Quantifying the benefits of spatial fisheries management – An ecological-economic optimization approach

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ABSTRACT

Improving fisheries management is a key challenge in addressing the United Nations Sustainable Development Goal 2 (Zero Hunger) and support Goals 1 (No Poverty) and 14 (Life Below Water). However, sustaining the ocean's living resources has important dimensions beyond food security, such as cultural values, which might be of equal importance in some settings. Fisheries management faces special challenges when there is a mismatch between biological units and management units, e.g., when ecological spatial structures are not reflected in how catch limits are set. This might result in overexploitation and even the loss of sub-stocks. We use a spatially structured ecological-economic model parameterized for a pelagic schooling fish to examine how the benefits of implementing spatially differentiated fisheries management depend on biological parameters. We focus on a subset of socio-ecological variables, i.e., fisheries yield, present value of economic surplus, and loss of spawning sites (which might be linked to loss of cultural values) to demonstrate that, in theory, ideally differentiated spatial management can be implemented without exact information about recruitment behavior. For imperfectly differentiated spatial management, however, knowledge about recruitment behavior becomes key to avoiding economic losses and to sustaining stock structure, especially when there is large spatial heterogeneity in biological parameters. Knowledge about variability in site-specific productivity determines the expectation of achievable sustainable harvest levels. Further research on such ecological issues is therefore warranted, both for ecological as well as economic reasons.

1. Introduction

Populations of fishes, like many species, display spatial structure. Their dynamics are driven by spawning migrations, ontogenetic habitat shifts, as well as movement to feeding and overwintering sites (Harden Jones, 1968; Aro, 2002; Secor, 2002). Within fish populations, sub-stocks may exist in some fish, often with multiple spatially segregated and discrete spawning grounds and limited connectivity among them (Reich and DeAlteris, 2009). For some species, "stocks" and "sub-stocks" may not be genetically distinguishable and can be difficult to

identify. As a consequence, researchers working in different regions may define and use these terms inconsistently. Fisheries assessment and management often lack ecological or genetic detail, and stock sub-structure is often not considered. Additionally, when management is spatially explicit, the spatial scale of management may differ from the spatial structure of stock units (Cadrin and Secor, 2009). Accordingly, the International Council for the Exploration of the Sea (ICES) Stock Identification Methods Working Group (SIMWG; ICES 2016) stated that "Traditionally, exploited stocks have been assessed and managed according to geographical features and ICES subdivisions (i.e., "lines on a map"), in order to facilitate decision-making and agreements among countries." In other cases, such as for Pacific herring (*Clupea pallasii*), management may be delineated by general spawning locations or occur at the aggregate stock level; determining finer-scale sub-stock structure is not yet possible with currently available scientific methods.

Overexploitation of stocks can lead to loss of spawning grounds through ecological extinction of sub-stocks, which could reduce total productivity and subsequently impair full recovery (Schmidt et al., 2009). Additionally, the loss of sub-stocks can happen in fisheries that are deemed sustainable at the stock level, but in which individual sub-stocks cannot sustain the localized fishing intensity that occurs, for example, because of differences in access costs (Reich and DeAlteris, 2009). Despite the appearance of large-scale sustainability, local depletion and related losses in potential catch are clearly inconsistent with policy goals related to sustainable fishing as well as food security and wellbeing for adjacent coastal peoples and communities (e.g. United Nations, 2015). In such cases, spatial management tools may thus lead to greater sustainability and improved human well-being. However, spatial management comes with increased costs. For example, data needs are greater, and monitoring costs are correspondingly higher. Additionally, regulations associated with management are ostensibly more complex and may lead to increased implementation and enforcement costs.

Detailed knowledge of fish behavior is needed to better understand the importance of spatially-explicit spawning components, including how fish recruit into certain sites or sub-stocks. The assumption of random diffusion versus other concepts, e.g. entrainment (Petitgas et al., 2006, 2010), might considerably alter management outcomes, as a broad literature on harvesting (fish) metapopulations has shown (e.g., MacCall et al., 2018; Armstrong and Skonhoft, 2006; Bulte et al., 1999; Sanchirico and Wilen, 2001, 2005; Supriatna and Possingham, 1999). These studies typically focus on two patches connected by movement. However, in many cases fish populations occur in many patches, and knowledge about exact spatial patterns of recruitment is not readily available, or conclusions about recruitment behavior are disputed among experts, thus competing assumptions need to be examined.

In addition to the economic benefits of fisheries, much recent work has highlighted the importance of considering the ecological and socio-cultural consequences of fisheries (e.g., Halpern et al., 2013; Tahvonen et al., 2014; Marshall et al., 2017). Careful evaluation of the costs and benefits of spatial management requires accounting for the full suite of trade-offs among ecological, economic, and socio-cultural objectives (Marshall et al., 2017). We take a first step in this direction by evaluating trade-offs between a subset of social, ecological, and economic objectives—fisheries yield, present value of economic surplus, and loss of spawning sites (which, in some cases, is linked to loss of cultural values). Between socio-ecological-economic objectives including: yield, present value of economic surplus, and loss of spawning sites (which might be linked to loss of cultural values).

In this analysis we use a generic spatially-structured ecological-economic model to explore the ecological and economic importance of knowledge about spatial patterns in harvested fish populations, in order to investigate the hypothetical benefits of implementing spatially-differentiated fisheries management. The model that we use is heuristic and simplified, motivated by the fishery for Pacific herring. Using our generic spatially-structured model, we explore the consequences for

fisheries management and ecosystem objectives of alternative, and equally plausible, spatial recruitment behaviors; heterogeneity in spawning site productivity; and global versus spatially-explicit fisheries management regulations. Using this conceptual model (*sensu* Mangel et al., 2001; Mangel and Levin, 2005), we illuminate the broad consequences of these biological assumptions as related to fisheries yield and maintenance of spawning sites.

2. Material and methods

The bio-economic model has spatial structure with several (in the baseline model, $n = 50$) spawning components that are partially connected by diffusion of adults and recruits among adjacent spawning sites. The general set-up and biological assumptions follow MacCall et al. (2018); stock dynamics within each site are described by a Ricker-type stock-recruitment function, in which the density-independent parameter may vary spatially.

Recruitment to the adult stock of each spawning component occurs according to one of two behavior models. Under the diffusion reproductive strategy (DIFF), recruits are distributed in fixed proportions among habitats near their natal habitat and subsequently tend to return to those spawning locations. Under the "Go With the Older Fish" (GWOF, Fig. 1; MacCall et al., 2018) strategy, recruits join a school of older migrating fish (repeat spawners) and adopt that school's migration behavior, with subsequent homing behavior following the migration path and spawning location of those older fish. Thus, under GWOF strategy, first-time spawners recruit to the same set of spawning sites as DIFF recruits, but proportional to the relative abundances of repeat spawners currently using those sites (MacCall et al., 2018).

For each combination of recruitment behavior and fishing mortality, we perform 100 iterations of the model, each with randomly drawn spatial distributions for the density-independent productivity parameter, when assuming site-specific variability in productivity. Each run simulates a 100 year projection, assuring that a steady-state equilibrium is reached.

The spawning sites are assumed to be organized around a circle, and diffusion of recruits occurs to five sites, i.e., from site i to sites i, $i-1$, $i-2$, $i+1$ and $i+2$. Similarly, diffusion from site $i+1$ is to sites $i+2$ and
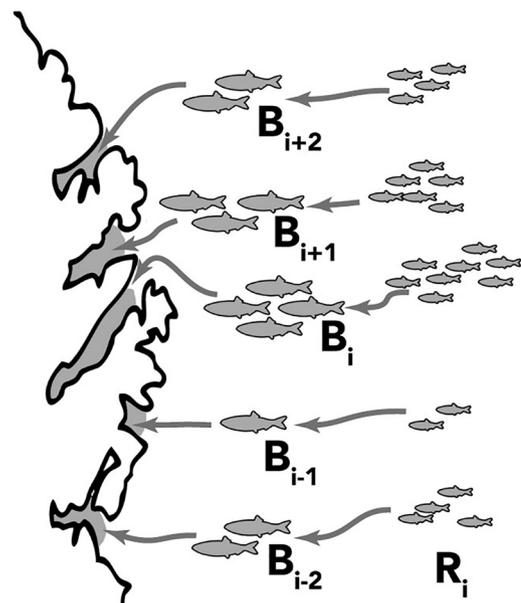

Fig. 1. Conceptual representation of the GWOF reproduction strategy: recruits adopt neighboring spawning sites in proportion to the relative abundances of older fish currently using those habitats. Recruits may stem from multiple spawning sites. The figure displays a small fraction of the circular spatial structure.

$i + 3$ as well as to sites i and $i − 1$. Returning spawners (adults) diffuse to three sites, i.e., if originating at site i, they can return to sites i, i-1, or i +1. This assumption of "periodic" or "circular" boundary conditions avoids boundary effects. The parameter L_i (as part of the Ricker stock-recruitment function) denotes site-specific, density-independent productivity.

Mathematical notation is as follows:

- biomass in sites $i = 1, ..., n$ is given by the vector B_t with elements B_{it}, with circular boundaries. To model this we extend the biomass vector with four extra elements set equal to the respective elements at the left and right boundaries of the vector, such that $B^{-1} \equiv B^{n-1}$, $B^0 \equiv B^n$, $B^{n+1} \equiv B^1$, $B^{n+2} \equiv B^2$. We need four such elements – two to the left and two to the right – to capture dispersal to the respective next and second next neighbor.
- Δ a matrix with elements $\Delta_{it} = \alpha \times (1 − 2\delta)$, $\Delta_{i,i-1} = \Delta_{i-1,i} = \alpha \times \delta$ and all other entries zero describes diffusion of adult fish. We set the overall survivability from natural mortality to $\alpha = 0.7$ and diffusion to $\delta = 0.1$ in the baseline parametrization. This means that 80% of adult fish remain in their current site, while 10% diffuse to the site to the left and another 10% to the site on the right (including the effects of the circular boundary).
- $R_t = \Phi(B_t)$ a vector of recruits with element i being the Ricker stock-recruitment function for site i, $\Phi_i(B_t) = B_{it} \exp(L_i − \varphi − \beta B_{it})$, having parameters $\beta = 0.01$ and L_i (as well as φ) set to zero in the scenario with homogeneous sites and assigned random numbers from a uniform distribution on $[−\sigma, \sigma]$, with σ varying between 0 and 1, or set equal to 1, in the scenario with heterogeneous site-specific productivities. At maximum heterogeneity the most productive sites are ca. 7.4 times more productive as compared to the least productive sites. We set φ such that $E[\exp(L_i − \varphi)] = 1$ [1] to keep the expected productivity for each site at the same level as for the case with fixed homogeneous site-specific productivity. For a particular randomly drawn set of productivity parameters the average productivity over sites can differ from the constant site-specific productivity. Diffusion of recruits in the DIFF model is described by a $(n + 4) \times (n + 4)$ matrix D with elements equal to zero except

$$D_{ii} = \frac{3}{9}$$

$$D_{i,i-1} = D_{i,i+1} = \frac{2}{9}$$

$$D_{i,i-2} = D_{i,i+2} = \frac{1}{9}$$

Circular boundaries are modeled by including diffusion from sites 1, and 2 to n, and n-1, and the other way around. We use the $(n + 4) \times (n + 4)$ matrix with two rows and two columns added at each border of the 'interior' $n \times n$ diffusion matrix to model these circular boundary conditions. Consequently, biomasses are described by an n +4-dimensional vector, where the first two elements are always identical to elements $n + 1$ and $n + 2$, and the last two elements are always identical toe elements 3 and 4. Thus, the elements 3 to $n + 2$ are the relevant, 'interior' biomasses.

- For the GWOF model, migration of recruits is described by a $(n + 4) \times (n + 4)$ matrix $G(B_t)$ with dispersal from i to j given by

$$G_{ij}(B_t) = \frac{B_{jt}}{B_{i-2,t} + B_{i-1,t} + B_{it} + B_{i+1,t} + B_{i+2,t}} \text{ for all } i \text{ and } j$$
$$\in \{i − 2, i − 1, i, i + 1, i + 2\}$$

Again, circular boundaries are modeled by including diffusion from sites 1, and 2 to n, and $n − 1$, and the other way around as above.

Biomass dynamics subject to harvesting are, in matrix notation:

$$B_{t+1} = \Delta E_t + DR_t \text{ in the "DIFF" model} \tag{1}$$

$$B_{t+1} = \Delta E_t + G(E_t)R_t \text{ in the "GWOF" model} \tag{2}$$

where Δ, D, and G are the matrices introduced above, $E_{it} = (1 − F_{it})B_{it}$ is "escapement" for site i at time t with fishing mortality Fit[2], i.e., Et is the biomass remaining after harvesting, and Rt = $\Phi(Et)$ is the recruitment produced by that biomass. As an initial condition we set the biomass in all sites equal to 100, i.e., the biomass where the Ricker stock-recruitment function peaks in expectation. In all of our computations, the steady state was unique and globally stable. Thus, assumptions regarding the initial biomass distribution have no impact on the steady state results. Yield levels can be interpreted with respect to this biomass. As this is a conceptual model, biomass as well as yield are handled without dimension.

We consider a schooling fish, and set the fish price – net of constant marginal harvesting costs – equal to one (Tahvonen et al., 2013). We consider the management objective to maximize the present value of economic surplus for the entire fishery. For the management scenario where fishing mortality is chosen independently for each site and time step, the optimization problem is:

$$\max_{\{E_{ij}\}} \sum_{t=0}^{\infty} \rho^t \sum_{i=1}^{n} (B_{it} − E_{it}), \tag{3}$$

that is, to maximize the present value of yield, discounted at a discount factor ρ (i.e. the discount rate is $\frac{1−\rho}{\rho}$). The model is implemented in Matlab and code is available in the online Supporting material.

We consider three scenarios for both recruitment behavior models (Table 1):

First, the model is used to compare the two alternative recruitment behavior scenarios, DIFF and GWOF, while spawning sites are assumed to be homogeneous and management ignores spatial structure (i.e., fishing mortality F is the same for all sites, hereafter termed "global F"). In this scenario, the density-independent parameter of the Ricker stock-recruitment function is pre-specified. The model is run for 100 years, and model output is used to construct a yield curve for the F range of 0–0.6. Here we ask the question: "How does the assumed recruitment behavior affect steady-state yield and the associated fishing mortality?"

In a second scenario, management is still assumed to be "global", but we additionally allow for heterogeneity in spawning site productivity, i.e., the density-independent parameter may vary spatially. Variation in productivity involves assigning a value randomly drawn from a uniform distribution. We perform 100 iterations of the model for each combination of recruitment behavior and fishing mortality. As before, results are used to construct yield curves over the range F = 0–0.6. Again, we determine optimal steady-state yields, and economically optimal exploitation rates (used here as a proxy for a management measure that limits fishing mortality, such as a spatial quota). Additionally, we calculate the number of "lost" spawning sites: A site is defined as being "lost" if its biomass drops below 10% of the biomass that would produce the maximum sustainable yield for that site, i.e., fishing at FMSY[3]. To explore the effect of the model assumptions, we perform a sensitivity analysis with respect to the number of sites n, the

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[1] This means, we set $\varphi = \ln([\exp(L_i)]) = \ln\left(\frac{1}{2\sigma} \int_{-\sigma}^{\sigma} \exp(L) dL\right) = \ln\left(\frac{1}{2\sigma}(\exp(\sigma) − \exp(−\sigma))\right)$.

[2] Strictly speaking this is an exploitation rate, as fishing mortality is in continuous time. Since there is a monotonic relationship between the two, we use the term fishing mortality for F_{it}.

[3] This doesn't necessarily reflect current fisheries practice, e.g. Pacific herring fisheries, where current F is assumed to be below F_{MSY}.

Table 1

Overview of model scenarios and corresponding results sections. DIFF denotes the diffusion reproductive strategy, GWOF denotes the "Go With the Old Fish" behavior assumption. See text for details.

Productivity of spawning sites	Spatial behavior of recruits	
	DIFF	GWOF
Homogeneous	Global *F* management Question: Impact of reproduction strategy on yield curve & optimal F Section 3.1	
Heterogeneous	Global *F* management Question: Impact of reproduction strategy on yield curve, optimal F, & loss of spawning sites Section 3.2 Local *F* management (site-specific) Question: Analytical results & quantification of benefits in yield and protection of spawning sites Section 3.3	

natural survivability α, and the diffusion rate δ to explore how the results depend on the parametrization of the numerical model.

The third scenario allows for fully spatially explicit management (i.e., setting site-specific fishing mortality *F*, hereafter referred to as "local *F*"; Table 1). Here, the model is analytically solved for the special case of optimal local *F* for heterogeneous sites. We also quantify potential benefits of spatially differentiated ("local") management compared to spatially homogeneous ("global") management, by varying the degree of spatial heterogeneity of spawning sites. Benefits are quantified in terms of both surplus yield and loss of spawning sites. We maintain the assumption that recruitment parameters are randomly drawn from a uniform distribution, but vary the range of the uniform distribution, keeping average productivity fixed. We refer to the upper bound of the range (equal to the absolute value of the lower bound) as the "spread" of site productivities. We perform 100 model iterations for each value of spread, with the optimal exploitation rate computed for each site at each iteration.

The results are presented in three sections, one for each scenario.

3. Results

3.1. Homogeneous productivity of spawning sites

The spatial recruitment mechanism, i.e. DIFF versus GWOF, has no effect on fisheries management or ecosystem objectives if all spawning sites are equally productive (no spatial structure, also in terms of fishing mortality, termed "homogeneous" in Table 1 & Fig. 2). Steady state harvest follows an almost symmetric concave function, with positive long-term harvest for fishing mortality up to a value $F_{crit} = 0.41$.[4] Higher fishing mortality than F_{crit} results in stock collapse in our idealized fishery. Optimal yield is equal for both models and optimal fishing mortality under these assumptions is $F_{hom} = 0.23$.[5] Two thirds of the maximum yield could be realized within the range of $F = 0.1$ to $F = 0.35$.

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[4] In the homogeneous case, equilibrium biomass is the same for all patches and described by equations 1 and 2. With exploitation rate *F,* natural survivability α and the parameter β of the Ricker function it is given by $B_{eq} = -\frac{1}{\beta(1-F)}\ln\left(\frac{1-\alpha(1-F)}{1-F}\right)$. It becomes zero when $F = F_{crit} = 1/\alpha - 1 = 1/0.7 - 1 = 0.41$.

[5] F_{hom} is the value of *F* that maximizes equilibrium yield $F B^{eq}(F) = \frac{F}{\beta(1-F)}\left(L - \varphi - \ln\left(\frac{1-\alpha(1-F)}{1-F}\right)\right)$ for the homogeneous case L-$\varphi = 0$, which is $F_{hom} = 0.233$ with harvest level $F_{hom} B_{eq} = 15.32$ for $\alpha = 0.7$ and $\beta = 0.01$.
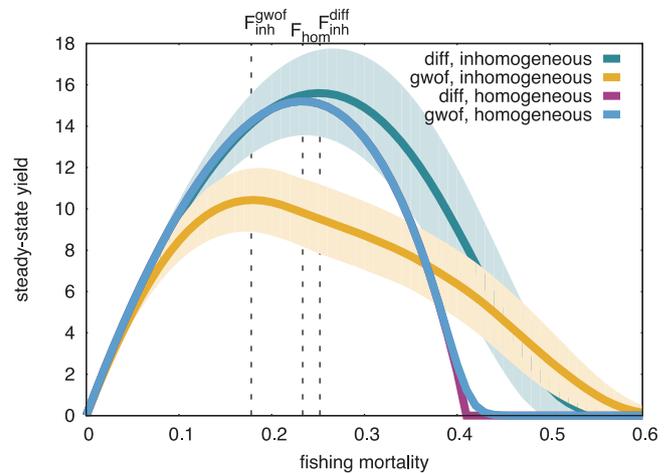

Fig. 2. Mean steady-state yield per site as a function of spatially uniform fishing mortality: results for two spatial recruitment models (DIFF versus GWOF, see methods), assuming either homogeneous or spatially-heterogeneous productivity of spawning sites. Results assuming inhomogeneity are displayed as mean (line) and one standard deviation (shaded area) of 100 model iterations. Vertical dashed lines indicate optimal fishing mortality for the assumptions of homogeneous sites (F_{hom}; both recruitment models lead to identical results), or heterogeneous sites using the DIFF recruitment behavior model (F_{inh_diff}) and GWOF behavior model (F_{inh_gwof}). Results are shown for the benchmark parametrization where $n = 50$, $\alpha = 0.7$, and $\delta = 0.1$.

3.2. Heterogeneous spawning sites – no spatial management

Results become more complex for the heterogeneous spawning sites scenario. Here, the DIFF strategy results in a slightly higher optimal yield as compared to the DIFF strategy with homogeneous sites, which is realized at a global exploitation rate of $F = 0.254$ (Fig. 2). As with homogenous productivity, the steady state yield curve is symmetric and concave. Variability in results from the 100 iterations with randomly drawn local density-independent productivity parameters is relatively large: one standard deviation covers a harvest range of 13.5–17.5 near the optimal *F*. The GWOF strategy in a system with heterogeneous habitats results in markedly reduced achievable steady-state harvest. Optimal *F* is lower (0.179), and the shape of the yield function becomes left-skewed.

In this scenario, optimal global F (i.e., management without spatial differentiation) depends on the biological setting. Assuming incorrect recruitment behavior might either lead to overfishing, or to underutilization, of the resource. Opportunity costs (i.e., a benefit that a person could receive, but gave up to take another course of action) of incorrectly applying spatial management rules are relatively low (see Discussion).

The DIFF migration strategy results in robustness of stock components to overfishing over a wide range of fishing mortality, i.e., up to a *F* of > 0.3 (Fig. 3). Managing for the optimal *F* (independent of the assumptions made regarding recruitment behavior) would never deplete any spawning component. However, under the GWOF strategy, an increasing *F* will lead to an increasing number of collapsed sites. Fishing mortality producing optimal harvest (in terms of biomass) would lead to ca. 19% of collapsed sites for the GWOF hypothesis. If management (wrongly) used the optimal *F* estimated based on the DIFF assumption, this would double to almost 40%.

Reducing the number of sites to $n = 20$ (shown in Fig. 4, panel a), or increasing it to $n = 100$ (panel b) has hardly any effect on expected outcomes, but increasing the number of sites clearly reduces variability due to spatial variation in productivity. Reducing dispersion to $\delta = 0.05$ (panel c), or increasing it to $\delta = 0.2$ (panel d), has hardly any effect in the homogeneous setting or in the heterogeneous setting for the DIFF model. In the GWOF model, reducing dispersion reduces
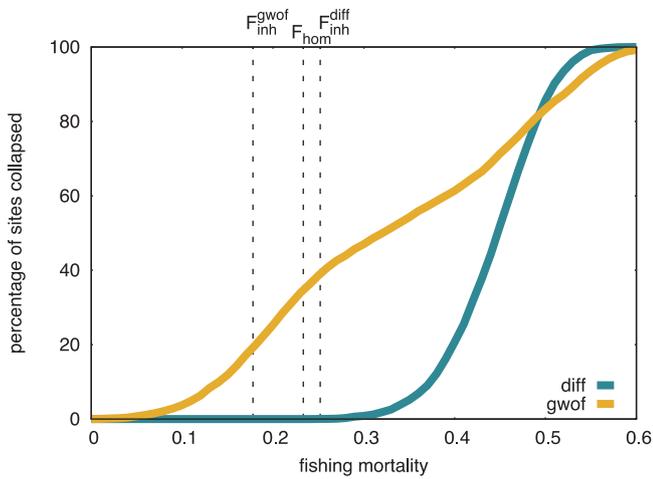
Fig. 3. Loss of spawning sites as a function of fishing mortality (average over 100 model runs for each level of fishing mortality), assuming heterogeneous spawning sites and either DIFF or GWOF recruitment behavior models. Optimal fishing mortality for different ecological assumptions are indicated by dashed lines: (F_{inh_diff}) indicates DIFF recruitment behavior model, and (F_{inh_gwof}) indicates GWOF behavior model.
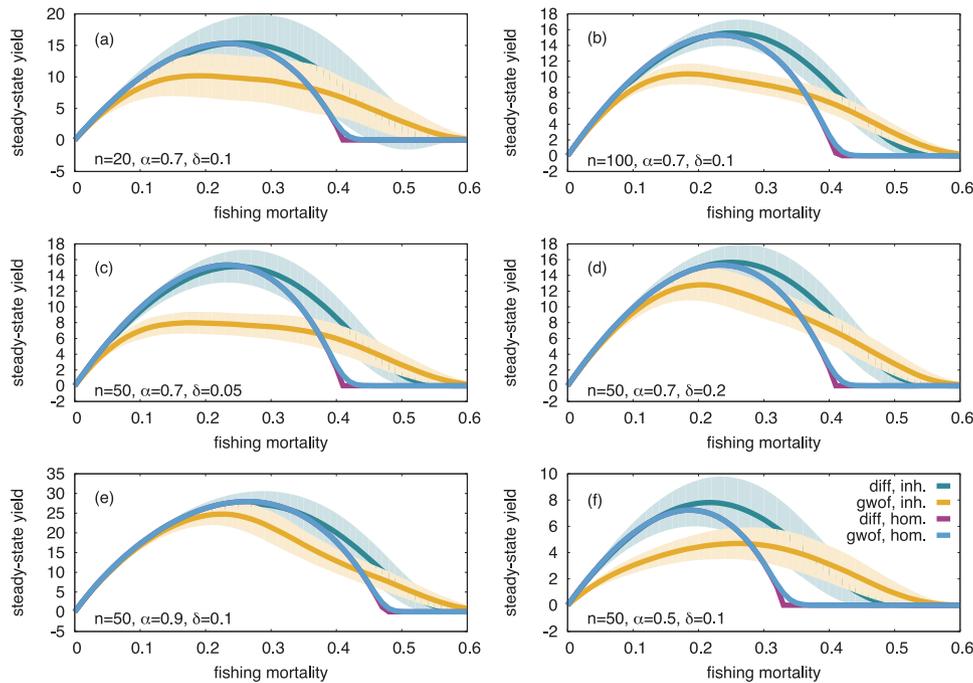
3.3. Optimal local F management

3.3.1. Analytical results

For the idealized case of optimal local *F* management, in which the fishing mortality is fixed for each spawning component individually, the assumed recruitment behavior model does not play a role, and knowledge about the recruitment behavior would accordingly not be needed for management purposes. This can be shown analytically as outlined below.

If the biomass dynamics are sufficiently fast (to exclude a corner solution), the optimal solution is a "constant escapement" strategy. The reason is that the state of the populations in all patches can be fully controlled by choosing the escapement levels, and thus the condition for the optimal next period's population sizes is independent of the current population size. We omit the proof, which follows the standard approach in the literature (e.g. Costello and Polasky, 2008). With the GWOF assumption, optimal constant escapement levels are given by the condition:

$$1 = \rho \frac{\partial}{\partial E_{kt}} \left(\sum_{i=1}^{n} \sum_{j=1}^{n} \left(\Delta_{ij} E_{jt} + G_{ij}(E_t) E_{jt} \exp\left(L_j \beta E_{jt}\right) \right) \right) \tag{4}$$

Condition 4 states that the marginal benefit of immediate harvest –

Fig. 4. Sensitivity analysis with respect to the number of sites (n = 50 in the baseline), natural survivability (α = 0.7 in the baseline), and diffusion rate (δ = 0.1 in the baseline). Fishing mortality *F* is held constant over sites.

maximum yield, and increasing dispersion increases the maximum yield, with less pronounced effects at fishing mortalities below or above the corresponding F_{MSY}. Increasing natural survivability to α = 0.9 (panel e) shifts the fishing mortalities that generate the maximum sustainable yield (and the fishing mortality where the fishery collapses in the homogeneous case) to larger values, and increases yields. In the GWOF model, the peak of the yield curve becomes more pronounced at high α. Decreasing natural survivability to α = 0.5 (panel f) decreases yields and shifts the fishing mortalities that generate the maximum sustainable yield (and the fishing mortality where the fishery collapses in the homogeneous case) to smaller values for all models except for the GWOF model in the heterogeneous case. In the GWOF model, yields decrease as well, but the fishing mortality that generates the maximum sustainable yield increases.

the fish price net of constant marginal harvesting costs set equal to one – on the left-hand side of the equation should equal the marginal benefit of leaving an extra unit of biomass in the ocean. This marginal benefit is given by the expression on the right-hand side of Eq. (4). It is the marginal increase in catches from all patches $i = 1,…,n$ that arises from a marginal increase in biomass of the fish stock in all patches $j = 1,…,n$ to which the patches *i* are connected by migration, due to the marginal increase of the escapement E_{kt} at site *k*. As the benefit arises one period in the future, it is discounted by the factor ρ. Using the fact that marginal benefits from harvesting are the same across patches, this condition can be substantially simplified. Rearranging we obtain:

$$
\begin{aligned}
1 &= \rho \sum_{i=1}^{n} \left(\Delta_{ik} + G_{ik}(E_t)(1 - \beta E_{kt}) \exp(L_k - \beta E_{kt}) \right. \\
&\quad \left. + \sum_{j=1}^{n} \frac{\partial G_{ij}(E_t)}{\partial E_{kt}} E_{jt} \exp(L_j - \beta E_{jt}) \right) \\
&= \rho \left(\alpha + (1 - \beta E_{kt}) \exp(L_k - \beta E_{kt}) \right. \\
&\quad \left. + \sum_{j=1}^{n} E_{jt} \exp(L_j - \beta E_{jt}) \sum_{i=1}^{n} \frac{\partial G_{ij}(E_t)}{\partial E_{kt}} \right) \\
&= \rho \left(\alpha + (1 - \beta E_{kt}) \exp(L_k - \beta E_{kt}) \right. \\
&\quad \left. + \sum_{j=k-2}^{k+2} E_{jt} \exp(L_j - \beta E_{jt}) \sum_{i=j-2}^{j+2} \frac{\partial G_{ij}(E_t)}{\partial E_{kt}} \right) \\
&= \rho \left(\alpha + (1 - \beta E_{kt}) \exp(L_k - \beta E_{kt}) + \sum_{j=k-2}^{k+2} E_{jt} \exp(L_j \right. \\
&\quad \left. - \beta E_{jt}) \left(\frac{1}{\sum_{i=j-2}^{j+2} E_{jt}} - \frac{\sum_{i=j-2}^{j+2} E_{it}}{\left(\sum_{i=j-2}^{j+2} E_{it}\right)^2} \right) \right) \\
&= \rho \left(\alpha + (1 - \beta E_{kt}) \exp(L_k - \beta E_{kt}) \right) \qquad (5)
\end{aligned}
$$

The same condition is obtained for the optimal escapement levels in the DIFF model. We thus have the following result:

Proposition 1. *Optimal, spatially differentiated management is identical under the DIFF and GWOF models.*

Human time-preferences are captured in bio-economic models by setting discount rates. Positive discount rates imply that realizing catches today is more valued than taking the same amount of fish at a later point in time. This seems to be a reasonable assumption, both under economic considerations as well as acknowledging the highly uncertain conditions in many fisheries. It is straightforward to show that the optimal escapement in each site decreases with the discount rate (i.e., increases with the discount factor). For no discounting, we obtain the corollary that all sites are harvested according to the respective site-specific maximum sustainable yield if there is no discounting, i.e. if $\rho = 1$:

Proposition 2. *Optimal, spatially differentiated management with no discounting, $\rho = 1$, is achieved when harvesting each patch according to its individual maximum sustainable yield, ignoring spatial movement.*

3.3.2. Economic benefits of applying optimal local F management

We now turn to the question how much harvest might be gained if spatially differentiated management optimally adapted to local productivities could be used. The potential benefits from the fishery rise with increasing spatial spread in productivity, following a convex function, i.e. local *F* management is increasingly rewarding if local differences in site-specific productivity are pronounced. When the spread of productivity reaches one, mean steady-state harvest could be increased by ca. 15% (Fig. 5), while no spawning components would be lost (see Section 3.2). The reason that yield increases with variability is that spatially-differentiated management adapts to the productivity of sites and thus can take advantage of more productive sites compared to the homogeneous case with equal average productivity. For the case without discounting, this can be easily demonstrated analytically: in this case the optimal spatially differentiated management is to harvest each patch according to its individual maximum sustainable yield, ignoring spatial movement. Maximum equilibrium yield (see footnote 6) is a convex function of site productivity, as the following argument shows
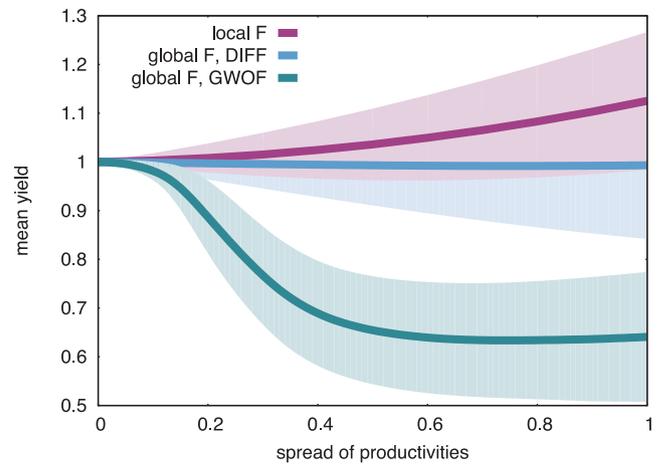

Fig. 5. Potential benefits of applying optimal spatially differentiated ("local") management compared to spatially homogeneous ("global") management, varying the degree of spatial heterogeneity of the spawning sites' productivity. Mean yield per site normalized to 1 for homogeneous sites. Increasing spread of productivities indicates increasing differences between sites. Mean (line) as well as standard deviation (shaded area) of 100 model runs.

$$
\frac{d^2}{dL^2}\left(\underbrace{\frac{F^{MSY}}{\beta(1-F^{MSY})}\left(L - \varphi - \ln\left(\frac{1-\alpha(1-F^{MSY})}{1-F^{MSY}}\right)\right)}_{F} \right) = \frac{d}{dL}\frac{F^{MSY}}{\beta(1-F^{MSY})}
$$

$$
= \frac{\frac{dF^{MSY}}{dL}}{\beta(1-F^{MSY})^2} > 0.
$$

Here, FMSY is the maximum sustainable yield fishing mortality which? is increasing in site productivity L. To derive the first equality we have used the Envelope Theorem, where the derivative of equilibrium yield with respect to FMSY is zero, as this is exactly the value of F that maximizes equilibrium yield. Thus, harvest from the more productive sites more than proportionally contributes to aggregate yield.

By contrast, the mean yield decreases with spatial heterogeneity applying a spatially homogeneous exploitation rate equal to the MSY level at the expected productivity – for the reasons discussed in Section 3.2. The benefit of spatially differentiated, local management thus increases with the spread of site productivities.

Fig. 5 shows the variability across model runs. As productivities are drawn randomly, spatial variability can also lead to an overall reduction in catches even with local *F* management. For the largest value of the spread, the catches of the least productive site are on average (over model runs) 0.36% of the average catches (over sites), for the most productive site, catches are 370% of the average over sites.

4. Discussion

Our results provide the methodological basis to quantify and evaluate potential economic and conservation benefits of applying spatially-explicit fisheries management. Furthermore, we analyze the risks associated with assuming incorrect migration behavior, and quantify the potential economics gains if such knowledge becomes available. Our work thereby offers general insights, rather than providing tactical management advice, and we discuss these below.

We explore two contrasting scenarios to describe migrational behaviour, which we consider to be simplified, but plausible, alternative assumptions. The DIFF scenario is behaviorally neutral, and applies basic diffusion rules founded in physics. On the other hand, the GWOF scenario incorporates active behavior of recruits and is based on the concept of "entrainment" (e.g. Corten, 2002; Petitgas et al., 2006). Both the GWOF and DIFF scenarios could result in observations for herring-like stocks, i.e. complex population structure without genetic

differentiation, variable migration patterns, or archaeological spatial patterns of herring abundance (Dickey-Collas et al., 2009; McKechnie et al., 2014). The GWOF behavior is consistent with traditional knowledge of Pacific herring, indicating that local spawning may consist of mixed or sequential waves of separate sub-stocks (MacCall et al., 2018).

Both migratory strategies incorporate homing to preferred spawning areas, which need not be the natal site in either case. In our simplified model, the distribution of recruits is limited to a local window of five adjacent sites. However, the spatial distances over which either mechanism would operate in actual fish populations are presently unknown. We have also considered symmetrical exchanges between sites. How other types of spatial movement (e.g., source-sink dynamics) would play out is still an open question.

In our model, optimal local F management becomes progressively more beneficial with increasing spatial variability in productivity. We estimate potential gains in yield of up to 15% in our theoretical setting. Under optimal local F management, knowledge of the underlying recruitment behavior is not relevant: each local site would be managed according to its maximum sustainable yield, ignoring spatial redistribution of adults and recruits. This theoretical result provides a reference point for optimal spatially differentiated management. Given the assumptions that the marginal net benefits of fishing are the same across patches (as prices and marginal costs are assumed to be spatially homogeneous) and that management is only concerned with total catch, the manager may not care from which patch the catch comes. The total catch is maximized by adjusting stock sizes in all patches, such as to maximize surplus production before spatial movement. Previous work on optimal fishing under biological uncertainties suggests that levels of optimal fishing mortality are fairly robust to uncertainties in, for example, the parameters of the recruitment function (Kapaun and Quaas, 2013; Tahvonen et al., 2017).

The spatial recruitment behavior would influence the optimal spatial management of the fishery if it matters from which site the catch is taken (for example if prices differ, transport costs matter, protecting local sites for traditional harvest is a priority, or distributing catch to avoid ecological implications of overharvesting individual patches is a priority). However, such theoretical optimal solutions for spatial management would require perfect, spawning site-specific implementation – a condition difficult to be met in reality.

If optimal local F management cannot be implemented (e.g. due to lack of administrative resources), the underlying migration behavior of recruits and adult fish becomes important. Unfortunately, migration behavior is unknown for many fish stocks and has been recognized as important and ongoing field of research (McQuinn, 1997; Huse et al., 2002; Petitgas et al., 2010; Planque et al., 2011). Therefore, a precautionary approach to the development of fisheries policy would be to adopt the scenario with the least negative impacts. For high natural survival rates ($\alpha = 0.7$ and $\alpha = 0.9$), the lowest risk is associated with the GWOF migration behavior hypothesis, and fishery managers would need to apply lower F values, as a less productive stock is implied. If the major management objective was to minimize the loss of spawning grounds, a maximum F of ca. 0.08 would be chosen, resulting in site losses < 5% (Fig. 3; Table 2). Maximum yield policies under the GWOF

recruitment behavior assumption would allow for $F = 0.18$ (Fig. 2). However, this relatively small increase in yield, as compared to yield under $F = 0.08$, would be accompanied by an approximately 15% loss of spawning sites (Fig. 3; Table 2). If management set $F = 0.23$ (the optimum F with DIFF recruitment hypothesis; Fig. 2) while in reality fish behave according to the GWOF model, this would result in a loss of 35% of all spawning sites, and a reduction of total catches (Table 2). The absolute values of fishing mortality discussed here relate to our theoretical example. They will change if ecological (e.g. natural mortality rates, diffusion rates) or economic (e.g. costs) conditions differ. Management could allow for higher F, and optimal yield limits could approximately be doubled without risking the loss of any spawning grounds if biological research could verify the DIFF migration behavior as the underlying process. Therefore, such quantification of potential benefits as well as the risks of adopting the wrong biological hypothesis might inform decisions on future research priorities.

We focused on *optimal yield* (involving ecological and social concepts) as our management objective. However, setting sustainable fishery harvest limits is only one element of Ecosystem-Based Fishery Management (EBFM) (Marshall et al., 2017). Here we show that spatial structure of fish populations is linked to optimal yield regulations, and that optimal yield management based on incorrect ecological assumptions can lead to overexploitation and local stock depletions. Spawning site loss will disproportionately affect harvesters and people from place-bound communities that do not or cannot move widely to alternative sites (i.e., small-scale commercial harvesters and/or those who harvest for food, social, ceremonial purposes). There is a further, hidden problem with losing individual spawning sites, and that is the risk of loss of the behavior associated with that site. This problem was investigated by Huse et al. (2010), who found that migratory knowledge begins to be lost when the fraction of repeat spawners was reduced below about 30%, and destruction of the behavioral knowledge became certain at 10%. Nevertheless, optimal yield (involving ecological and social concepts) remains a valuable concept, as it provides an existing governance framework for the operationalization of EBFM, by requiring that fisheries balance ecological, economic, and social goals (Patrick and Link, 2015).

Using optimal yield (OY) within an EBFM framework by definition (and statute) requires a multiobjective approach, and a challenge in operationalizing the use of multiattribute decision tools is identifying the objectives with which to measure performance of each potential strategy (Patrick and Link, 2015). This should be a multi-step process, starting with first bounding the problem, or essentially identifying the stakeholder groups and objectives to include in any tradeoff analyses (Levin et al., 2016). Knowing the specific social, ecological and economic objectives of different stakeholders, it is then possible to craft management strategies that attempt to meet these goals. In the U.S. management system, for instance, MSY is estimated first and subsequently, quota can be reduced below MSY in order to achieve other objectives (Patrick and Link, 2015).

Successful non-spatial fisheries management, e.g., applying uniform fishing mortality across sites, should be predicated on understanding spatial dynamics of fish populations, especially recruitment. Otherwise, economic benefits might be wasted either by overfishing (losing yield and spawning sites by wrongly assuming DIFF behavior) or by being overly precautionary (wrongly assuming GWOF behavior). In this case, knowledge of recruitment behavior might increase allowable long-term catches by ca. 100% (Table 2). Conservation of spawning sites, eventually even of low productivity sites, might in some cases be economically sub-optimal. It might, however, be of considerable importance when socio-cultural objectives are included, e.g. the interest of indigenous fisheries (Levin et al., 2016).

We should, however, be aware that applying uniform fishing mortality across sites is actually a special form of spatial management as F is forced to be similar across sites, when in practice global management using TACs does not ensure that removals occur at the same proportion

Table 2
Management outcomes for different levels of global fishing mortality F associated with two recruitment behavior hypothesis, GWOF and DIFF (see text for details).

	GWOF		DIFF	
F	Lost sites	Yield	Lost sites	Yield
0.08	< 5%	7.5	0%	8
0.18	19%	10.2	0%	14
0.23	39%	9.5	0%	15.6

of the biomass across sites.

Further research concerning migration behavior, site-specific productivity, and spatial structures of exploited fish populations is warranted for Pacific herring as well as other species (Levin et al., 2016). As long as such crucial knowledge is missing, precautionary management should aim at lower *F* and lower yield targets.

Acknowledgements

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