually non-cooperative behavior across TURFs produce outcomes under connectivity that are worse than when species are immobile. Our results demonstrate that joint accounting of species dispersal habits and behavioral organization of communities within spatial property rights are critical when demarcating property rights boundaries.

JEL Codes: Q22, C72

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Background

Small scale fisheries provide an important source of protein and sustainable livelihoods for much of the world’s population. Coastal communities in developing countries are especially reliant on the nutrition and income generated from fisheries. In spite of this importance, practical fisheries management in small scale fisheries remains poorly understood. Factors complicating the ability to effectively manage fisheries in these environments include weak
governance institutions and ill-defined property rights. Such conditions contribute to depressed fish stocks and lowered economic returns [1].

Recent estimates are that small-scale fisheries account for nearly one-half of global marine and inland fish catches [2]. In terms of employment, over 30 million capture fishers and 85 million people in accompanying industries are supported by small-scale fisheries [3]. However, small scale fisheries in developing countries present particular challenges to management and reform due to their integration in local communities and household dependence [4]. Lack of baseline monitoring and assessment data, weak ability to enforce regulations, and incentives to carry out illegal, unreported, and unregulated fishing further challenge reform [5, 6 and references therein]. These conditions make the establishment of top-down, market based fisheries management difficult.

In many of the developed world’s managed fisheries, managers allocate harvest rights under market based transferable quota systems. An alternative is to allocate rights to harvest in particular geographic space. Space-based rights, such as territorial use rights fisheries (TURFs), can be designated as rights to any layer(s) of the water column and are generally granted to groups of fishers [7]. In situations with little or no management capacity to implement market-based tools such as ITQs, development of spatial property rights (e.g. TURFs) can lead to effective rights-based management [8, 9]. Moreover, granting spatial property rights may be preferable in situations where fishermen behave territorially according to local social norms [10].¹ A recent online survey of fisheries experts and stakeholders identified over 1,000 TURFs existing in 41 countries [11]. However, it is likely that many more TURFs exist given that

¹ Co-management regimes in Kenya and Madagascar provide such examples
approximately 700 are currently operational in Chile alone [12]. Developing countries where TURFs are implemented include India, Bangladesh, Fiji, Sri Lanka, Jamaica, Philippines, and Vietnam [13]. In spite of wide spread use as a management tool, the efficient design of spatial property rights remains poorly understood.

The design of spatial property rights is complicated by spatial externalities and the internal costs of organization of fishers. Harvest behavior at the local level can impose external costs in neighboring spaces when resource populations disperse. Increasing resource mobility between patches degrades the exclusivity of in-situ ownership and can thus lead to strategic responses by fishers between patches which creates lower stock levels. Where TURF rights are held by multiple agents, the spatial extent of property right determines, in part, the catch share. In turn, size of the catch share affect incentives to act non-cooperatively [14, 15] and the resulting harvest externalities.2 Thus, accounting for spatial dynamics and internal organization of the TURF informs the design of resilient spatial property rights in fisheries management.

Prior attempts to address spatial fisheries management have overlooked the significance of internal costs of organization of economic agents [e.g. 16, 17]. Models relying on sole-ownership of spatial harvest rights do not reflect the reality that most space-based rights regimes are group-allocated [18-20]. Moreover, when it comes to game-theoretic fisheries literature, models have either addressed interactions between sole owners of jurisdictions harvesting a straddling or migratory stock [e.g. 21, 22-25] or interactions of multiple agents within the same jurisdiction harvesting a common stock [e.g. 15, 26]. However, we are unaware

2 Secured access and shared control of resources, as in the formation of a TURF fishing union, is often insufficient for achieving cooperative outcomes without the use of regulations and sanctions to disincentivize non-cooperative behaviors [12].
of any literature accounting for spatial dynamics and agent interactions both *between* and *within* jurisdictions.

The subject of scale concerns the geographic, spatial, or biological extent over which property rights are granted. Recognizing the inefficiencies arising from spatial externalities, a tempting notion is to assign “large scale” property rights such that any potential spillovers are effectively internalized [16, 17]. However, empirical relations between areal extent of TURFs and fishery outcomes do not necessarily support the conclusion that large scale rights confer efficiency [11]. Additionally, arguments that spatial rights be sufficiently “large” in fact neglects the importance of intra-TURF agent interactions and the effect that scale has on agents’ incentives to behave cooperatively or not. The implication of not including this could be an overestimate of the gains accruing to large scale spatial property rights.

In this paper, we present a spatially explicit model of a renewable resource in the context of a small scale developing country fishery. The model incorporates spatial movement of the resource between patches and the interactions of agents both within and between patches. We characterize cooperative and non-cooperative fishery outcomes in terms of patch size and biological networks. We find that when neighboring TURFs are independently cooperative, the profits under high larval-stage dispersal are greater than the profits under species immobility. However, when neighboring TURFs are mutually non-cooperative, then profits under species immobility are always greatest, regardless of TURF size. When

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3 Note that scale in geographical, spatial, and biological contexts are likely to be closely related, but are not necessarily so. For instance, holding harvest rights to a particular reef in its spatial entirety may correspond to equally complete rights to the population of species dependent on that reef. On the other hand, for species with low site-fidelity, spatial coverage and population coverage will be less direct.
cooperation fails, the relative magnitude and spatial distribution of the defection depends critically on dispersal and patch size. With high larval dispersal and low adult dispersal, the relative costs of a defection is mostly borne by the local patch. When adult dispersal is high, the relative cost of a defection can either be borne more by the local or neighboring patch, depending on relative patch sizes. These results highlight the value of accounting for intra-TURF interactions while providing theoretical validation to recent empirical evidence suggesting disconnect between areal TURF extent and fishery outcomes [e.g. 11]. Lastly, our findings provide basis to inform the likelihood of successful communal harvest regimes as well as the likely enforcement costs needed to maintain stable cooperative behaviors.

The spatial biological model is first outlined, after which the game theoretic elements are described. In section four we present results and illustrate the model implications using numerical illustrations. The paper closes with a discussion and concluding remarks.

**The Spatial Biological Model**

We begin with a spatial metapopulation model with two patches with populations $x_1$ and $x_2$, with no loss of generality. The total population distribution range of the system is defined to be unity. The population distribution range of patches 1 and 2 are therefore defined to be $m$ and $1 - m$, respectively. Following Sanchirico [27] and Flaaten and Mjølhus [28], the model assumes that each sub-population has its own carrying capacity, where carrying capacity is proportioned to the size of its respective sub-area. Based on Pezzey et al. [29] and Sanchirico [27], the spatial biological model captures an implicit juvenile growth and settlement process. In particular, populations have an adjusted logistic growth function, which depends on the total population in the system and own-patch population density. Specifically, we have
\[ F_1(x_1, x_2) = r \left( \alpha_1 x_1 + \psi_1 ((1 - \alpha_1)x_1 + (1 - \alpha_2)x_2) \right) \left( 1 - \frac{x_1}{m} \right) \] (1)

\[ F_2(x_1, x_2) = r \left( \alpha_2 x_2 + \psi_2 ((1 - \alpha_1)x_1 + (1 - \alpha_2)x_2) \right) \left( 1 - \frac{x_2}{1-m} \right) \] (2)

where \( r \) is the intrinsic growth rate, \( a_i \) is the probability that larvae from patch \( i \) remain in patch \( i \), \( 1 - \alpha_i \) is the probability that larvae leave patch \( i \) to enter the larval pool, and \( \psi_i \) is the probability that larvae from patch \( i \) survive the trip to and from the larval pool. As in Sanchirico [27] we assume that all larvae that do not settle in their local patch will mix perfectly in the larval pool and then redistribute evenly to all patches in the system.

The production of larval organisms is a density independent function, while eventual larval settlement into the patch is subject to density dependent mechanisms. Consider the case where all larvae enter the larval pool (i.e. \( \alpha_i = 0 \)). In this case, larval production is a function of the total system population ((1 - \( \alpha_1 \))\( x_1 \) + (1 - \( \alpha_2 \))\( x_2 \)), yet growth is driven by local density dependent effects ((1 - \( \frac{x_1}{m} \), (1 - \( \frac{x_2}{1-m} \)). The larval portion of the model predicts higher total and marginal biological growth than its spatially independent analogs. The marginal effect of the population in patch 1 on patch 2’s production is greatest when patch 2’s population is low or, holding patch 2’s population constant, when patch 2 is large in size (i.e. \( \frac{\partial F_2(x_1, x_2)}{\partial x_1} = r\psi(1 - \alpha_1) \left( 1 - \frac{x_2}{1-m} \right) \)). As the population in any patch approaches its maximum capacity, the effect of neighboring patches population levels diminishes due to competition for limited resources.

For many species, the spatial behavior during juvenile and adult stages are likely to be distinct. For instance, juvenile dispersal may rely on currents while adults have the ability to move purposefully to seek out unoccupied habitats. Here, the movement of adult organisms is
consistent with Sanchirico and Wilen [30] by specifying that net adult migration is dependent upon relative patch densities, i.e. $\frac{x_1}{m}$ and $\frac{x_2}{1-m}$. Coupling this adult organism dispersal with the production and settlement of juvenile organisms specified in (1) and (2), the total population dynamics within each patch are

$$\frac{dx_1}{dt} = r \left( \alpha_1 x_1 + \psi_1 \left( (1 - \alpha_1) x_1 + (1 - \alpha_2) x_2 \right) \right) \left( 1 - \frac{x_1}{m} \right) + b \left( \frac{x_2}{1-m} - \frac{x_1}{m} \right) - h_1$$

$$\frac{dx_2}{dt} = r \left( \alpha_2 x_2 + \psi_2 \left( (1 - \alpha_1) x_1 + (1 - \alpha_2) x_2 \right) \right) \left( 1 - \frac{x_2}{1-m} \right) + b \left( \frac{x_1}{m} - \frac{x_2}{1-m} \right) - h_2$$

where $h_i$ is the catch level in patch $i$ and $b$ is the adult transfer coefficient, which can be interpreted as the fraction of total adults that are mobile. Under isolation, the population in patch 1 increases logistically with growth rate $r_1$. Under connectivity, patch 1 receives new juvenile recruits as a function of own-patch density (represented by the term $r_1 \psi_1 (1 - \alpha_2) x_2 (1 - \frac{x_1}{m})$) and, depending on the relative densities of both patches, either loses or gains individuals at the rate $b$. The biological model thus captures common pool growth, density dependent juvenile settlement, and adult migration processes based on relative densities.

TURFs are used to manage both immobile species (e.g. crustaceans and molluscs) and mobile species (e.g. finfish) [20]. We therefore investigate four different dispersal scenarios representing a range of inter-patch species mobility (Table I). The first scenario we refer to as ‘low adult dispersal’, where 10% of the absolute difference between patch densities is exchanged and larval production is common pool ($\alpha_i = 0$). The low adult dispersal scenario represents species with high site fidelity within their adult home range but perfect larval mixing (e.g. molluscs). In the ‘high adult dispersal’ scenario, we increase the adult dispersal parameter from $b = 0.1$ to $b = 1$ while maintaining common pool larval production. Under this scenario,
100% of the absolute difference between patch-specific densities are exchanged between patches. The high adult dispersal scenario represents finfish species with dispersal in both larval and adult phases (e.g. anchovetta, snapper). In the ‘no larval dispersal’ scenario, we eliminate the common pool larval growth effect (i.e. \( \alpha_i = 1 \)), while maintaining high adult mobility. Under this scenario, growth is a function of own-patch population only and represents either oceanographic or biological factors which might limit larval displacement. In the ‘source-sink’ scenario, all larvae from patch 2 remain and settle in patch 2 (\( \alpha_2 = 1 \)). Hence, under this scenario, patch 1 acts as a source of larval production for patch 2. In all four scenarios we assume that survivability is unity. Isoclines for the four dispersal cases are presented in Appendix A.

The Economic and Behavioral Model

Building on [31], the decision process on effort investment in a communally held spatial property right is a two-stage game, where cooperative agents agree on a total level of effort to invest in the fishery in the first stage, and members individually choose their effort levels in the second stage. The aggregate cooperative effort level in the first stage is arrived at based on a voluntary agreement which maximizes profits jointly to all agents. We first present the second stage non-cooperative game as a way to motivate the incentives to establish voluntary cooperative behaviors in communally held harvest rights.

The Second Stage: Non-cooperative Effort Game

Consider an \( n \)-person game over the amount of effort (\( e_{1,1}, e_{2,1}, \ldots, e_{n,1} \)) to invest within patch \( j \). We assume that agents within patch \( j \) do not observe the play of the other agents within patch \( j \) nor the agents in patch \( l \) (e.g. an open loop model). Agents are assumed to have
knowledge of the species dispersal patterns. Under this assumption, we allow for agents to adjust effort levels in response to changes in in-situ biomass which manifests through changing aggregate effort outside the patch. For tractability, we evaluate biomass at its equilibrium and assume agents take this biomass level as given. Formally, the system biomass is at equilibrium if \(3) = (4) = 0\). Suppose that entry is exogenously restricted and that patch \(j\) membership is \(n_j = N_j\) while patch \(l\) membership is \(n_l = N_l\). The individual rents conferring to each agent \(i\) in entry-restricted patch \(j\) are a function of his effort and the equilibrium biomass which reflects aggregate effort across the whole system:

\[
\pi_{i,j} = p q_{i,j} e_{i,j} x_j \left( e_{i,j} + \sum_{k \neq i}^{N_j} e_{j,k} + \sum_{h}^{N_l} e_{l,h} \right) - e_{i,j} (c_{i,j} + w)
\]  

(5)

where \(q_{i,j}\) is the agent- and patch-specific Schaefer harvest coefficient, \(c_{i,j}\) is the patch- and agent-specific per unit harvest cost, \(w\) is the opportunity cost of labor common to all agents, and \(x_j \left( \bullet \right)\) is the equilibrium biomass levels for patch \(j\) as a function of effort by all agents in both patches \(j\) and \(l\). Given this rent specification, each agent within patch \(j\) considers two strategies. One strategy is to behave non-cooperatively and invest the effort consistent with individual maximization given the effort level of other agents in patch \(j\) and patch \(l\):

\[
e_{i,j}^0 \left( e_{k,j}, e_{h,l} \right) = \text{argmax} \left( \pi_{i,j} \right), \forall i \neq k
\]  

(6)

where \(\pi_{i,j}\) is as defined in (5). That is, each agent \(i\) chooses his effort level given the effort level of each agent \(k\) within patch \(j\) and each agent \(h\) in patch \(l\) using (5) as a decision rule. Let the patch-specific Cournot-Nash equilibrium level when no player cooperates be \(e_{j}^{0,0}\).

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4 Assumptions of exogenously fixed membership is consistent with small scale fisheries governance via customary marine tenure, where access is controlled by well-defined social units [20, 32].
The other choice of strategy open to agents is to behave cooperatively by investing the jointly optimal patch-specific individual effort level, which we denote $e_{i,j}^*$.  

**Incentives to Voluntary Cooperation and Defection**

Rents conferring under Cournot-Nash non-cooperative solutions are lower than those conferring under joint maximization (Fig. B1). The value added to individual agents behaving cooperatively within patch derives from the ability to capitalize on rents conferring from jointly owned biomass. Hence the per capita gains conferring to cooperation within patch $j$ given the aggregate effort in neighboring patch $l$ ($E_l = \sum_{h}^{N_i} e_{h,i}$) are

$$\Delta_{i,j}^C = \pi_{i,j}(e_{i,j}^*, \sum_k e_{k,j}^* | E_i) - \pi_{i,j}(e_{i,j}^{00}, \sum_k e_{k,j}^{00} | E_i), \quad \forall i \neq k \quad (7)$$

The larger (7) is, the more likely agents are to engage in voluntary cooperation (see Appendix B). Note that the gains from cooperation in patch $j$ depend on whether aggregate effort in patch $l$ ($E_l$) is cooperative or not. Conversely, if agent $i$ believes that agents $k \neq i$ will behave cooperatively, then his best response may be to act non-cooperative, and invest greater than the agreed upon effort. This represents the incentive to defect from cooperative agreements in an entry-restricted spatial property rights fishery, which is equal to the difference between the profits conferring from optimal cheating and the profits conferring from internal cooperation:

$$\Delta_{i,j}^{Ch} = \pi_{i,j}(e_{i,j}^{0}(\sum_k e_{k,j}^*),\sum_k e_{k,j}^* | E_i) - \pi_{i,j}(e_{i,j}^{*},\sum_k e_{k,j}^* | E_i), \quad \forall i \neq k \quad (8)$$

The larger (8) is in magnitude, the more difficult it is to enact durable cooperative exploitation of the common property right.

**The First Stage: Cooperative Equilibrium**
In the first stage, patch members collectively choose the effort levels that maximize the aggregate rents conferring to the group. The aggregate cooperative effort and population levels can be determined for patch $j$ by each agent choosing individual effort level, $e_{i,j}$, in order to jointly maximize the following program:

$$\Pi_j = \sum_i^{N_i} \left( p q_i e_{i,j} x_j \left( \sum_i^{N_i} e_{i,j} + \sum_h^{N_i} e_{h,l} \right) - e_{i,j} (c_{i,j} + w) \right)$$  \hspace{1cm} (9)$$

Where $x_j(\square)$ is the equilibrium biomass in patch $j$ as a function of the aggregate coordinated effort in patch $j$ and total exogenously given effort in patch $l$. The solution to (9) is denoted $e_{i,j}^*$ and the aggregate cooperative effort is thus $E_j^* = \sum_i e_{i,j}^*$. Note that when agents are homogeneous in fishing skill and effort costs, then individual effort levels $e_1, j, e_2, j, \ldots e_{N_j,j}$ will be equal under cooperation. To maintain tractability, we assume that cooperation, when it exists, takes place on voluntarily basis (i.e. without costly enforcement). Indeed, the incentives to defect from voluntary agreements (e.g. (8)) inform the likely enforcement costs necessary to maintain cooperation.

**Numerical Illustrations**

Closed form solutions to equilibrium biomass are not feasible. Therefore, the simultaneous solutions to (6) and (3) = (4) = 0 (Cournot-Nash outcomes) as well as (9) and (3) = (4) = 0 (cooperative outcomes) are best elucidated using numerical techniques. We simulate the model using the stylized biological life histories outlined in Table I. For the economic parameters, we set price and Schaefer harvest parameters to unity and per unit effort cost and wage rate to 0.05 each.

Let patches 1 and 2 operate under limited entry with $n_j = n_m = 3$ and effort levels determined either by Cournot-Nash outcomes from (6) or internal cooperation outcomes from
We evaluate the system under symmetric biological and economic conditions as a means to benchmark the model. In this case, each player $i$ in patch $j$ takes the effort of the other players within and outside the patch as given. The length of the line plots represents the range of economically feasible patch sizes. Leftward of the line segment, costs of the first marginal unit of fishing effort in patch 1 exceed the revenues, while rightward of the line segments, the costs of fishing in patch 2 exceed the revenues. For instance, under Cournot-Nash equilibrium, the minimum economically viable patch size ranges from about 15% of the system total ($m \approx 0.15$) under low adult dispersal to approximately 45% of the system total ($m \approx 0.45$) under no larval dispersal. Hence, the critical patch sizes under spatial property rights regimes depend critically on the nature of the connectivity.

Generally, we find that scenarios where species exhibit high adult mobility will impose lower bounds on patch sizes that are larger than their low mobility counterparts. For instance, holding larval dispersal constant, we find that the critical patch size under high adult dispersal is over 130% greater than the critical patch size under low adult dispersal (Fig. 1 a). Moreover, the presence of the larval dispersal effect meaningfully increases the range of feasible patch sizes. Holding adult dispersal constant at the ‘low adult dispersal’ rate, we find that the presence of the larval dispersal effect reduces the critical patch size by approximately 30%.

Profits are generally highest under biological parameters conferring the most ‘complete’ ownership of adult species to property rights holders (e.g. when adult dispersal is ‘low’) (Fig. 1)

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5 Solving the model under symmetric economic and biological conditions across the two TURFs permits evidence that the solution for one of the TURFs is a reflection of the solution for the other TURF across the range of patch sizes. The assumption of homogeneity yields interior solutions where all agents invest positive effort in the fishery.
a). Profits conferring under Cournot-Nash equilibrium with spatial connectivity are always lower than the profits that would confer under Cournot-Nash equilibrium with spatial independence. The reduction in profitability relative to spatial independence, in fact, captures the magnitude of spatial externalities occurring between patches as a result of species connectivity. Under Cournot-Nash equilibrium, spatial externalities are increasing in adult dispersal and decreasing in larval dispersal. The finding that, with Cournot-Nash competition, spatial connectivity is less profitable than spatial independence is consistent with the original views by Christy [33] that TURFs are most effective when targeting immobile species.

In-situ biomass levels under spatial connectivity are lower than when all the patches are independent (spatial independence) for all four dispersal cases (Fig. 1 b and d). Moreover, patch 1 biomass under Cournot-Nash equilibrium decrease as the degree of adult mobility increases (Fig. 1 b). We find that for both Cournot-Nash and cooperative behavior, there is a critical patch size where biomass under source-sink scenarios exceed biomass under the low adult dispersal scenario (Fig. 1 b and d). To see why, consider that under the source-sink scenario, the marginal cost of fishing in patch 1 (the source patch) increases due to the decreases in in-situ biomass density resulting from the loss of juveniles. Per capita profits in patch 1 decline as a result of the higher fishing costs and lower effort. In response, we find that biomass in the source patch actually increase relative to the scenario of common pool larval dispersal over much of the feasible range of patch sizes. Outcomes in the sink patch are similar to the base scenario of low adult dispersal.

Biomass under the high adult mobility scenarios (i.e. ‘high adult dispersal’ and ‘no larval dispersal’) are significantly lower than the spatially independent scenario for both Cournot-
Nash and cooperative behavior. Spatial connectivity via density dependent exchange manifests inter-patch strategic behaviors amongst the harvesters. This gives rise to the double tragedy of the commons, where agents not only fail to account for the costs their harvest imposes on others, but in fact actively seek to entice assets away from their neighbors [17]. Under scenarios of high adult mobility, agents in patch $i$ strategically depress in-situ population until the increased marginal fishing cost from removing an individual in patch $i$ just equal the marginal gain in profits from enticing an individual away from patch $j$.

Per capita profits for patch 1 when both patches are independently cooperative are again highest under conditions of high larval dispersal and low adult dispersal (Fig. 1 c). For the other scenarios, we find that profits conferring to patch 1 under connectivity exceed the profits that would confer under spatial independence when $m \geq 0.14$ for low adult dispersal, $m \geq 0.60$ for high adult dispersal, and $m \geq 0.66$ for source-sink. In particular, we find that profits under the low adult dispersal scenario are greater than the spatially independent scenario for nearly the entire feasible patch size range. Larval growth occurring as a common pool across the entire system, along with rational investment of effort across both patches, results in a fishery that can support higher exploitation than it otherwise could under spatial independence. In fact, the peak in patch 1’s per capita cooperative profits under low adult dispersal when $m \cong 0.2$ reflects nearly a 400% increase in effort relative to spatial independence.

Lowering the larval dispersal rate, as in the source-sink scenario, generally lowers profits. However, even though patch 1 is a net exporter of larvae in the source-sink scenario, they record greater profits than the spatially independent scenario for patch sizes exceeding
\( m = 0.66 \). This is because patch 1 is a net importer of adults for \( m \geq 0.66 \) due to their lower population density. The profits accruing to patch 2, the receptor patch, are always greater than the spatially independent scenario. Hence, some degree of adult mobility is necessary in order for both patch 1 and patch 2 to benefit in the source-sink scenario.

As the adult dispersal rate is increased, the ability for agents operating in small patch sizes to capitalize on the common pool growth effect is negated by the loss of adults. Where adult dispersal is high, larger patch sizes present agents with greater ability to influence biomass density and, accordingly, better ability to capitalize on inter-patch biomass density gradients. Hence, from the perspective of patch 1, low values of \( m \) correspond to net exportation of adults (with exports from patch 1 increasing inversely with \( m \)) and lower profits relative to spatial independence. The high adult dispersal scenario therefore confers greater profits to patch 1 than spatial independence scenario for \( m \geq 0.60 \) due to the added influence that large patch size accords to the exchange of adults.

Cooperative biomass levels for patch 1 are lower under connectivity than spatial independence (Fig. 1 d). This result follows from both the higher exploitation levels that are supported by the larval growth effect and the aforementioned incentives to reduce in-situ biomass densities to stimulate the exchange of adults.

Unlike with Cournot-Nash behaviors, the presence of mobility during larval life stages actually increase TURF returns relative to species immobility. This is counter to the conventional wisdom that a necessary condition for TURFs to be effective management tools is species sedentarism [e.g. 16, 17, 33]. In fact, relative to spatial independence, both patches 1
and 2 are strictly better off when $0.14 \leq m \leq 0.86$ under low adult dispersal and $0.66 \leq m \leq 0.88$ under source-sink dispersal.

**Heterogeneity**

To introduce between-patch heterogeneity in behavior and characterize the stability of cooperative outcomes in a TURF, we consider the case where patch 1 has a defection while patch 2 remains cooperative. To maintain consistency with the open loop model, we assume that within each patch the defective behavior of any agent $i$ is not publicly known to other agents $i \neq j$. The open loop model states that if an agent defects in the second stage, then the effort of those who remain cooperative is held at the first stage levels. However, to maintain consistency with the steady state biological solution, the inter-patch dispersal must re-equilibrate. Thus, the model allows for outside agents to adjust their optimal effort levels according to any changes in dispersal levels resulting from defections. For instance, if aggregate effort in patch 1 increases through defection during the second stage of the game, then we allow agents in patch 2 to adjust their effort levels to new profit maximizing levels according to the new dispersal patterns. We assume that these responses occur in the second stage of the game as the defector chooses his optimal non-cooperative response.

To test the model, we first examine the case where there is no connectivity between patches (i.e. $b = 0, a_2 = 0, d_1 = 0$). We find the effort response of the defector is positive along the entire feasible patch size range and increases with patch size (Fig. 2 a). Biomass under cheating is strictly less than those under cooperation (Fig. 2 b). The absolute incentives to

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6 Naturally, by virtue of the lack of connectivity, the economic and biological conditions in patch 2 are unaffected by cheating within patch 1.
defect (i.e. the additional gains in profit from defecting) are strictly positive and increasing in patch size (Fig. 2 c and d). The relative incentive to defect, measured against the profits that would confer under internal cooperation, are constant across the feasible range of patch sizes (Fig. 2 d). Those agents who remain cooperative are strictly worse off after the defection (Fig. 2 c).

We next consider the effect that defection has on the system under connectivity. The gains from defection for an agent in patch 1 appear in Fig. 3. The absolute and relative gains from defecting are highest under the low adult dispersal and source-sink scenarios (Fig. 3 a and d). Hence, incentives to defect from cooperative behavior are highest when adult mobility is low. All else equal, a lower adult dispersal rate limits capacity for agents to interact between patches, thus limiting the spatial biological externality. Put another way, low adult dispersal confers the greatest ownership of the in-situ population (Fig. 1 c and d). The ability of defective agents to capitalize on cooperative behaviors of agents within the patch are therefore highest when the fishery is in a state of low adult dispersal. Cooperation under these biological conditions would likely require significant regulation and sanctioning.

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Richter et al. [15], who examine the interactions of multiple agents harvesting a single common pool stock, find that incentives to cheat increase inversely to stock size. In their model, cooperative agents take into account the negative dynamic harvest externalities and, thus, cooperators are more responsive to stock depletions than defectors. As the stock is depleted, the cooperators lower their effort, yet defectors act to appropriate the rents left behind by those acting cooperatively. Declining shares of the common pool resource trigger additional defections, thereby leading to a tipping point of widespread non-cooperative behavior. The analogous result in our model, is a “race to the bottom” under high adult dispersal conditions, where stock reductions in the neighboring patch incentivize further local reductions as a means to balance the dispersal ledger.
Recall that cooperative profits for patch 1 under source-sink are generally lower than under low adult dispersal, as patch 1 is a net exporter of larvae. Hence, because total biological productivity are lower for patch 1 when it is a source patch, the incentives to defect are greater under low adult dispersal than source-sink. Consequently, eliminating larval dispersal has the effect of lowering total and marginal biological productivity, which also lowers the ability of defectors to capitalize on the rational behavior of cooperators within and outside the patch. Note that the relative incentives to defect under source-sink are increasing in patch size (Fig. 3 d) because importation of adults from the neighboring patch increases with patch size (Fig. 1 d).

The gains to defection under high adult dispersal and no larval dispersal are significantly lower than the cases where adult mobility is low (Fig. 3 b and c). Recall that when adult mobility is high, the patch-specific biomass levels for both patches are significantly lower than the spatially independent scenario due to strategic fisher interactions between TURFs (Fig. 1 b and d). These inter-patch strategic interactions give rise to the incentives to depress own-patch population in efforts to entice further adult settlement from the neighboring patch. Spatial externalities occurring from fisher interactions between patches thus limit the potential gains of defection within any given patch. By increasing biological production in both patches, larval dispersal acts to somewhat attenuate the density gradient between patches and, in the process, tempers the spatial externality. Hence, the gains from defection under high adult mobility are larger in the presence of larval dispersal. Without larval dispersal, the gains from cheating are lower, yet more variable since the biomass gradient does not experience attenuation by the common pool larval process.
**Spatial distribution of costs from defective behavior**

Losses to the remaining cooperators in patch 1 are on the order of 30-50% of their original per capita profits, representing significant within-patch harvest externalities (Fig. 4). In relative magnitudes, the within-patch losses to the remaining cooperative agents resulting from cheating exceed the between-patch losses for most of the patch sizes across the four dispersal cases. However, the within patch losses are relatively constant across the feasible range of patch sizes. By contrast, the relative profit losses outside the patch are highly sensitive to the size of the cheating patch. In fact, we find a range of feasible patch sizes for which losses to the neighboring patch exceed, in relative terms, the losses within the cheating patch. Namely, under scenarios of high adult dispersal, for $m \geq 0.50$, the relative losses outside the patch exceed those inside the patch (Fig. 4 b and c). Per capita losses summed over both patches are largest under the scenarios involving high adult mobility and lowest under the source-sink scenario (Fig. 4 d).

**Discussion**

Small scale fisheries create meaningful value at both local and (collectively) global scales. In spite of their importance, practical fisheries management and reform remains a challenge in many small scale fisheries. Where fisheries governance lack the institutional power to implement strict market based management tools, decentralized measures such as TURFs and other space-based rights are increasingly being considered as potential tools for reform. However, the design of TURFs is complicated by communal management and spatially dependent resource mobility. Many space-based rights regimes are operated on a communal basis [18] and therefore are exposed to the risk of defective behavior and harvest externalities.
At the same time, exchange of individuals at both the adult and larval stages establishes strategic interactions between agents in neighboring TURFs. Thus, when designing spatial property rights in the small scale fisheries context, accounting for the ability to internally coordinate rational exploitation as well as the inefficiencies arising from incomplete resource ownership is critical.

Fishery outcomes depend critically on the scale of the TURF and the biological connectivities. We find that when two neighboring TURFs are each internally cooperatively exploited, then spatial connectivity via a common pool larval growth and settlement process can, even in the presence of modest rates of adult dispersal based on relative densities, increase profits significantly relative to spatial independence. Each TURF can thus capitalize on the cooperative behavior of its neighbor without any attendant formal unification agreement. Even in the presence of source-sink larval dispersal and low adult dispersal based on relative densities, profits to both patches can exceed those under spatial independence. Moreover, incentives to defect from cooperative harvest agreements also change along the dimension of community scale. If per capita catch shares decrease as communal membership increases, then the potential gains from defection increase [14] and cooperative stability falls [34]. Thus, it is critical to account for how membership scales when designing ‘large’ spatial property rights aimed at achieving complete dispersal coverage. The widely held notion of always demarcating spatial property rights boundaries such that complete dispersal range is covered [16, 17, 33] is therefore no panacea.

Conversely, for either Cournot-Nash or cooperative behaviors, a lack of a common pool larval growth and settlement process and a very high adult dispersal process results in high
spatial externalities that produce fishery outcomes that are substantially worse than spatial independence. Along these lines, accounting for the behavioral organization of agent communities within spatial property rights as well as the particular dispersal habits of the species are a critical part of the design calculus when demarcating property rights boundaries.

Our numerical illustrations demonstrate that the scale and connectivity properties of the TURF critically inform the likelihood of durable internal cooperative behaviors. In particular, we find that small patch sizes and species exhibiting either absence of common pool larval dispersal or very high rates of adult dispersal are most conducive to maintaining lasting voluntary cooperative agreements within a TURF. Yet, TURFs under these conditions are exposed to significant spatial externalities originating from resource users outside the TURF. When agents are tempted to capitalize on the cooperative behaviors of those within and outside the TURF, the likelihood of lasting voluntary cooperation goes down. Somewhat surprisingly, such situations arise when adults are relatively immobile. That is, the spatial scale and dispersal characteristics which enable the best cooperative outcomes also tend to establish the largest incentives to defect from voluntary cooperative behaviors. Such results inform the internal costs to behavioral enforcement that may be necessary to preserve beneficial communal fisheries regimes.

When cooperative arrangements fail, we find that the fallout is largely borne by those within the defective patch. However, the precise burden of harvest and spatial externalities depends on the size of the defective patch and the dispersal patterns of the harvested species. With mid to large patch sizes and under conditions where adults are highly mobile, the cost of
any defection is likely to be borne more by the neighboring TURF.\footnote{Even when each patch is cooperative, spatial externalities arise because cooperative agents in patch $i$ do not account for the effect of harvest in patch $j$. The external costs from a defection is therefore in addition to the spatial externalities arising from each patch operating in independence.} These result raises complex political-economy questions concerning the distribution of costs and benefits in networks of communally managed spatial property rights regimes.

Designing practical reform in small scale developing world fisheries is an ongoing pursuit. The current vogue in fisheries reform frequently center on community-based co-management and fisheries cooperatives [e.g. 35 and references therein]. However, there is scant analyses concerning such arrangements. What are the conditions under which communal management will form? Can characteristics be identified ex-ante which correlate with successful communal management? What costs are necessary to maintain durable cooperative relationships in the fishery? These are questions that must be answered if headway is to be made in developing world fisheries governance. In order to answer these questions and more, we must begin with conceptual structures of the style developed in this paper, which bring together spatial biological networks, economic incentives, and strategic interactions within and across harvester networks.

Appendix A

\textit{Biological Isoclines}

Isoclines for $\frac{dx}{dt} = 0$ for patch 1 and patch 2 in the absence of exploitation and for equal patch size (i.e. $m = 0.5$) are shown in Fig. A1. To generate the isoclines, we solve for the zeros
of the biological equations of motion in (3) and (4) when $h_1$ and $h_2$ equal zero and given a range of stock levels in the neighboring patch. If the patches were independent, then the isoclines would be straight lines equal to their carrying capacity. Likewise, under larval connectivity yet absent exploitation and adult dispersal, the isoclines would be straight lines equal to carrying capacity and would intersect when both patches were at carrying capacity. The curvature of the isoclines reflects the fact that the adult dispersal process draws individuals from high to low densities. The larger the dispersal rate, the more individuals exchange to equalize inter-patch density gradients and, thus, the closer the isoclines shift toward the 45 degree line. The common pool larval growth effect acts to attenuate the density gradient by increasing the effective growth rate of low-density patches. As a result, the isoclines shift outward relative to the scenario where there is no common pool growth effects. Because the two patches thus far do not differ in mortalities, then the steady state in the independent case coincides with the integrated scenarios.

A key feature when integrating scale in models of biological dispersion is accounting for behavior of the model at the limits of the scale parameter (i.e. as $m \to 0$ and $m \to 1$). Isoclines for patch 1 in the absence of exploitation in the vicinities of the upper and lower patch size are presented in Appendix A. We find that the model is able to sensibly represent patch 1 steady state population as the patch size limits to zero (Fig. A2 b). At the upper limits, the model performs qualitatively similar to the isoclines in Fig. 1 (Fig. A2 a).
Fig. A1. Isoclines for Patches 1 and 2 under equal patch size in the absence of exploitation. Isoclines for Patch 1 are labeled with the number ‘1’. Example trajectories are displayed as curved arrows. The solid isoclines represent the base scenario of ‘low adult dispersal’. The dashed lines represent the high adult dispersal scenario. The dotted lines represent the no larval dispersal scenario. The dash-dot lines represent the source-sink scenario. Note that since Patch 2 acts as the sink in the source-sink scenario, the isocline for Patch 2 is equivalent to the base scenario.

**Limit Behavior of the Spatial Biological Model**

A key feature when integrating scale in models of biological dispersion is accounting for behavior of the model at the limits of the scale parameter (i.e. as $m \to 0$ and $m \to 1$). Isoclines for $\frac{dx}{dt} = 0$ for Patch 1 in the absence of exploitation in the vicinity of the upper ($m \to 1$) and
lower \((m \to 0)\) limits of patch size are presented in Fig. A1. To generate the isoclines, we solve for the zeros of the equation of motion for Patch 1 in (3) using fixed values for Patch 2 biomass that are consistent with the patch sizes evaluated. In particular, we evaluate the upper and lower limits of Patch 1 using Patch 2 biomass values of \(x_2 = 0.01\) and \(x_2 = 0.8\), respectively. These biomass values are consistent with Patch 2 carrying capacities under the range of evaluated patch sizes. The model is able to sensibly represent Patch 1 steady state population as the patch size limits to zero (Fig. A1 b). The steady state behavior of Patch 1’s population at the lower patch size limit is approximately linear due to the restricted carrying capacities. At the upper limit of patch size, the model performs qualitatively similar to the isoclines in Fig. 1 (Fig. A1 a). However, the isoclines for the ‘high adult dispersal’ and ‘no larval dispersal’ scenarios exhibit additional curvature due to the exchange of adults as the size of Patch 2 increases (Patch 2 density decreases from \(\approx \frac{1}{1}\) to \(\approx \frac{1}{10}\) as Patch 1 size decreases from \(m = 1\) to \(m = 0.90\), thus facilitating exchange). By contrast, the lower adult dispersal rates under the ‘low adult dispersal’ and ‘source-sink’ scenarios cause the isoclines to be relatively level.
Cooperative Outcomes Relative to Cournot-Nash

Rents conferring under cooperative harvesting behavior are always greater than rents conferring under Cournot-Nash competition for the four dispersal scenarios (Fig. B1). Gains to cooperation generally increase with patch size. This finding is consistent with the result that harvest externalities borne outside the patch are highest when the offending patch is large in size. For the largest economically feasible patch size in a two-patch network, the gains to cooperation are roughly 200% of what would be earned under Cournot-Nash. When patch 2 behaves according to Cournot-Nash competition, patch 1 has the least to gain from cooperative behavior when biological connectivity is characterized as source-sink larval dispersal (Fig. B1 a).
When patch 2 behaves internally cooperatively, patch 1 has the most to gain from cooperative behavior when connectivity is characterized as either high adult dispersal or no larval dispersal (Fig. B1 b). Recall that under no larval dispersal, the ability of one patch to influence the between-patch biomass density gradient increases with patch size. Hence, the relative gains to cooperation for patch 1 when patch 2 behaves internally cooperatively are highest for small patch size. However, when patch 2 behaves non-cooperatively and under no larval dispersal, agents in patch 1 have limited incentive to lower their collective effort, as the density gradient will favor the patch with the highest aggregate effort.

Fig. B1. Per capita profits conferring under cooperation relative to Cournot-Nash. Panel a is the relative gains from cooperation in patch 1 when patch 2 is behaving non-cooperatively. Panel b is the relative gains from cooperation in patch 1 when patch 2 behaves cooperatively.
References


Fig. 1. Per capita profits (Panel a) and biomass (Panel b) for Patch 1 under Cournot-Nash equilibrium and per capita profits (Panel c) and biomass (Panel d) under two-patch simultaneous cooperative. The Cournot-Nash and cooperative results are measured relative to their spatially independent analogs.
Fig. 2. Per capita effort, biomass, and per capita profits for Patch 1 in a closed patch system when there is a cheater. Panel a is the per capita effort under cooperation and by the cheater. Panel b is the biomass under cooperation and under cheating. Panel c is the per capita profits conferring under cooperation, to the cheater, and to the two agents who remain cooperative. Panel d is the absolute and relative gains to cheating, where relative gains are measured as a percentage of the initial cooperative per capita profits.
Fig. 3. Absolute and relative gains from cheating under the four different dispersal scenarios.

Relative gains to cheating are measured as a percentage of the initial cooperative per capita profits. Panel a is the ‘low adult dispersal’ scenario. Panel b is the ‘high adult dispersal’ scenario. Panel c is the ‘no larval dispersal’ scenario. Panel d is the ‘source-sink’ scenario, with Patch 1 acting as the source.
Fig. 4. Per capita losses from having a cheater in Patch 1. Panel a is the low adult dispersal scenario. Panel b is the high adult dispersal scenario. Panel c is the no larval dispersal scenario. Panel d is the source-sink scenario. Losses are given relative to the profits that conferred under cooperative behavior.
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