

Matching spatial property rights fisheries with scales of fish dispersal

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Abstract. Regulation of fisheries using spatial property rights can alleviate competition for high-value patches that hinders economic efficiency in quota-based, rights-based, and open-access management programs. However, efficiency gains erode when delineation of spatial rights constitutes incomplete ownership of the resource, thereby degrading its local value and promoting overexploitation. Incomplete ownership may be particularly prevalent in the spatial management of mobile fishery species. We developed a game-theoretic bioeconomic model of spatial property rights representing territorial user rights fisheries (TURF) management of nearshore marine fish and invertebrate species with mobile adult and larval life history stages. Strategic responses by fisheries in neighboring management units result in overexploitation of the stock and reduced yields for each fishery compared with those attainable without resource mobility or with coordination or sole control in fishing effort. High dispersal potential of the larval stage, a common trait among nearshore fishery species, coupled with scaling of management units to only capture adult mobility, a common characteristic of many nearshore TURF programs, in particular substantially reduced stock levels and yields. In a case study of hypothetical TURF programs of nearshore fish and invertebrate species, management units needed to be tens of kilometers in alongshore length to minimize larval export and generate reasonable returns to fisheries. Cooperation and quota regulations represent solutions to the problem that need to be quantified in cost and integrated into the determination of the acceptability of spatial property rights management of fisheries.

Key words: adult spillover; catch shares; fishery yield; game theory; larval export; Nash equilibrium; nearshore fisheries; population connectivity; spatial property rights; territorial user rights fisheries (TURFs).

INTRODUCTION

Most organisms exhibit a dispersive phase as a part of their reproductive life cycle. The exchange of individuals among locations through dispersal can profoundly influence the density and persistence of local populations (MacArthur and Wilson 1963, Stacey and Taper 1992, Wing et al. 1998, Armsworth 2002). Consequently, biologists, and more recently economists, have increased their focus on evaluating the implications of space and alternative spatially explicit regulatory policies on the efficacy in achieving goals in wildlife conservation and renewable natural resource management (Sanchirico and Wilen 1999). Bioeconomic modeling and empirical results indicate that successful management depends on our ability to align the spatial scales of regulatory procedures with the natural spatial scales characterizing the dispersal processes of the resource (Botsford et al. 1998, Palumbi 2004, Kaplan 2006).

Rights-based management policies that secure exclusive access to portions of a resource offer a promising solution to excessive exploitation rates that degrade populations and generate the unsatisfactory economic

returns experienced under common pool (open-access) management (Fujita and Bonzon 2005, Newell et al. 2005, Grafton et al. 2006, Costello et al. 2008). In fisheries, regulation of individual harvest quotas is a common form of rights-based management that can provide incentives for efficient and sustainable harvest practices (Costello et al. 2008). Spatial property rights are a special form of rights-based management in which exclusive access to a resource is granted within spatially delineated areas. Management of renewable natural resources via spatial property rights is widespread in terrestrial ecosystems (e.g., forestry, livestock industries) and occasionally used in nearshore marine fisheries (e.g., Molares and Freire 2003, Cancino et al. 2007). Management with spatial property rights can increase economic returns (e.g., yields, profits) over those attainable under quota-based management programs by reducing unnecessary competition for high-valued spatial units (Copes 1986, Cancino et al. 2007, Costello and Deacon 2007). (See Christy [1982], Thwaites et al. [1998], Li et al. [2007], Costello and Kaffine [2008], and Goodhue and McCarthy [2009] for exceptions and a detailed discussion of challenges and failures in marine and terrestrial spatial property rights management programs.) However, when growth of an exploited natural resource disperses, overexploitation similar to that observed in open-access management can develop under spatial-rights-based management when agents

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own a fixed area too small to contain the dispersing resource (Janmaat 2005). Conversely, proper scaling of parcels (e.g., grazing areas) relative to the mobility of a natural resource (e.g., herbivores) is expected to promote efficient management of the resource (Schmidt and Willott 2003). Consequently, the degree to which spatial-rights-based management can achieve maximum potential returns of a renewable natural resource (and thus the benefit of this form of management over open-access- and alternative rights-based policies) is sensitive to how well the spatial scale represented by the delineation of use rights aligns with the spatial scale of dispersal of the resource.

Dispersal of the juvenile stage typically outdistances that by the harvested, adult stage of many renewable natural resource species, especially in nearshore, non-pelagic marine fisheries (Kinlan et al. 2005, Nathan 2006). Yet, few fisheries management programs with spatial property rights (commonly termed territorial user rights fisheries, or TURFs [Christy 1982]) appear to be appropriately scaled to adequately capture dispersal of the preharvest, juvenile stage. For example, in a national TURFs program established along the Chilean coast in the 1990s for a suite of benthic (predominantly shellfish) fishery species with relatively sedentary adult stages, the majority of spatial management units with exclusive fishing rights are exceedingly small (≤ 1 km alongshore length) compared with the estimated mean dispersal distances (10–100+ km) of the pre-recruit, larval stages of the harvested species (González et al. 1987, Parma et al. 2001, Kinlan and Gaines 2003, Siegel et al. 2003, Molinet et al. 2005). Similarly, in Japan, thousands of historically based TURF area boundaries are typically seaward extensions of municipal boundaries on land, delineating small management units not expected to contain dispersive larval stages of harvested fishery species that are otherwise relatively sedentary as adults (Uchida and Makino 2008). Similar examples exist in Fiji, the Philippines, along the Baja California peninsula in Mexico, and U.S. Maine coast of fisheries characterized by exclusive or limited access within small spatial zones (less than tens of kilometers in alongshore length) to species with relatively sedentary adult stages and dispersive pelagic larval stages (Acheson 1975, Smith and Panayotou 1984, Cooke et al. 2000, Baticados 2004, SCS 2004).

Amidst praise for the observed and expected ecological, economic, and social benefits of TURF-based fishery management is awareness that appropriate spatial scaling of the management units, or TURFs, can influence their efficacy (Allison and Ellis 2001, Baskaran and Anderson 2005, Schumann 2007). Yet there exist few explicit evaluations of how large TURFs need to be to satisfactorily minimize overfishing in response to dispersal and lost yields. Conversely, few have quantified the gains expected from TURFs over open-access management in relation to TURF size. In this study we constructed a simple game-theoretic

bioeconomic fisheries model and considered the effect of size of individual TURFs relative to scales of movement of adult and larval stages on managed stock density and fishery yield. We estimated connectivity between adjacent TURFs in relation to TURF size and levels of adult spillover and larval export due to adult movement and larval dispersal, respectively. We then compared effects of connectivity on equilibrium stock levels and yields within TURFs managed by independent fisheries that do not cooperate with one another, to maximum stocks and yields achievable in the TURFs if they were managed collectively or cooperatively (i.e., as if by a sole owner). We also compute stock levels and yields to the fishery under open access, which provides a benchmark against which to compare the TURF and sole-owner cases. While others have shown the inability of spatial property-rights-based management to maximize fishery yield for resources that disperse (Janmaat 2005), explicit consideration of the differential effects on yields caused by adult spillover vs. larval export is often ignored. In deconstructing our analysis to consider adult and larval movement we demonstrate that overexploitation of stocks and reductions in fishery yield are predominantly driven by high connectivity by the larvae, the life history stage, and associated dispersal scale that is poorly aligned with TURF design in many property-rights-based fishery management programs. Further, direct estimates of movement in fishery species are difficult to obtain, especially for larval stages. Yet, key demographic characteristics, such as adult home range area and length of the larval dispersal phase, are more readily available and can be used to approximate spatial scales of adult spillover and larval export from a delineated region (Kramer and Chapman 1999, Siegel et al. 2003). Consideration of these demographic factors has been shown to play a critical role in determining the optimal scaling of conservation patches (Ovaskainen 2002) and no-take spatial closures (marine reserves) used in fishery management (e.g., Shanks et al. 2003, Kinlan et al. 2005, Kellner et al. 2008, White et al. 2008). In these cases the management unit serves to preserve stocks within and possibly enhance economic yields outside. Consideration of these demographic factors in relation to the optimal scaling of TURFs, i.e., management units within which fishery yields are expected, is lacking. We advance the evaluation of the efficacy of spatial property-rights-based fishery management by relating adult and larval demographic values characterizing their movement rates to the scaling of TURFs and the ability of TURF management to maximize long-term yields. Finally, we present a case study of five nearshore fishery species in California: kelp bass, California sheephead, blue rockfish, red urchin, and spiny lobster (see Plate 1). In this case study we show how differences among these species in their potential levels of adult spillover and larval export influence the efficacy of TURF management. In all cases, the movement scale of the larval stage of the fishery species

dominates that of the adult stage in affecting managed stock levels and yields within the TURFs.

METHODS

We focused on nearshore fish and invertebrate species characterized by a mobile adult stage subject to density-independent mortality and a pelagic larval stage that disperses. Adult movement and larval dispersal connect neighboring patches. Survival of larvae to the adult stage (i.e., recruitment) is dependent upon settler density in the patch. We developed a discrete-time model with these elements of life history:

$$N_x^{t+1} = (N_x^t + M_x^t)(1 - \delta) + \frac{S_x^t}{1 + \alpha S_x^t} \quad (1)$$

where t and x represent time in years and patch number, respectively, N is adult stock density, M is a function describing net adult movement (see Eq. 2), S is a function describing settler density (see Eqs. 3 and 4), α is a scaling parameter that characterizes the overall strength of density dependence, and δ is the natural annual mortality rate of adults (e.g., following Walters et al. 2007). The final term on the right-hand side describes settler survival to adulthood, which is density dependent (the maximum number of new adults per settler is 1). In our analysis we implicitly assume an infinitely long, homogenous coastline divided into an array of TURFs identical in size, ecological condition, and management. Because of the symmetry of the system and our consideration of population dynamics in units of density, the entire system can be represented by two patches: a focal patch representing one TURF and secondary patch representing the remainder of the coastline. Either patch (i.e., $x = 1$ or 2) can be the focal patch, and for the secondary patch stock density also equals density within any single TURF in that patch.

Patches are connected by adult and larval movement. Because conditions are homogenous throughout and the focal patch is scaled to the size of a TURF and population dynamics are measured in units of density, immigration and emigration rates into and out of the focal patch equal those for the secondary patch as well as for any TURF in the system. Adult movement between patches is assumed to be affected by the gradient in stock density between the patches relative to each patch's equilibrium carrying capacity:

$$M_1^t = -M_2^t = -mN_1^t \left(\frac{N_1^t}{K_1} - \frac{N_2^t}{K_2} \right) + mN_2^t \left(\frac{N_2^t}{K_2} - \frac{N_1^t}{K_1} \right) \quad (2)$$

where m is the maximum rate of movement of adults between patches (i.e., maximum spillover rate from a TURF) and $K_x = K$, equilibrium unfished carrying capacity. Larval production occurs after adult movement and prior to adult mortality, and settler density is determined following larval production and dispersal:

$$S_1^t = P((N_1^t + M_1^t)(1 - c) + (N_2^t + M_2^t)c) \quad (3)$$

$$S_2^t = P((N_2^t + M_2^t)(1 - c) + (N_1^t + M_1^t)c) \quad (4)$$

where P is the per capita production of larvae by adults and c is the proportion of larvae that disperse to the other patch (i.e., larval export to the other TURF; the remainder stay). In the wild, adult densities are typically in the relatively linear portion of any kind of density-dependent function (e.g., influencing their mortality or fecundity), mostly because densities are reduced by more intense density-dependent settler-recruitment mortality and, for fished species, harvest mortality. For these reasons we modeled adult mortality and fecundity as density independent (e.g., as done by Walters et al. 2007). Larval dispersal, c , is assumed to be influenced by exogenous factors such as duration of the pelagic larval phase and oceanographic circulation dynamics.

Following standard convention (e.g., Walters et al. 2007), we set carrying capacity and annual natural mortality rate to default values ($K = 1$ and $\delta = 0.05$), then parameterized the recruitment relationship and adult productivity in terms of δ , K , and the Goodyear compensation ratio (CR, the ratio of maximum larval survival at low densities to survival at carrying capacity) by solving

$$\alpha = \frac{CR - 1}{CR\delta K} \quad (5)$$

and

$$P = \frac{\delta}{1 - \delta\alpha K}. \quad (6)$$

In solving Eqs. 5 and 6 we set $CR = 4$, a value typical for representing nearshore fishery species (e.g., kelp bass, kelp rockfish, sea urchin, and sheephead; Costello et al. 2010).

Eq. 1 is solved for steady-state conditions:

$$Y_x^* = M_x^* + \frac{S_x^*}{1 + \alpha S_x^*} - \delta(N_x^* + M_x^*) \quad (7)$$

where Y is equilibrium adult population density growth rate or, in the context of fishery management, sustainable annual yield of adult fish per unit coastline (hereafter referred to as yield). Thus, harvest occurs following larval production and recruitment and adult movement and natural mortality. Given positive values for m and/or c , yield in a patch is a function of adult density in both patches. Representing a simple spatial property-rights-based fishery management program, we assumed each TURF to be privately controlled by an agent (or collective of yield-sharing agents, or fishermen) able to exclude competing harvesters without cost. Each agent's strategic objective is to harvest local population density down to a chosen stock level (i.e., escapement level) that maximizes yield in the TURF (Eq. 7), given complete knowledge of but no influence over the managed stock densities in the neighboring TURFs. Each agent chooses to harvest simultaneously so we compute the Nash equilibrium of this noncooperative

game (Fudenberg and Tirole 1991). The Nash equilibrium occurs where each owner's choice is optimal taking the other owner's choice as given. We label this equilibrium the noncooperative yield, Y_{nc} . We focus on yield to help keep the model analytically tractable, while recognizing that fishery profit in relation to revenue and cost is another important measure of management efficacy (see *Discussion*).

We compared Y_{nc} with maximum yield attainable in the system. Under the latter scenario, fishery management is assumed to be governed by a sole owner of the entire stock or by TURF owners who coordinate local harvest rates to maximize joint yield. The resulting yield is the cooperative maximum sustainable yield, MSY.

With no connectivity between TURFs (i.e., $m=c=0$), the stock is assumed immobile and/or each TURF is assumed to be infinitely large. Consequently, ownership is exclusive and Eq. 7 simplifies to describe management of two independent stocks with identical cooperative and noncooperative managed stock levels and yields. Setting the derivative of Eq. 7 to zero and solving for density produces

$$N_{x,MSY} = N_{x,Y_{nc}} = \frac{-\sqrt{\delta} + \sqrt{P}}{\alpha P \sqrt{\delta}} \quad (8)$$

which, when substituted into Eq. 7, generates a simple closed-form expression for yield

$$MSY = Y_{nc} = \frac{\delta - 2\sqrt{\delta P} + P}{\alpha P}. \quad (9)$$

Eq. 9 describes the maximum long-term, annual yield achievable via regulation of adult stock density, given the demographics and life history of the fishery species.

Analytic consideration of positive m and c values produces unwieldy $N_{x,Y_{nc}}$ and Y_{nc} equations that do not readily illustrate effects of connectivity on stock and yield. Instead, we determined $N_{x,Y_{nc}}$ and Y_{nc} numerically for given connectivity conditions by evaluating Eq. 7 across an exhaustive sampling of managed stock levels in each TURF. This approach is practical and allows for comparison of stocks and yields generated among the full range of managed densities in addition to those associated with MSY and Y_{nc} . For each combination of adult spillover and larval export rates (i.e., m and c values), we quantified the relative reduction in stock from $N_{x,MSY}$ to $N_{x,Y_{nc}}$, and the relative reduction in yield from MSY to Y_{nc} , that is, the relative reduction in stock and yield achieved under noncooperative management compared with those under cooperation or sole ownership.

We also used our model to calculate equilibrium resource stock level and yield expected under open-access management, to be used as a benchmark against which to compare our results from the uncoordinated TURF and sole owner (or fully coordinated TURF owner) cases. Under open-access (i.e., unlimited entry) management without costs, entrants will continue to

enter the fishery until the stock and harvest are both driven to zero (see *Discussion* for consideration of effects of harvest costs). Thus, in the long term the fishery will be extirpated.

Consideration of fish life history traits not included in our simple model, such as recruitment of settlers to a juvenile stage prior to the adult stage and adult growth and increased fecundity with age, may be considered to influence results. To investigate the possible effect of these life history characteristics on our analysis we constructed an age-structured model with juvenile and adult growth after recruitment and fecundity scaling with biomass and compared the results generated using this more complex model with those produced by the simpler model presented above. Including this complexity leaves our qualitative conclusions unchanged and has only a minor effect on quantitative results. A detailed description of this model is presented in Appendix B.

To quantify effects of connectivity on fisheries yield, we linked m and c in our model with empirical estimates of adult movement and larval dispersal. Variables m and c are functions of the spatial scale of movement of the life stage in relation to the spatial scale of the TURF. Accordingly, we calculated values for m and c by relating alongshore adult home range sizes and larval dispersal patterns estimated in nearshore fish and invertebrates with a range of alongshore TURF widths. We assumed individual TURFs extend sufficiently far offshore (e.g., beyond the edge of a rocky reef, kelp forest, or coral reef subtidal habitat boundaries) to capture adult movement perpendicular to shore. Because larvae are not harvested, TURFs need not be assumed to capture the entire offshore spatial extent of larval dispersal trajectories.

With few exceptions, nearshore fishery species exhibit strong site fidelity within adult home ranges spanning <1 km (the majority <300 m) in the alongshore domain (Kramer and Chapman 1999, Botsford et al. 2009). This generalization does not include pelagic fishery species (e.g., anchovy) that visit the nearshore environment and are highly mobile. We use, from Kramer and Chapman (1999), a calculation of the proportion of an adult population that moves outside a patch, i.e., spillover, in relation to home range length of the species and patch width: $m = 1/(4W)$ when $W \geq 0.5$; $m = 1 - W$ when $W \leq 0.5$, where in the context of this study W is alongshore TURF width in units of alongshore home range length (Appendix A: Fig. A1). Kramer and Chapman's geometrically based calculation assumes home range area to be roughly circular and uniform use of the home range area (Low 1971, van Rooij et al. 1996). Consideration of irregular home range shape may increase expected adult spillover. Consideration of more concentrated use of the center of the home range (e.g., via a normal probability density distribution) would decrease adult spillover. Given TURF widths that captured the range observed in management programs (see *Introduction*), we considered a range of alongshore

TABLE 1. Life history characteristics of California nearshore fishery species used in the case study.

Common name	Scientific name	PLD (d)	Home range (m)	δ	Sources
Kelp bass	<i>Paralabrax clathratus</i>	25–31	65	0.033	Cailliet et al. (2000), Lowe et al. (2003)
California sheephead	<i>Semicossyphus pulcher</i>	39	139	0.033	Cailliet et al. (2000), Shanks and Eckert (2005), Topping et al. (2005)
Blue rockfish	<i>Sebastes mystinus</i>	80–130	106	0.04	Cailliet et al. (2000), Jorgensen et al. (2006)
Red urchin	<i>Strongylocentrotus franciscanus</i>	50	100	0.01	Cameron and Shroeter (1980), Kato and Schroeter (1985), Ebert and Southon (2003)
Spiny lobster	<i>Panulirus interruptus</i>	210–270	100	0.05	Shaw (1986)

Notes: Lower bounds of pelagic larval duration (PLD) values were used in the analysis to avoid overestimating larval export. Calculations of alongshore home range lengths are based on empirical estimates of home range area, when available, assuming a circular home range area. Upper bound estimates of home range area were used in the analysis to avoid underestimating adult movement. We calculated δ as inverse mean life span in years.

home range lengths characteristic of nearshore fishery species. We then estimated adult spillover and its effect on the relative reduction in stock and yield attained under noncooperative management compared with those under cooperation or sole ownership.

In nearshore fishery species, mean displacement of dispersing larvae between release and settlement locations ranges from less than 100 m to hundreds of kilometers (Kinlan and Gaines 2003, Planes et al. 2009) and has been described with good first-order accuracy by oceanographic models that approximate dispersal patterns in relation to circulation processes and the duration of the pelagic stage of larvae (Siegel et al. 2003). Although direct estimates of dispersal are lacking, pelagic larval duration (PLD) is known for many fishery species, enabling us to combine an empirically estimated range of PLDs in nearshore fishery species with an oceanographic model of larval dispersal (Siegel et al. 2003) to calculate larval export in relation to alongshore TURF width. In their model, Siegel et al. simulated dispersal trajectories of passive larvae in an idealized nearshore region parameterized with surface velocity statistics typical of coastal currents. The resulting dispersal probability density function is Gaussian, with a standard deviation (σ_d , characterizing the width of the probability density function) calculated in relation to PLD (T_{PLD}) and the root mean square of the fluctuating current velocity (σ_u) in the flow field: $\sigma_d = 2.238\sigma_u T_{PLD}^{1/2}$. Because most marine larvae are small and weak relative to prevailing ocean currents, PLD is often used as a proxy for dispersal ability (Shanks et al. 2003); however, a variety of biological and oceanographic features can prevent larvae from reaching their full passive dispersal potential (Swearer et al. 2002) causing Siegel et al.'s (2003) model to overestimate dispersal distance. Although incorporating such features is beyond the scope of this study, we mitigated overestimating larval export by setting fluctuating current velocity to a conservatively low value, $\sigma_u = 1$ km/d (compared with $\sigma_u > 5$ km/d observed empirically [Harms and Winant 1998, Andrade et al. 2003]). We

calculated the Gaussian probability density distribution based on $\sigma_d(PLD)$, then calculated c , the proportion of larvae that disperse outside a TURF of length L , as the cumulative probability density across the distribution $[-\infty -L/2, L/2 \infty]$, as illustrated in Appendix A: Fig. A2. All larvae that disperse from the TURF (focal patch) settle in the secondary patch, which, because of the homogeneity and symmetry of the model system, corresponds with settler density in any TURF within that patch (the cumulative effect of larval import into a TURF from all neighboring TURFs can be represented by that from the focal patch). We considered a range of TURF widths and PLDs characteristic of nearshore fishery species and estimated larval export and its effect on the relative reduction in stock and yield attained under noncooperative management compared with those under cooperation or sole ownership.

Finally, we calculated changes in stock and yield under cooperative vs. noncooperative TURF management of nearshore fishery species in California. In this hypothetical case study (there are currently no TURFs in California) we explicitly accounted for the estimated natural annual mortality rate, home range dimension, and PLD for each species (Table 1). Changes in stock and yield were estimated in relation to alongshore TURF width.

RESULTS

Consideration of all possible combinations of managed stock densities in each of the two TURFs connected by adult spillover and/or larval export revealed a relationship between stock density in each TURF and yield that did not exist in the absence of connectivity. Fig. 1 illustrates this effect with non-connected (Fig. 1a, b) and positive connectivity (Fig. 1c, d) scenarios. With positive connectivity, private yield in a TURF managed at a given density increased with increasing density in the neighboring TURF. Also in response to connectivity, local density that maximized yield within a TURF in the noncooperative scenario in relation to density in the neighboring TURF (indicated

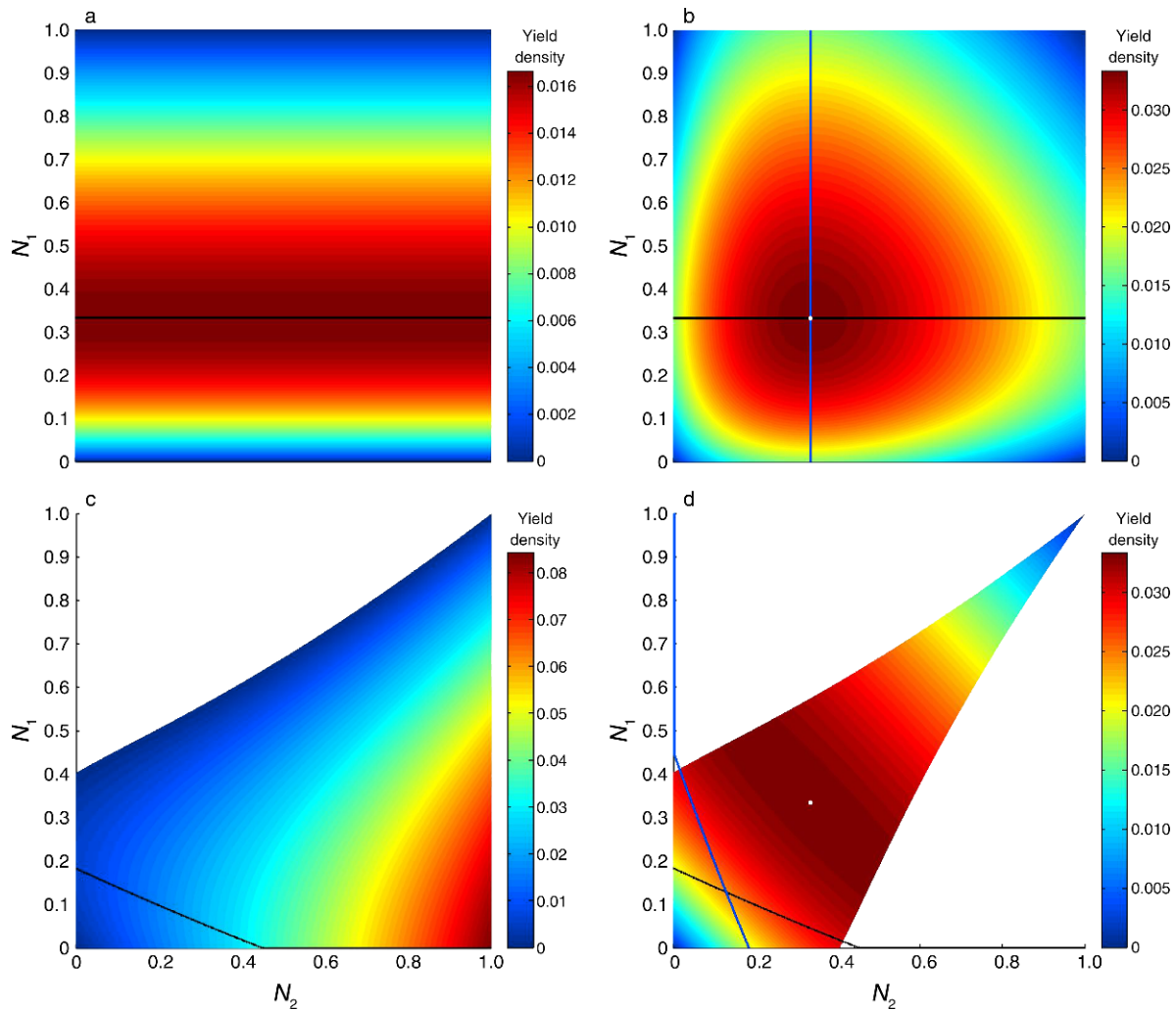


FIG. 1. Equilibrium yield density (number of adults/unit length coastline) in relation to postharvest local population densities in neighboring territorial user rights fisheries (TURFs). N_x refers to post-harvest population density in patch x scaled to the size of a TURF. Two example connectivity scenarios are presented. (a, b) No inter-TURF connectivity; (c, d) TURFs connected by adult movement ($m = 0.05$) and larval dispersal ($c = 0.40$). (a, c) Yield in TURF 1, given fixed population density N_2 in TURF 2, and management of population density in TURF 1 at N_1 . The black line indicates the level of N_1 that maximizes sustainable yield in TURF 1, given fixed values of N_2 . (b, d) Total yield in both TURFs in relation to managed local population densities N_1 and N_2 . White space in panels (c) and (d) represents biologically unsustainable relations. Black lines in panels (b) and (d) correspond with those in panels (a) and (c); blue lines indicate the managed level of N_2 that maximizes sustainable yield in TURF 2, given fixed values of N_1 . Lines intersect at the noncooperative Nash equilibrium density, $N_{x,Y_{nc}}$ and associated yield, Y_{nc} . Maximum sustainable yield, MSY, associated with management of local population densities at the cooperative optimum, is indicated by the white point. In the bottom row, $N_{x,Y_{nc}}$ and Y_{nc} represent a 41% and 27% reduction in managed stock level and yield, respectively, from the optimum stock level and MSY at the white point.

by the lines in Fig. 1) declined with increasing density in the neighboring TURF and was less than $N_{x,MSY}$. Consequently, all values of noncooperatively managed stock density that maximized yield generated yields less than MSY. In particular, connectivity caused Y_{nc} , corresponding with $N_{x,Y_{nc}}$, the Nash equilibrium of noncooperative stock densities between TURFs, to be less than MSY.

Maximum adult spillover between patches, m , increased exponentially to nearly 30% with increasing

home range length (to 1 km) and decreasing TURF width (to 1 km width; Fig. 2a). Regardless of home range length, adult spillover was typically low, limited to <5% for TURFs >5 km wide.

Using Siegel et al.'s formulation (2003) we calculated larval dispersal probability density functions in relation to a range of pelagic larval durations, 5–90 days, that captured mean PLDs characteristic of most fishery species (Lester and Ruttenberg 2005). Larval export, c , increased approximately monotonically with increasing

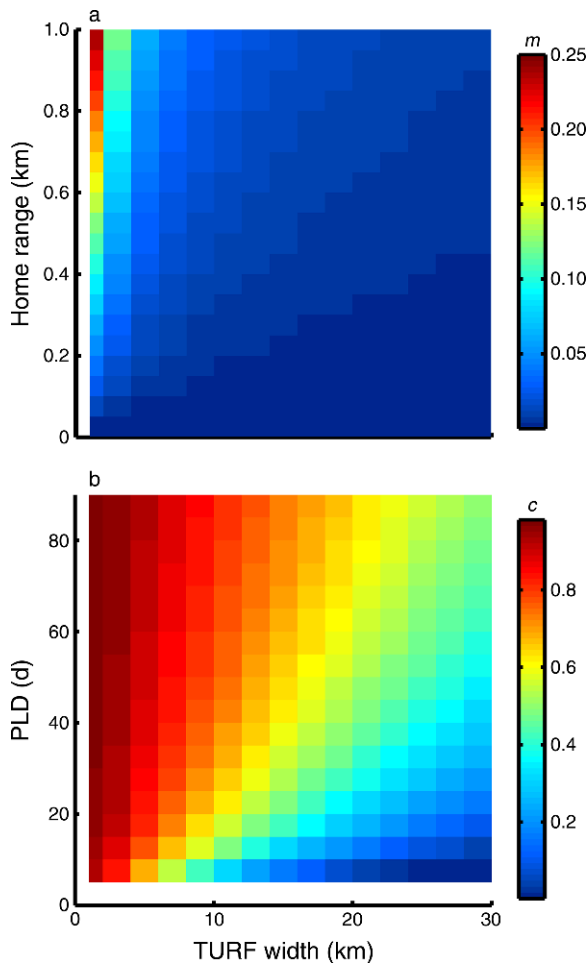


FIG. 2. Adult movement and larval export rates in relation to fish demography and territorial user rights fishery (TURF) width. (a) Maximum proportion of adults leaving a patch, m , between TURFs, in relation to adult home range size and TURF width. (b) Proportion of larval export (the proportion that disperses out of a patch), c , between TURFs in relation to pelagic larval duration (PLD) and TURF width.

PLD and decreasing TURF width, excepting when PLD was relatively short (<30 d) and TURF width large (>20 km) (Fig. 2b). Larval export ranged from $\sim 0\%$ (given 5-d PLD, 30-km wide TURF) to $>90\%$ (TURF width ≤ 1 km, regardless of PLD).

We calculated Nash equilibrium stock densities and associated yields and quantified the proportional reduction in stock and yield attained under noncooperative management compared with those under cooperation or sole ownership, across the range of adult spillover (m) and larval export (c) rates presented in Fig. 2 (Fig. 3). Thus, parameters m and c in Fig. 3 represent calculated levels of connectivity by nearshore fishery species in relation to patches 1–30 km in alongshore width. Given any level of connectivity via adults and/or larvae, the Nash equilibrium stock density in the noncooperative scenario was always less than the density that maximized

yield (i.e., $N_{x,Y_{nc}} < N_{x,MSY}$; Fig. 3a). Connectivity also always induced a positive proportional reduction in yield (i.e., $Y_{nc} < MSY$). Consideration of adult spillover only (i.e., $c = 0$, $m > 0$) generated approximately monotonic proportional reductions in stock and yield. Given the greatest level of spillover considered (i.e., $m = 0.5$) stocks and yields were reduced by $\sim 80\%$ and $\sim 50\%$ from $N_{x,MSY}$ and MSY , respectively. With consideration of larval export only (i.e., $c > 0$, $m = 0$) proportional reductions in stock and yield changed nonlinearly and eventually reached 100% when larval export was large ($c > 70\%$). That is, use of relatively small TURFs and/or targeting of species with long PLDs (i.e., conditions represented by dark red in Fig. 2b) resulted in such high larval export that the Nash equilibrium was characterized by total extirpation of local stocks (i.e., $N_{x,Y_{nc}} = 0$) and a Y_{nc} equal to zero, conditions also found under

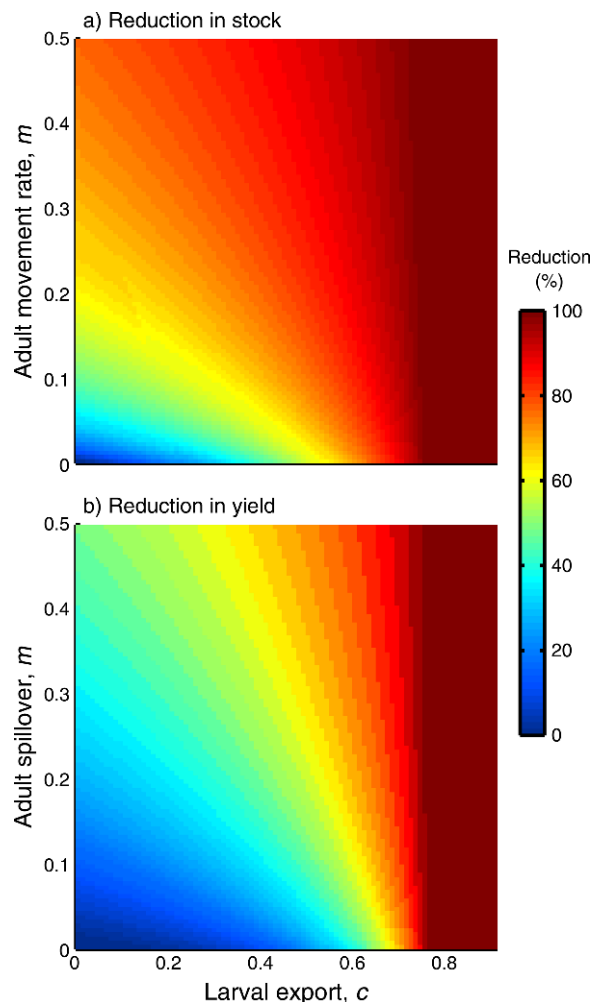


FIG. 3. Percentage reduction in (a) managed stock level and (b) fishery yield attained under noncooperative management compared with those under cooperation or sole ownership, evaluated in relation to rates of adult movement and larval export.

open access. Restricting the analysis to only consider TURFs >5 km wide severely limited adult spillover to $m < 5\%$ while only limiting larval export to $c < 80\%$ (see x -axes in Fig. 2), causing reductions in yield to be almost exclusively due to connectivity via larval dispersal. Qualitative and quantitative interpretation of the results did not change with consideration of recruitment of settlers to a juvenile stage prior to the adult stage or adult growth and increased fecundity with age, using the age-structured biomass model (see Appendix B for comparison of results).

In all five nearshore fishery species considered in the case study, stocks and yields were reduced considerably under noncooperative management across a range of TURF widths (Fig. 4). Reductions were severe (20–100%) when TURF width was <10 km. For kelp bass, California sheephead, and red urchin, species with relatively large home ranges but with the shortest PLDs, reductions in yield tapered to lower levels ($\sim 25\%$ in stock, $<10\%$ in yield) as TURF width approached 30 km. For blue rockfish and spiny lobster, whose PLDs were the longest at 2.6 and 7 months, respectively, reductions in stock and yield remained large for TURFs ≤ 30 km and only tapered to low levels for TURFs >50 km (result not shown).

DISCUSSION

Conservation and economic benefits of rights-based management programs may erode when ownership is not exclusive. This study demonstrates for nearshore fisheries how the level of exclusivity of ownership in a spatial property-rights-based management program is strongly contingent on movement rates of the fishery resource in relation to the size of the management unit. The potential for long-distance dispersal of the larval stage in particular can generate strong connections between management units and compromise ownership. Strategic responses by fishermen to compromised ownership leads to overly intensive local harvest rates and generates lower stock densities and unsatisfactory yields. Increasing resource connectivity between management units increases the reduction in stocks and yields, and, given enough connectivity, the situation reverts to open access. Described differently, infinitely large TURFs and/or targeting of immobile species allows for complete ownership of the natural resource within each TURF, promoting optimal harvesting practices that avoid overexploitation and maximize yield. Conversely, use of tiny TURFs and/or targeting of highly mobile species reduce stock ownership to near zero, resulting in intensive overharvesting akin to that found under open-access management. Scenarios in between these two extreme management conditions are represented by moderate-sized TURFs and targeting of species with moderate mobility levels. In these cases, ownership is partial and stocks and yields are an improvement over those under open access, but a reduction compared with MSY.

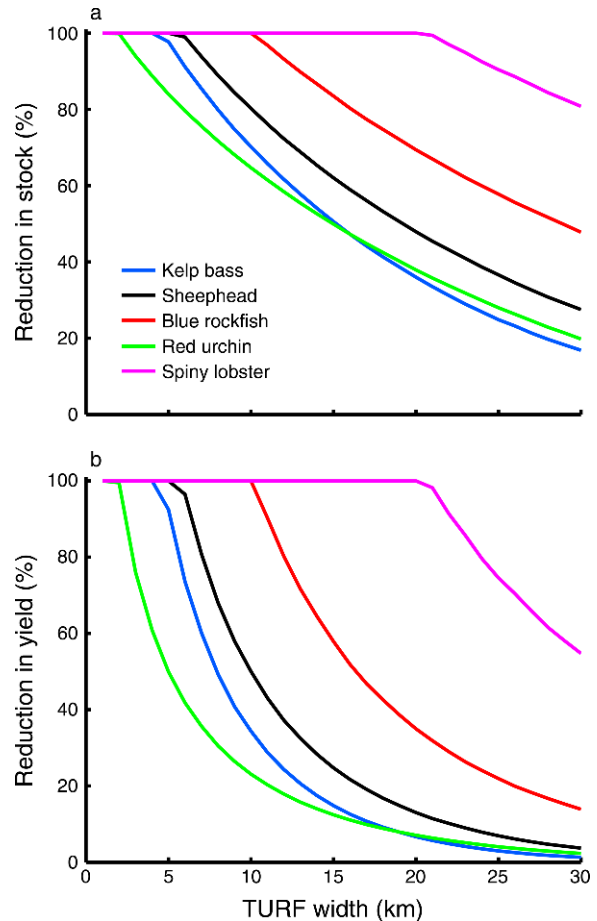


FIG. 4. Proportional reduction in (a) managed stock level and (b) fishery yield under noncooperative vs. cooperative spatial management for five nearshore fishery species in California, USA, in relation to territorial user rights fishery (TURF) width. See Table 1 for demographic values.

In considering differential effects of adult and larval movement we find reductions in stock and yield to be driven predominantly by the potential for long-distance dispersal of larvae. Other studies also emphasize the influence of connectivity caused by larval dispersal on stock size and fishery harvest (e.g., Botsford et al. 2001, Costello and Polasky 2008, Watson et al. 2010). However, scant empirical evidence for larval export between management units (Cudney-Bueno et al. 2009) and the conspicuousness and direct value of the adult stage encourage trivializing the potential effect of larval dispersal on spatial patterns of stocks and fishery yields. Yet, results suggest that expected yields will be overestimated when TURFs are scaled relative to adult home range size but stock ownership is gauged in relation to both adult and larval mobility. To highlight the solitary effect of variation in scales of connectivity on relative changes in stock and yield, we focused on symmetry among patches. Larval dispersal patterns are hardly expected to be symmetrical (Cudney-Bueno et al.



PLATE 1. California sheephead commercial fisherman near Los Angeles, California, USA. Photo credit: C. White.

2009, Mitarai et al. 2009). Results from bioeconomic modeling studies of marine reserves suggest that consideration of asymmetrical patterns of connectivity between TURFs may further reduce managed stock levels and yields when effort is not coordinated between patches (Gaines et al. 2003, Kaplan 2006).

We considered adult home range lengths 0–1 km, corresponding to the majority of nearshore tropical and temperate system fishery species that exhibit strong site fidelity within home range areas less than $\sim 10^5$ m² (Kramer and Chapman 1999, Botsford et al. 2009). Our calculations included several highly mobile fishery species (e.g., greasy grouper and giant trevally, with home range areas = 344 000 m² and 492 250 m², corresponding with estimated alongshore home range lengths = 662 m and 792 m, respectively [Botsford et al. 2009]), yet the effect of adult spillover on reductions in yield was still typically low compared with that by larval export. Although factors influencing connectivity not considered in this study (e.g., home range shape, migratory patterns) may increase the influence of spillover, results here suggest that for most nearshore fishery species the greatest reductions in yield in a region characterized by a network of neighboring TURF are due to larval dispersal.

One solution to the problem of reduced stocks and yields in a TURF system is to limit the lower bound of

escapement through exogenous regulation of harvest levels. Empirical examples exist in Japan and Chile where TURF systems are constrained by total allowable catches imposed at the federal level that maintain stock densities at presumably more productive levels than would occur otherwise (Cancino et al. 2007). Although this approach may increase long-term stocks and yields, it undermines the simplicity of spatial property rights management and introduces costs (e.g., administrative, enforcement) that need to be considered explicitly in the overall assessment of the program's efficacy. An alternative or supplementary remedy to reduced stocks and yields involves coordination among TURF agents in harvest strategies. In our analysis we consider only the extreme example of complete coordination, e.g., by a cooperative of TURF owners who share all yield. Others have shown how more moderate levels of coordination among agents can lead conditions away from the Nash equilibrium and toward greater economic returns (Costello and Deacon 2007). Incentives for coordination can be created by pooling yields or profits (Gaspart and Seki 2003) and/or driven exogenously (e.g., via regulation); a challenge is formalizing costs to contracting coordination and integrating them into the analysis of harvest strategies (Johnson and Libecap 1982, McCarthy et al. 2001, Potter 2003, Erdlenbruch et al. 2008). With TURFs, the level of coordination necessary

to achieve satisfactory returns will depend on management unit size and connectivity rates (C. Costello and D. Kaffine, *unpublished manuscript*). Within fisheries management and development policy, the importance of sustaining small-scale (thus, incidentally, highly connected) fisheries is being increasingly vocalized (Pauly 1997, Allison 2001, Prince 2003), placing a premium on effectively and efficiently organizing coordination in spatial property-rights-based management programs in order to mitigate lost returns.

Our model makes several important simplifying assumptions. In our estimation of larval export we assume passive transport, despite vertical migratory swimming behavior in many pelagic larvae and its potential effect on reducing dispersal distance (Marta-Almeida et al. 2006; but see Edwards et al. 2008, Siegel et al. 2008). We also assume no larval mortality during dispersal, which can reduce mean dispersal distance (Cowen et al. 2000), and for dispersal to be diffusive (i.e., non-stochastic). We avoid explicitly considering these processes because their quantitative effects on dispersal remain difficult to estimate and are specific to local oceanographic conditions. As a proxy, we mitigate overestimating larval export by considering the near-shore flow field to be conservatively calm (i.e., low fluctuating current velocity) when calculating the larval dispersal probability density function. Also, with specific regard to our case study that is focused primarily on species in southern California, the thermocline (where stratification occurs and velocity changes rapidly in speed and direction with depth) in the Southern California Bight is relatively deep (>50 m depth) compared with the lower depth range of many pelagic larvae exhibiting vertical migratory behaviors (e.g., Queiroga and Blanton 2005), and above the thermocline the current profile changes slowly with depth compared with other coastal regions (e.g., Caribbean continental shelf; Harms and Winant 1998, Andrade et al. 2003, Dong et al. 2009). Consequently, incorporating larval behavior in simulations of dispersal patterned after the California Current altered dispersal scales only minimally (Siegel et al. 2008). Thus considering vertical migratory behavior may only have a small influence on our case study results. Stochastic larval dispersal processes do not necessarily change the long-term dispersal pattern (e.g., mean distance), but they do introduce spatial patterns of directed dispersal that vary among locations from year to year (Mitarai et al. 2008). Maximizing yield when dispersal is stochastic (as opposed to diffusive) is especially sensitive to a management strategy's ability to explicitly control harvest dynamically across the entire spatial domain and over time (Costello and Polasky 2008). Such a strategy is only possible by a sole owner or with complete cooperation among TURFs. Consequently, consideration of stochastic larval dispersal may further reduce yields achieved under noncooperative management compared with those under cooperation or sole

ownership. We focus on fishery yield without consideration of the negative effects of cost of harvest on fishery gains (e.g., profit). Marginal cost of harvest may increase nonlinearly (e.g., exponentially) with decreasing local fish density (Clark 1990). Consequently, decreased Nash equilibria stock densities with increased connectivity could introduce exponentially larger harvest costs and thus greater proportional reductions in fishery profit due to connectivity than that suggested here. However, consideration of harvest cost in relation to stock density also generates an incentive for all fisheries to mitigate costs by harvesting less intensively (i.e., maintain higher escapement) than that presented here. How these two factors trade off in determining harvesting strategies and fishery profit in response to connectivity will depend on the form and severity of the harvest cost function. Our simple model without age structure assumed settlers recruit into fishable adults within a single year and for there to be no increase in adult biomass and fecundity with age. These assumptions contrast with true life history characteristics of nearly all fishery species, yet explicit consideration of these life history characteristics using an age-structured model did not change the results. Although population stage structure and individual growth are seen to influence fish population dynamics and fishery yield (Gaylord et al. 2005), these factors may be less important than often supposed in affecting strategies for maximizing fishery yield compared with other life history characteristics such as density dependence (White and Kendall 2007). In the context of this study, consideration of stage structure and fish growth had similar effects on the strategic decisions for maximizing yield by both noncooperative and cooperative (or sole owner) fisheries. Consequently, the relative differences in stock levels and associated yields resulting from their strategic decisions were no different than those found using the original (i.e., non-stage-structured) model.

Economic theory of natural resource management predicts the emergence of private property rights in fisheries (Hannesson 1991), and a growing body of empirical evidence suggests that fishing rights should have a central place in the fisheries management and conservation toolbox (Hilborn et al. 2005, Costello et al. 2008). However, establishing fishing rights is not a panacea to open access or common-property management, nor is any single style of rights-based program appropriate for all fisheries. Management based on spatial property rights can alleviate competition for high-value spatial units that hinders efficiency in quota-based, rights-based, and open-access fisheries, yet such gains may be partially eroded by the delineation of spatial rights with incomplete ownership that degrade the local value of the resource. This study highlights how TURF size and species mobility levels interact to determine the efficacy of spatial property rights management. We focused on managed stock levels and yields in a TURF system, compared with those expected under

open access at one extreme and sole ownership or perfectly cooperative management at the other extreme. Under certain conditions TURF management alone generates enough ownership to incentivize an improvement in management strategy over open access. However, for most nearshore fishery species the large dispersal potential of their larvae challenges the ability to secure resource ownership via spatial regulations. Consequently, when TURF size matches adult home range size only, spatial-rights-based management typically is not expected to maximize stock conservation or fishery economic outcomes without cooperation or additional controls. Assessing the costs of these controls and negotiations and quantifying the resulting net conservation and economic returns with their use in spatial right-based management of fisheries are key factors contributing to the evaluation of the efficacy and acceptability of catch share programs.

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APPENDIX A

Estimating adult spillover and larval export (*Ecological Archives* A021-020-A1).

APPENDIX B

Effects of stage structure and growth on managed stock levels and fishery yields (*Ecological Archives* A021-020-A2).