Accounting for spatial complexities in the calculation of biological reference points: effects of misdiagnosing population structure for stock status indicators[1]

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Abstract: Misidentifying spatial population structure may result in harvest levels that are unable to achieve management goals. We developed a spatially explicit simulation model to determine how biological reference points differ among common population structures and to investigate the performance of management quantities that were calculated assuming incorrect spatial population dynamics. Simulated reference points were compared across a range of population structures and connectivity scenarios demonstrating the influence of spatial assumptions on management benchmarks. Simulations also illustrated that applying a harvest level based on misdiagnosed spatial structure leads to biased stock status indicators, overharvesting, or foregone yield. Across the scenarios examined, incorrectly specifying the connectivity dynamics (particularly misdiagnosing source–sink dynamics) was often more detrimental than ignoring spatial structure altogether. However, when the true dynamics exhibited spatial structure, incorrectly assuming panmictic structure resulted in severe depletion if harvesting concentrated on more productive population units (instead of being homogeneously distributed). Incorporating spatially generalized operating models, such as the one developed here, into management strategy evaluations will help develop management procedures that are more robust to spatial complexities.

Résumé : La caractérisation erronée de la structure spatiale de populations peut se traduire par des niveaux de prises ne permettant pas l'atteinte d'objectifs de gestion. Nous avons développé un modèle de simulation spatialement explicite pour déterminer comment des points de référence biologiques varient entre différentes structures de population répandues et pour étudier la performance de quantités établies pour la gestion dont le calcul repose sur une dynamique spatiale de la population incorrecte. Les points de référence simulés ont été comparés entre différentes structures de population et différents scénarios de connectivité qui démontrent l'influence d'hypothèses spatiales sur les points de référence de gestion. Les simulations illustrent également le fait que l'application d'un niveau de prises reposant sur une structure spatiale mal caractérisée mène à des indicateurs biaisés de l'état des stocks, à la surpêche ou à des pertes de rendement. Pour l'ensemble des scénarios examinés, le fait de spécifier incorrectement la dynamique de connectivité (en particulier la caractérisation erronée d'une dynamique source–puits) est souvent plus nuisible que le fait de ne pas tenir compte de la structure spatiale. Cependant, dans les cas où la dynamique réelle présente une structure spatiale, le fait de spécifier incorrectement une structure panmictique se traduit par un important appauvrissement si la pêche est concentrée dans des unités de population plus productives (plutôt que d'être uniformément répartie). L'intégration de modèles opératoires spatialement généralisés, comme celui développé dans la présente étude, aux évaluations de stratégies de gestion facilitera l'élaboration de procédures de gestion plus robustes en présence de complexités spatiales. [Traduit par la Rédaction]

Introduction

Fish movement and dispersal stem from a variety of biotic and abiotic factors (Bowler and Benton 2005) and contribute to a continuum of genetic variation and associated population structures (Reiss et al. 2009; Ciannelli et al. 2013). Spatial connectivity is an important facet of fish population dynamics that helps safeguard population units against natural and anthropogenic perturbations and maintains population stability (Kerr et al. 2010*a*, 2010*b*). The spatial distribution of fishing effort can also influence population structure, and displacement of effort has been used as a management tool for implementing conservation strategies (e.g.,

implementing marine protected areas, MPAs; Punt and Methot 2004; McGilliard et al. 2015). Protecting and conserving spatial population structure has been a central concern for rational fisheries management for over a century (Hjort 1914; Beverton and Holt 1957; Sinclair 1988; Cadrin and Secor 2009).

There has been increasing effort in recent decades to incorporate spatial heterogeneity in population and fishery dynamics into stock assessment (and ecosystem) models that underlie management advice (see review by Goethel et al. 2011) and to develop marine policies that directly protect spatial population structure, including subpopulation components (e.g., spawning populations;

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Kritzer and Liu 2014). However, spatial structure is rarely concurrently and holistically evaluated across the entire assessment–management interface. The spatial scale of stock assessment models is often limited by the available data, which, until recently, has typically been reported by broad-scale management units (Wilen 2004). Consequently, the ability to achieve the desired objectives of fine-scale fishery regulations is severely hampered by using outputs of stock assessments that do not match the desired spatiotemporal scale (Cope and Punt 2011; Goethel et al. 2016).

Simulation experiments that evaluate spatial processes can be useful tools for understanding the importance of spatial population structure for the sustainable management of marine resources (e.g., Pelletier and Mahévas 2005; Kerr and Goethel 2014). In certain cases, it has been demonstrated that spatially aggregating data or assessment results across known spatial components may be warranted or even statistically advantageous, particularly if there is little genetic differentiation or sample sizes are limited (Li et al. 2015; Benson et al. 2015; Goethel et al. 2015; Punt et al. 2015). However, the majority of spatial simulations have indicated that ignoring spatial structure is likely to be detrimental either to the resource or the harvesters or both (for reviews see Kerr and Goethel 2014 and Goethel et al. 2016).

When management (e.g., setting of catch quotas) ignores population structure or connectivity among population units, there is increased potential for overharvesting, and system productivity is often incorrectly estimated (Fu and Fanning 2004; Kerr et al. 2014; de Moor and Butterworth 2015). Even when population structure is recognized and accounted for within the management framework, if the spatial dynamics of the fishery (e.g., gear selectivity or effort) are ignored, the possibility of overharvesting can remain (Fahrig 1993; Mchich et al. 2006; Ling and Milner-Gulland 2008; Benson et al. 2015; Hoshino et al. 2014). Concomitantly, underharvesting can also occur when effort is not efficiently allocated between spatial units, resulting in foregone yield and lower net revenue for fishing fleets (Tuck and Possingham 1994). Because harvest strategies are often context-dependent, no single, optimal approach to distributing fishing effort exists when spatial structure is present (Steneck and Wilson 2010). For instance, the optimal strategy when source–sink dynamics are modeled has been shown to differ between focusing harvest on the source or the sink population, exclusively, depending on modeling assumptions and management objectives (Tuck and Possingham 1994; Sanchirico and Wilen 2001, 2005; Wilberg et al. 2008).

Spatial dynamics can complicate the determination of management benchmarks, because of the multilevel spatiotemporal interactions that occur among individual fishermen behavior (targeting), differences in gear selectivity among fleets, regulatory management, and the underlying population demographics (Steneck and Wilson 2010; Goethel et al. 2016; Thorson et al. 2017). Surplus production models have been used to estimate maximum sustainable yield (MSY) when metapopulation dynamics exist and subpopulations are linked through movement or recruitment dynamics (Carruthers et al. 2011; Takashina and Mougi 2015). For instance, using a metapopulation operating model, Ying et al. (2011) demonstrated that ignoring metapopulation structure led to localized depletion, because biased stock status indicators were estimated from spatially aggregated surplus production models. Yield-per-recruit and spawner-per-recruit (SPR) models have also been adapted to account for spatial structure within a population by allowing movement among population patches (e.g., Beverton and Holt 1957; Punt and Cui 2000) or by addressing heterogeneity in effort and population distribution using individual-based models (IBMs) for sessile species (Hart 2001, 2003; Truesdell et al. 2016). When stock–recruitment dynamics are accounted for directly, slightly more complex simulation models can be utilized to calculate a suite of potential spatially explicit reference points. For example, Kerr et al. (2014) illustrated how accounting for population structure and genetic straying (i.e., connectivity among spawning components) in Gulf of Maine cod (*Gadus morhua*) could lead to different interpretations of population productivity and system yield compared with spatially aggregated models.

However, there are few instances of integrated assessment–management frameworks that incorporate spatial structure into both the stock assessment model and the resulting simulations of management benchmarks or yield projections. For tuna in the western and central Pacific Ocean, the MULTIFAN-CL software program (Fournier et al. 1998; Hampton and Fournier 2001) is used to provide spatially explicit estimates of exploitation by modeling catch by region and allowing connectivity among regions. In many applications, a single interbreeding population is modeled allowing equilibrium yield-based or depletion-based (relative to unfished levels) reference points to be defined for the entire population (or system) without a mismatch in spatial structure. However, recent modeling additions allow performing these analyses regionally, thereby preserving the same connectivity and fishery dynamics utilized in the assessment model (J. Hampton, SPC, Nouméa, New Caledonia, personal communication, 2016). Similarly, assessment of the snapper (*Pagrus auratus*) resource in New Zealand is undertaken utilizing a spatially explicit model (i.e., a customized version of the CASAL software program; Bull et al. 2012) to simultaneously model the three populations in the SNA1 management unit (Francis and McKenzie 2015). This model assumes that each population exhibits natal fidelity (i.e., natal homing), and connectivity is incorporated by calculating the degree of spatial overlap within each geographic zone while allowing individuals to perform instantaneous spawning migrations to their natal population's spawning area. Population-specific virgin biomass (B_0) estimates are utilized in conjunction with deterministic B_{MSY} simulations to determine stock status, which explicitly accounts for connectivity dynamics and provides reference points both by geographic area and by population unit. Although SNA1 snapper provides one of the few examples of a complete spatially explicit assessment–management framework, many uncertainties exist particularly regarding population structure and connectivity assumptions (Francis and McKenzie 2015).

Despite increasing awareness that fishery and population spatial structure have important implications for defining management benchmarks and resulting harvest levels, investigations have often been focused on a single application involving only one or two assumed population structures. We develop a spatially explicit simulation framework that can account for a variety of spatial processes, then apply it across a relatively comprehensive range of common spatial population structures and connectivity dynamics to provide a broad comparison of resulting biological reference points. Next, we demonstrate the management implications of misdiagnosing population structure by exploring the potential for overharvest and loss of yield when harvest levels are applied based on incorrect management benchmarks. By improving our understanding of the consequences associated with misidentifying population structure at the assessment–management interface (e.g., the conversion of assessment outputs into management advice), resource managers will be better able to identify potential harvest policy pitfalls and prioritize limited management resources (e.g., to determine the cost–benefit of fine-scale data collection; Goethel et al. 2016).

Methods

A generalized simulation framework was built to utilize stock assessment input (e.g., life history and demographics) and output values (e.g., terminal year abundance, natural mortality, fishery selectivity, and recruitment parameter estimates) to project resource dynamics assuming a particular spatial population structure and associated connectivity dynamics. The purpose of the framework was twofold: to determine reference points under a variety of assumed spatial dynamics and to address the manage-

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Fig. 1. Outline of the two-stage generalized simulation model. Maximum sustainable yield (MSY)-based biological reference points (BRPs) were chosen for illustrative purposes, but other depletion or yield-based management benchmarks could be defined. Similarly, u_{MSY} (i.e., the harvest rate that achieved the maximum system yield) in stage 2 could be replaced with any input harvest rate or yield level. Stages were run independently.
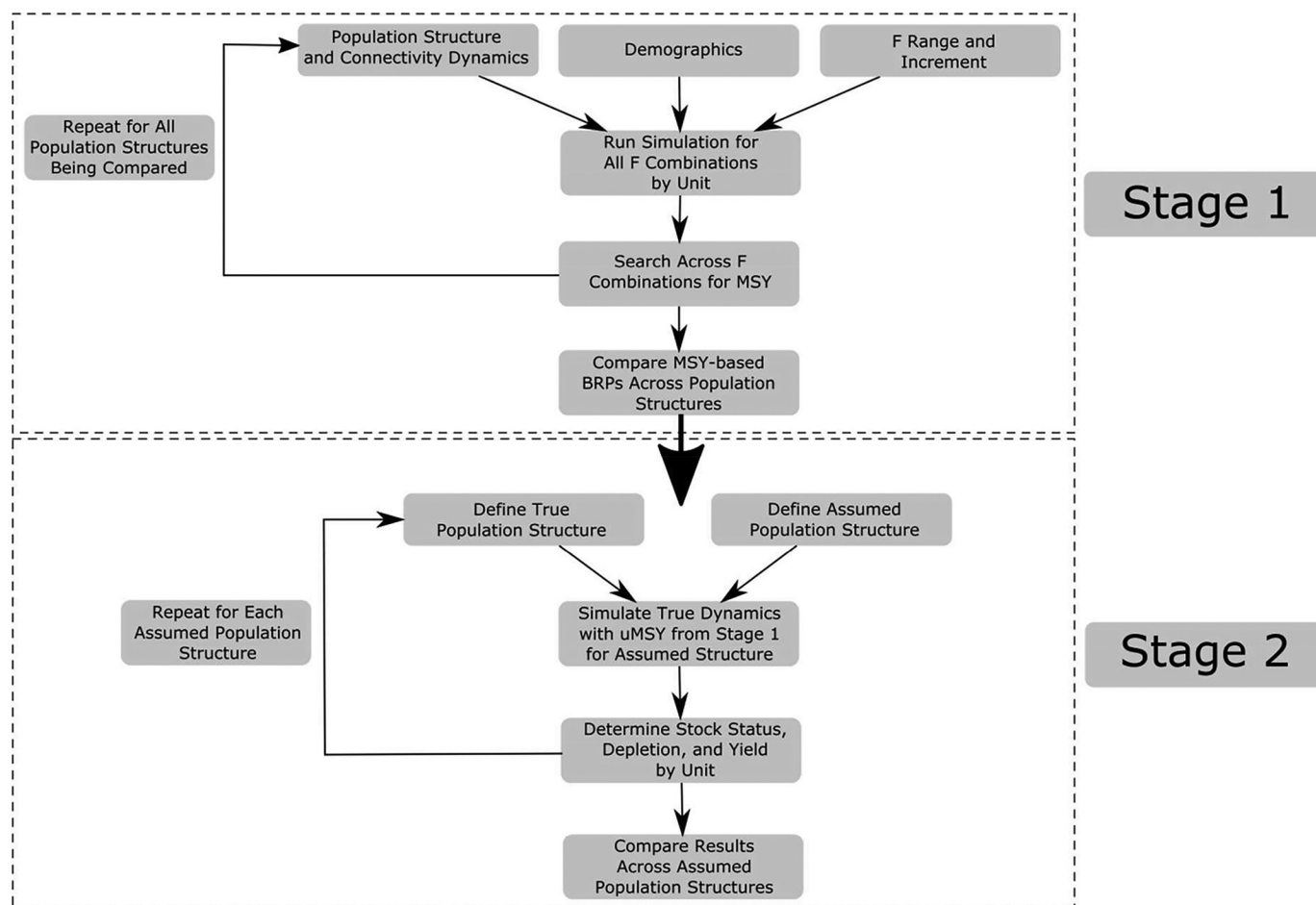
ment implications of applying a harvest level developed with misdiagnosed spatial dynamics (Fig. 1).

Generalized simulation model

The age-structured population dynamics are described below, but for further details see Goethel et al. (2011, section 4). Each implementation of the model differs only in the assumed population structure and connectivity dynamics. Table 1 provides a glossary defining important terms used throughout the article.

The model was designed to perform simulations in two stages using both AD Model builder (ADMB; Fournier et al. 2012) and Program R (R Core Team 2012) statistical computing software. The first stage determined biological reference points (BRPs; Fig. 1). Model inputs were used to simulate population dynamics forward through time until equilibrium was reached. An iterative search algorithm was implemented that ran the model across combinations of fishing mortalities (according to a defined step size for each fleet and area) to find the desired BRP. In the current study, SSB_{MSY} (spawning stock biomass achieved by fishing at the harvest rate, u_{MSY}, that resulted in the maximum system yield) was used as a BRP for comparative purposes. However, the model search algorithm could be setup to achieve any number of alternative depletion or yield-based BRPs.

The second stage determined the impact of fishing at alternative harvest levels (Fig. 1). Instead of using the search algorithm to find the desired BRP, a harvest rate (or yield) was specified and the model dynamics were simulated forward using this value at the appropriate scale (i.e., system-wide or area-specific values could be input). The primary function was to investigate the impact of misdiagnosing spatial population dynamics by fishing at the harvest rate that achieved the desired BRP in stage 1, but for an incorrectly assumed spatial structure (i.e., the input harvest rate did not achieve the BRP for the true simulated population structure). The Newton–Raphson method was utilized to iteratively tune the model until the fishing mortality that corresponded to the desired harvest rate by area was approximated within a certain error threshold. The default assumption when applying harvest rates was that fishing effort was homogeneously distributed across areas. When the applied harvest rate was for an assumed single area population, but the true dynamics contained multiple areas, the harvest rate was evenly applied to all areas. Other effort allocation assumptions could be applied across areas to approximate concentration of fishing effort while still being constrained to maintain the same overall (i.e., system-wide) input harvest rate.

Population structure

The population structure was defined by the number of population units, the interactions among units, and the recruitment dynamics. Four types of population structure were considered corresponding to the main types typically modeled in spatially explicit stock assessments (Goethel et al. 2011): panmictic, single population with spatial heterogeneity, multiple populations with natal homing, and metapopulation structure (Fig. 2A). When defining each of these population structures, careful consideration

Table 1. Glossary of terms used throughout the article.

Term	Definition
Spatial population structure	The spatiotemporal distribution of a resource resulting from environmental or ecosystem interactions (i.e., connectivity) and reproductive dynamics.
Connectivity	Movement of individuals among geographic areas at any life stage (e.g., larval or adult).
Area	A geographic unit representing the spatial extent over which a homogeneous fishing mortality acts. Depending on the type of population structure, an area may contain a segment of a single population, an entire population, or segments of multiple populations.
Population	A self-reproducing biological entity within which all fish are able to reproductively mix, resulting in a single spawning stock biomass (SSB) that determines population-specific recruitment values based on a unique stock–recruit function.
System-wide	The entire spatial domain of the model.
Panmictic	A single, unit population with no spatial heterogeneity.
Single population with spatial heterogeneity	A single population with abundance distributed over multiple areas.
Metapopulation	A network of populations each with unique stock–recruit relationships, but that can reproductively mix. It is assumed that environmental factors drive demographic rates.
Natal homing	A population structure wherein multiple populations overlap spatially, but do not reproductively mix. Fish always retain the life history characteristics of their natal population, which assumes that genetics drive demographic parameters.
Unidirectional movement	Movement among areas is only allowed in one direction (e.g., source–sink dynamics).
Bidirectional movement	Movement is allowed among all areas.
Spawning migration	An instantaneous migration at the time of spawning that allows a fish to reside outside of its natal area throughout the year, but still add to the SSB of its natal population.
Natal return	A return migration at a specific age (i.e., a_{RET}) that emulates an ontogenetic migration.
Harvest rate	The fraction of the biomass that is harvested within a given area (i.e., yield/biomass).

of definitions is warranted, especially in the determination of geographic units versus population units. For the purpose of this study, an "area" was defined as a geographic unit representing the spatial extent over which a homogeneous fishing mortality acted. Depending on the type of population structure, an area may contain a segment of a single population, an entire population, or segments of multiple populations. A population was defined as a self-reproducing biological entity within which all fish were able to reproductively mix, resulting in a single SSB that determined population-specific recruitment values based on a unique stock–recruit function. Depending on the type of population structure, area and population may be synonymous or a population may be scattered across multiple areas.

Panmictic structure was defined as a single reproductively mixing population where no spatial structure existed (i.e., fish were well-mixed throughout the area). A unit population was assumed such that all fish were homogeneously distributed across a single area and no immigration or emigration occurred. A single stock–recruit function was utilized with all mature fish in the population contributing to the SSB. Panmictic structure represents the simplest possible population structure and is one of the most common assumptions in stock assessment models.

When spatial structure was assumed to occur within a single population, the resulting spatial heterogeneity was modeled by allowing multiple areas within the population. A single stock–recruit function was utilized with SSB summed across all areas. A single genetic population was assumed to come from a single larval pool. Total population abundance before movement ($\mathbf{N}_{BEF}^{\Sigma r}$) at the youngest age ($a_0$) for a given population (j) and year (y) was a function (based on the stock–recruit relationship) of the total SSB summed across all areas (r), while the area-specific abundance ($\mathbf{N}_{BEF}^{r}$) at the youngest age was the total abundance multiplied by the apportionment factor (ξ) for that area:

$$
(1) \quad \begin{aligned} N_{j,y,a_0,\mathrm{BEF}}^{\Sigma r} &= f\left(\sum_a \mathrm{SSB}_{j,y,a}^{\Sigma r}\right) \\ N_{j,y,a_0,\mathrm{BEF}}^{r} &= \xi_j^r N_{j,y,a_0,\mathrm{BEF}}^{\Sigma r} \end{aligned}
$$

A wide variety of species exhibit some degree of spatial heterogeneity in distribution, despite maintaining a single reproductive population (e.g., Gulf of Alaska sablefish (*Anoplopoma fimbria*); Hanselman et al. 2015).

Metapopulation structure was defined similarly to a single population with multiple areas, except that multiple populations were modeled simultaneously. Reproductive mixing occurred among populations through the movement of mature individuals, but each population was assumed to maintain its own larval pool. For metapopulation dynamics, area and population delineations were now synonymous (i.e., $r = j$), because once a fish moved into another area, it assumed the reproductive dynamics and demographics of the population residing in that area. Basically, a fish was instantaneously exposed to the dynamics of the population that inhabited the area that it currently occupied, which assumed that environment was the main driver of life history (not genetics). The recruitment dynamics followed eq. 1, but multiple populations were modeled simultaneously, each of which maintained its own stock–recruit function defined by the SSB of all fish currently residing in the corresponding area. Metapopulation structure is becoming a more widely observed form of population structure for marine fish and is frequently detected in reef fish and small pelagics (e.g., Atlantic herring (*Clupea harengus*); Kritzer and Sale 2004; Kerr et al. 2010*b*).

Natal homing (also known as the overlap model; Porch 2003) was the most complex population structure evaluated. Multiple populations were modeled, but no reproductive mixing occurred among them. Similar to a metapopulation, each population unit maintained its own stock–recruit relationship. However, fish only contributed to the SSB of their natal population. As individuals moved among population areas, they cohabitated with fish of other natal populations but were unable to reproduce with them. Because of the overlap of non-interbreeding populations within an area, area was no longer equivalent to population (i.e., $r \neq j$). Once again, recruitment was based on eq. 1. Contrary to metapopulation structure where recruitment was determined from all the SSB in the given population area, natal homing implied that individuals not within the confines of their natal population area

Fig. 2. Spatial (A) and spatiotemporal (B) dynamics of the simulation model (see eqs. 1–5 and associated text for a description of terms). Large circles represent geographic areas within which multiple populations can mix (for spatial heterogeneity, smaller circles represent areas within a single population). Mixing (dark overlap regions) is depicted as taking place in partial areas for illustrative purposes, but actually takes place across the extent of the given geographic area. Dotted lines illustrate movement, while narrow solid lines represent recruitment. The small circles in panel B represent the segment of a population (population is denoted by the subscript) outside its natal area, which overlaps with the natal population of the geographic area (large circles; area is represented by the superscript).
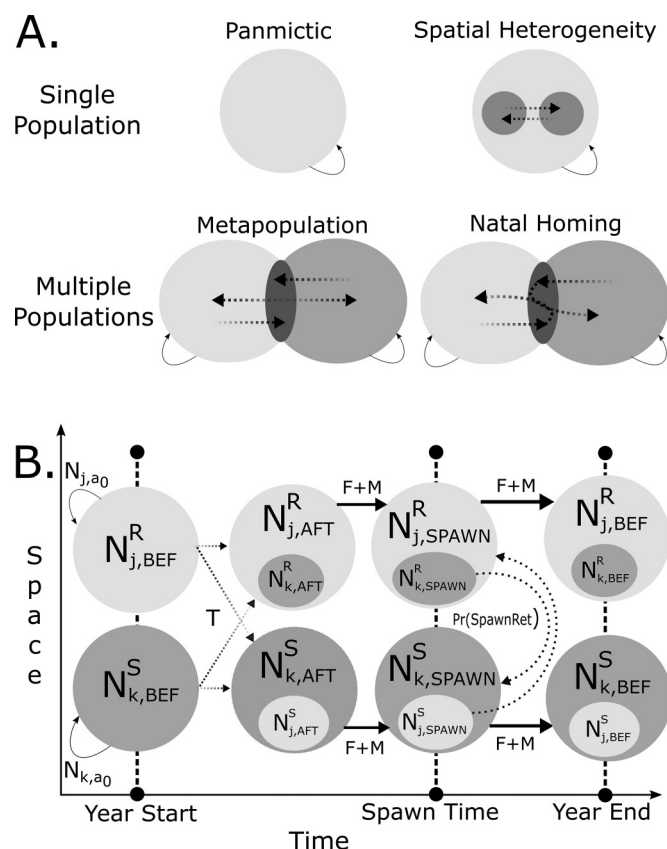
could not reproduce unless they underwent a spawning migration (see eq. 2 in the following section for a description of SSB calculations for alternative natal homing scenarios). Demographics were now assumed to be defined by the natal population (i.e., vital rates no longer changed as an individual moved among areas), which implied that life history characteristics were determined by genetics (not environment). Natal homing has been hypothesized for many large pelagics (e.g., Atlantic bluefin tuna (*Thunnus thynnus*); Rooker et al. 2008) and is a well-known trait for salmon.

Movement parametrization

Simulated movement used the box-transfer method, which assumed a certain fraction of the population instantaneously moved to the other areas at the beginning of the year. The movement parameter ($T_{j,y,a}^{r \to s}$) represented the fraction of fish from population j in year y at age a that moved from area r to area s (for the simulation scenarios presented here, movement was time-invariant). The population subscript changed to the new population area superscript (i.e., movement was a Markovian process) for metapopulation structure, but not for natal homing (i.e., movement characteristics were defined by the natal population).

Age-specific movement was incorporated by allowing different movement rates for the youngest age class compared with all other age classes. The primary assumption was that if, for example, the model started at age-0 (i.e., the stock–recruit function provided the number of age-0 eggs or larvae), then age-0 movement would represent larval drift and would be characterized by different dynamics than the movement of older fish. Additionally, it was assumed that apportionment of larvae and larval drift were separate processes (i.e., age-0 larvae were apportioned to area and then allowed to move among areas).

Two unique movement scenarios were examined using the natal homing population structure. Spawning migrations were incorporated by defining a probability of returning (Pr(SpawnReturn)) as the fraction of the natal population not in the natal area that returned to spawn, and the spawning migration was assumed to occur instantaneously at the time of spawning. In this case, a fish could add to the SSB of its natal population, despite residing in a non-natal area (i.e., as a result of the instantaneous spawning migration):

$$(2) \quad N_{j,y,a_0,\text{BEF}}^{r=j} = f\left\{ \sum_a \text{SSB}_{j,y-1,a}^{r=j} + \sum_{r,r \neq j}\left[\text{Pr(SpawnReturn)}_j^r \cdot \sum_a \text{SSB}_{j,y-1,a}^{r \neq j} \right] \right\}$$
$$N_{j,y,a_0,\text{BEF}}^{r \neq j} = 0$$

By accounting for fish that did not contribute to SSB, the spawning migration probability effectively allowed for skipped spawning (i.e., mass resorption of oocytes), which has been observed in some species that demonstrate natal homing (e.g., Atlantic cod and bluefin tuna; Rideout and Tomkiewicz 2011).

The second movement scenario (termed natal return; Table 1) was defined to approximate ontogenetic movement. Movement was allowed at the initial age (i.e., larval drift). A permanent return migration to the natal area could then occur at a certain age (a_{RET}) with a probability given by Pr(PermReturn). Movement was not allowed at any other ages. Recruitment was thus a function of the SSB in the natal population area plus the corresponding SSB of fish that moved back to the natal population at a_{RET}:

$$(3) \quad N_{j,y,a_0,\text{BEF}}^{r=j} = f\left\{ \sum_a \text{SSB}_{j,y-1,a}^{r=j} + \sum_{r,r \neq j}\left[\text{Pr(PermReturn)}_j^r \cdot \text{SSB}_{j,y-1,a=a_{\text{RET}}}^{r \neq j} \right] \right\}$$

With this scenario, fish that did not return (according to a_{RET}) never contributed to the SSB. This configuration was meant to approximate an ontogenetic migration back to the natal population once a fish had reached maturity. The basic ecological premise was that larval or young-of-the-year fish settled and spent their juvenile stage in various areas (e.g., nursery grounds) where they did not contribute to the SSB. Then, once maturity was reached, adult fish would move back to the natal population and contribute to SSB (assuming negligible straying). Ontogenetic migrations have been observed in a number of species (e.g., Gulf of Alaska sablefish; Hanselman et al. 2015) and has been hypothesized in conjunction with natal homing for some large pelagics (e.g., Atlantic bluefin tuna; Rooker et al. 2008). Although the implemented natal return scenario does not explicitly match any known ontogenetic migration patterns, it represents a first approximation to the more complex versions seen in the real world.

Population dynamics

Abundance was projected forward from input initial abundance-at-age and calculated recruitment at the minimum age (Fig. 2B). Recruitment calculations assumed a Beverton–Holt stock–recruit model, where SSB was calculated based on mass and was adjusted based on the assumed population structure and movement dynamics (as described above) and for the time of spawning. Mortality was assumed to be a function of area. Fishing mortality was separated into an area- and fleet-specific yearly multiplier (*F*) and

an age-specific selectivity component. Selectivity (v) for each of the modeled fleets (f) was input directly by age. Any number of fleets was allowed within each area (for the simulation scenarios presented here, only one fleet per area was modeled). Natural mortality (M) was input directly and could vary by age, year, and area. In the recruitment year, mortality was discounted for the fraction of the year that fish underwent mortality based on the time of spawning (and hence birthdate). Abundance-at-age at the beginning of the year before movement in area r from natal population j in year y and at age a was calculated from the abundance after movement (N_{AFT}) in the previous year and age as

$$
(4) \quad \begin{aligned} N^r_{j,y,a,\text{BEF}} &= N^r_{j,y-1,a-1,\text{AFT}} e^{\left[-\left(F^{\Sigma f}_{r,y-1,a-1} + M_{r,y-1,a-1}\right)\right]} \\ F^{\Sigma f}_{r,y-1,a-1} &= \sum_f v^f_{r,y-1,a-1} F^f_{r,y-1} \end{aligned}
$$

The terminal age was assumed to be a plus group that was the summation of all fish that survived to the plus group age from the previous age along with all fish already in the plus group that survived to the next year. Instantaneous movement immediately followed at the start of the year, and abundance-at-age after movement was

$$
(5) \quad N^r_{j,y,a,\text{AFT}} = \sum_s T^{s \to r}_{j,y,a} N^s_{j,y,a,\text{BEF}}
$$

Catch-at-age (C_a) was calculated using Baranov's catch equation based on the area- and fleet-specific mortality and selectivity values and the available abundance after movement, while yield (Y) was the summation over age of catch-at-age multiplied by the mass-at-age (w):

$$
(6) \quad \begin{aligned} C^{r,f}_{j,y,a} &= N^r_{j,y,a,\text{AFT}} \left\{1 - e^{\left[-\left(F^{\Sigma f}_{r,y,a} + M_{r,y,a}\right)\right]}\right\} \frac{v^f_{r,y,a} \cdot F^f_{r,y}}{F^{\Sigma f}_{r,y,a} + M_{r,y,a}} \\ Y^{s,r,f}_{j,y} &= \sum_a \left(C^{r,f}_{j,y,a} \cdot w_{j,y,a}\right) \end{aligned}
$$

The general spatial and spatiotemporal dynamics are illustrated in Figs. 2A and 2B.

Model outputs

Several output quantities that are typically important for making management decisions were provided for each year of the simulation and at all spatial scales (i.e., system-wide or by area). By providing results at different spatial scales, the impacts of applying a given mortality rate could be examined at different levels, which can be particularly useful when comparing different types of assumed population structures. Results were also provided by area and by natal population to allow comparison among different population structures. Biological metrics included abundance-at-age, recruitment, biomass, SSB, depletion (biomass$_{\text{Current}}$/biomass$_{\text{Initial}}$), and spawning potential ratio (SPR = SSB$_{\text{Current}}$/SSB$_0$, where SSB$_0$ was calculated based on unfished equilibrium SSB and the parameters of the stock–recruit curve). Mortality-based metrics included catch-at-age, yield, and harvest rate or exploitation fraction (yield/biomass).

Model application

The generalized framework was applied to evaluate three main study objectives using MSY-based reference points. MSY-based reference points were chosen for illustrative purposes, because they are widely used (as explicit or proxy reference points) and discussed in fisheries management. However, their use is not meant to represent the basis for any particular real-world harvest pol-

Table 2. Input parameters for a midwater pelagic, hake-like species used to evaluate BRP_Dev and HL_App models.

Age	Selectivity	Maturity	Initial abundance	M	Mass
1	0.00	0.00	3 125 000	0.226	0.101
2	0.12	0.12	2 538 636	0.226	0.273
3	0.54	0.54	2 062 295	0.226	0.377
4	0.71	0.71	1 675 333	0.226	0.473
5	0.87	0.87	1 360 979	0.226	0.545
6	1.00	1.00	1 105 610	0.226	0.622
7	1.00	1.00	898 157	0.226	0.674
8	1.00	1.00	729 630	0.226	0.754
9	1.00	1.00	592 725	0.226	0.805
10	1.00	1.00	481 508	0.226	0.833
11	1.00	1.00	391 159	0.226	0.909
12	1.00	1.00	317 764	0.226	0.952
13	1.00	1.00	258 139	0.226	0.938
14	1.00	1.00	209 703	0.226	0.918
15+	1.00	1.00	170 355	0.226	0.982
R_0	3 125 000				
SSB$_0$	2 397 000				
Steepness	0.814				

Note: Abundance and recruitment are in 1000s of fish, mass is in kilograms, and SSB is in metric tons.

icy. For the first objective (BRP_Dev), the stage 1 model (Fig. 1) was run for several alternative spatial population structures and various connectivity dynamics, and the resulting MSY-based reference points were compared. The second objective (HL_App) applied results from the stage 1 model runs to the stage 2 model (Fig. 1), where an MSY-based harvest level was applied based on an incorrect assumption regarding spatial structure and connectivity dynamics. Thus, the dynamics of the true population structure were simulated using the harvest rate that achieved MSY for the assumed population structure. Model outputs (e.g., level of depletion, foregone yield, and bias in stock status indicators) were then compared across scenarios. The simulation model for objectives one (BRP_Dev) and two (HL_App) was conditioned to loosely emulate a midwater pelagic, hake-like species with many of the life history characteristics borrowed from the Pacific hake (*Merluccius productus*) stock assessment (Grandin et al. 2016). This species was chosen to provide realistic parameters to initialize the model (see Table 2 for input values), but, given the many simplifying assumptions made, the results were not meant to be representative for any particular species and thus were not suitable as the basis for management advice. The third objective (Snapper_App) was to apply the generalized simulation framework (stages 1 and 2) to a species with alternative life history parameters and to explore the impact of spatial effort allocation. The input parameters, spatial population structure, and connectivity scenarios were based on aspects of Gulf of Mexico red snapper (*Lutjanus campechanus*), though model evaluations are exploratory and not suitable as the basis for management advice.

Base dynamics and scenarios: midwater pelagic

The simulation model used to evaluate objectives one (BRP_Dev) and two (HL_App) was first parameterized by a base set of population dynamics and then adjusted to evaluate alternative spatial structure and connectivity scenarios. The base model assumed 15 ages and deterministic simulations were carried out for 200 years, a time period meant to allow equilibrium conditions to occur. The initial age structure was setup so that abundance at the youngest age class was equivalent to R_0 (virgin recruitment; 3.125 billion fish), and the abundance-at-age was at unfished equilibrium assuming an age-invariant natural mortality of 0.226, but adjusted such that the total SSB was equivalent to SSB$_0$ (virgin spawning stock biomass; 2.397 million t). A Beverton–Holt stock–recruit function was assumed with a steepness of 0.814, and no

stock–recruit deviations were incorporated. SSB was in mass and mass-at-age was input in kilograms. A single fleet was assumed for each area and selectivity was set equivalent to maturity to avoid any influence of differences in these quantities on results. All parameters were time-invariant (see Table 2 for input parameter values).

For population structures assuming multiple areas, the number of areas was two for tractability and ease of interpretation of results. The vital rates were assumed constant across all areas or populations, and R_0, SSB_0, and initial abundance-at-age were evenly apportioned among populations to ensure that results were not influenced by differential population demographics and that differences in spatial dynamics were the axis of evaluation. For scenarios where differential recruitment apportionment or productivity among areas was assumed, the first area had the potential to produce up to 30% of the total recruitment, while the second area could produce up to 70%. For a single population with multiple areas, this was accomplished by splitting the recruitment apportionment factor 30/70 (instead of the base 50/50 split). For multiple population scenarios, the split was achieved by scaling the population-specific R_0 and associated SSB_0, which then also required rescaling the initial abundance-at-age by area.

Movement rates and types differed according to objective and scenario set. Movement was separated between larval drift (constant movement at age a_0) and adult movement (constant movement for ages greater than a_0). Two levels of movement were evaluated (high or low residency) along with two types of movement (bidirectional or unidirectional), and both could occur at the larval or adult stage. Bidirectional movement allowed fish to move between both areas, while unidirectional movement represented source–sink dynamics (i.e., fish moved in one direction). For bidirectional movement, high residency indicated that 80% of fish stayed in area 1 and 85% stayed in area 2 in any given year, while low residency indicated that 60% stayed in area 1 and 65% stayed in area 2. For unidirectional movement, fish were only allowed to move from area 2 to area 1 (representing movement from the more productive area to the less productive area when productivity differed) with high residency set to 85% and low residency to 65%. For natal homing scenarios, spawning migrations and natal return were considered. The probability of return was 75% for spawning migrations and constant across population areas, which represented a plausible level given recent literature on skipped spawning (Rideout and Tomkiewicz 2011). For the natal return models, high and low return probabilities (85% or 65%, respectively) were evaluated, where the age of return was set to age-4 (roughly corresponding to 75% maturity). Alternative movement levels were chosen to provide a reasonable range of plausible rates but, again, were not meant to reflect any particular species.

Scenarios for the first objective (BRP_Dev) were developed to calculate and compare reference points across different spatial structures and connectivity assumptions. The first subset of scenarios focused on the role of adult movement (Adult_Move; a complete listing is provided in the online Supplementary material, Table S1[2]). The second subset looked at the impact of larval connectivity (Larval_Move; Supplemental Table S2[2]). The third subset allowed both adult and larval connectivity (All_Move; Supplemental Table S3[2]). The fourth subset demonstrated the impact of full connectivity dynamics along with variation in recruitment (i.e., productivity) across areas (Move+Prod; Table 3).

Scenarios for the second objective (HL_App) were developed using model output harvest levels from the high adult and high larval residency scenarios of objective one, subset four (Move+Prod), as these represented the most inclusive set of MSY-based harvest levels examined. For each scenario, there was a true underlying

spatial structure that determined the dynamics of the system and an assumed spatial structure that was used to guide management (i.e., the implemented harvest level) for the true system. The applied harvest rate was that which maximized yield (u_{MSY}) for the assumed spatial structure. For situations where the assumed spatial structure was panmictic, the panmictic u_{MSY} was applied to each of the areas in the true population structure. On the other hand, when multiple areas were assumed but the true structure was panmictic, the system-wide u_{MSY} from the assumed structure (i.e., the total u_{MSY} across all areas) was used as the harvest rate for the panmictic population. When multiple area spatial structures were examined for both the assumed and true dynamics, the assumed u_{MSY} for the first (second) area was applied to the first (second) area in the true dynamics. Resulting area-specific and system-wide terminal year outputs (e.g., SSB, yield, and SPR) allowed comparison of how misdiagnosing spatial structure and unknowingly implementing inappropriate management harvest levels may affect the ability to achieve long-term management goals.

Base dynamics and scenarios: red snapper-like

The simulation model used to evaluate objective three (Snapper_App) was also parameterized by a base set of population dynamics (Supplemental Table S4[2]), but some simplifying assumptions were made compared with the current assessment (e.g., only a single fleet per area was modeled here). Reference points were evaluated based on various hypothesized spatial structure and connectivity scenarios. For red snapper, spatial structure is known to exist, but the causes and levels of potential mixing among areas is not well known (Patterson 2007; Karnauskas et al. 2013). The current stock structure applied to the assessment of red snapper is essentially two populations (eastern and western Gulf of Mexico) with management treating them as a single population, but tagging studies and larval drift models indicate that metapopulation structure may exist (Patterson 2007; Karnauskas et al. 2013).

Life history parameters were derived from the most recent stock assessment (SEDAR 2015), but some parameters were altered to fit the various modeling assumptions. All parameters were assumed constant across areas (as was done in the stock assessment) and were time-invariant. Selectivity was taken from the dominant fishery (the recreational fleet in the eastern area) to avoid the added complexity of averaging selectivity across fleets when a single panmictic population was assumed. The assessment fixes steepness at 1.0, but allows a time-varying recruitment distribution parameter to accommodate the independent recruitment that is thought to exist between the eastern and western populations. For this study, steepness was fixed at 0.85 to maintain the reliance of recruitment on SSB. When evaluating a single population with two areas, the recruits were apportioned using the time-averaged apportionment factor estimated from the stock assessment (66% of recruits were apportioned to the western area, referred to as area 2 here). When evaluating metapopulation models, R_0 was apportioned using the same ratio.

Three types of population structure were investigated based on previously hypothesized connectivity dynamics (Patterson 2007): panmictic, a single population with two areas, and metapopulation. For the two spatial population structures, different connectivity dynamics were investigated based on larval connectivity hypothesized from a larval individual-based model (IBM) developed for red snapper (Karnauskas et al. 2013). Five movement scenarios were considered: no movement; bidirectional larval movement with mean values from the larval IBM (~97% residency for each population); unidirectional larval movement at maximum values from the larval IBM (either the eastern (i.e., area 1) or western (i.e., area 2) areas are treated as a source with residency of

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Table 3. Scenario list for the Move+Prod subset of BRP_Dev models.

Scenario	Population structure	Residency level		Movement type				
		Adult	Larval	None	Unidirectional	Bidirectional	Spawning migration	Natal return
1	1 population, panmictic	All	All	×				
2	1 population, 2 areas	All	All	×				
3		High	Low		×			
4		Low	High		×			
5		High	High		×			
6		Low	Low		×			
7		High	Low			×		
8		Low	High			×		
9		High	High			×		
10		Low	Low			×		
11	Metapopulation	All	All	×				
12		High	Low		×			
13		Low	High		×			
14		High	High		×			
15		Low	Low		×			
16		High	Low			×		
17		Low	High			×		
18		High	High			×		
19		Low	Low			×		
20	Natal homing	High	Low		×		×	
21		Low	High		×		×	
22		High	High		×		×	
23		Low	Low		×		×	
24		High	Low		×			
25		Low	High		×			
26		High	High		×			
27		Low	Low		×			
28		High	Low			×	×	
29		Low	High			×	×	
30		High	High			×	×	
31		Low	Low			×	×	
32		High	Low			×		
33		Low	High			×		
34		High	High			×		
35		Low	Low			×		
36		High	Low		×			×
37		Low	High		×			×
38		High	High		×			×
39		Low	Low		×			×
40		High	Low			×		×
41		Low	High			×		×
42		High	High			×		×
43		Low	Low			×		×

Note: For natal return and spawning migration models, adult residency actually corresponds to the rate of return. "All" indicates 100% residency, "high" means the high residency values are used, and "low" signifies that the low residency values are used. For unidirectional movement, 100% residency is implied for the sink (area 1).

93%); unidirectional larval movement based on hypothesized maximum values (either the eastern (area 1) or western (area 2) areas are treated as a source with residency of 80%); and bidirectional mean larval movement (97% residency) with bidirectional adult movement based on hypothesized movement rates (90% adult residency for each population).

Associated reference points were developed for each population structure (see Supplemental Table S5[2] for a list of scenarios), and then MSY-based harvest levels were applied to investigate the impact of misdiagnosing spatial structure when effort was apportioned evenly among areas (Snapper_Even_Eff; see Supplemental Fig. S14[2] for specific scenarios). Uneven apportionment of effort was also evaluated when panmictic stock structure was assumed (Snapper_Uneven_Eff; see Fig. 7 for specific scenarios), such that the input harvest rate on the eastern population (area 1) was halved and the harvest rate on the western population (area 2) was increased until the panmictic u_{MSY} was achieved for the entire complex. The Snapper_Uneven_Eff scenarios illustrated the detriments of ignoring population structure when management failed to limit harvesting aggregation and were meant to touch upon the potential impact that spatial fleet dynamics (and lack of subpopulation catch allocations) might have on naïve management strategies.

Graphical analysis

For all scenarios, model output comparisons were carried out through graphical analysis of important management quantities (e.g., MSY, SSB_{MSY}, and u_{MSY}). When evaluating the impact of misdiagnosing spatial population structure, results were presented as the ratio of the terminal yield or SSB compared with either the true MSY or SSB_{MSY} or the assumed MSY or SSB_{MSY}. Yield comparisons provided an indication foregone yield, while SSB comparisons indicated the level of depletion and bias in a common stock status indicator (i.e., when compared with the true stock status).

Table 4. Qualitative summary of BRP_Dev results describing the relative value of each factor (SSB, yield, and harvest rate) for various population structures and movement types.

Population structure	Movement type	Factor	System-wide	Area 1	Area 2
1 population, panmictic	No movement	SSB	High	—	—
		Yield	High	—	—
		u_{MSY}	Moderate	—	—
1 population, 2 areas	Unidirectional	SSB	High	High	Low
		Yield	High	High	Low
		u_{MSY}	Moderate	Moderate–high	Low–moderate
	Bidirectional	SSB	High	Moderate–high	Moderate
		Yield	High	Moderate	Moderate
		u_{MSY}	Moderate	Moderate	Moderate
Metapopulation	Unidirectional	SSB	Low–moderate	Moderate	Low–moderate
		Yield	Low–moderate	High	Low
		u_{MSY}	Moderate–high	High	Low
	Bidirectional	SSB	High	Moderate	Moderate–high
		Yield	High	Moderate–high	Low–moderate
		u_{MSY}	Moderate	High	Low–moderate
Natal homing	Unidirectional, spawning migration	SSB	High	Low–moderate	Moderate–high
		Yield	High	Low–moderate	Moderate
		u_{MSY}	Moderate	Low–moderate	Moderate–high
	Bidirectional, spawning migration	SSB	High	Low–moderate	Moderate–high
		Yield	High	Low	Moderate–high
		u_{MSY}	Moderate	Low–moderate	Moderate–high
	Unidirectional, natal return	SSB	Moderate	Low–moderate	Moderate–high
		Yield	Moderate	Low	Moderate
		u_{MSY}	Moderate	Low–moderate	Moderate–high
	Bidirectional, natal return	SSB	Moderate	Low–moderate	Moderate–high
		Yield	Moderate	Low	Moderate–high
		u_{MSY}	Moderate	Low	Moderate–high

Note: Results are averaged across movement levels within each movement type to provide an overview of results. Qualitative values (low, medium, or high) represent relative comparisons for that factor across population structure and movement types within that geographic area (i.e., system-wide or area-specific).

Results

Development of BRPs (BRP_Dev)

Spatial population structure had important implications for resulting spatially explicit management harvest levels and biological reference points (Move+Prod scenario results are described here and qualitatively summarized in Table 4; Adult_Move, Larval_Move, and All_Move scenario results are shown in Supplemental Figs. S1, S2, and S3[2], respectively). Although system-wide (total) u_{MSY} was relatively constant across population structures and connectivity dynamics (with the exception of a few cases), resulting SSB_{MSY} varied considerably across scenarios (Table 4; Fig. 3). In addition, different area-specific harvest rates were required to maximize utilization across population structures (Fig. 3). For instance, when source–sink dynamics were present, the source population remained relatively unfished (u_{MSY} was less than 0.05), whereas the sink population was fished much harder (u_{MSY} was near 0.4). These results held for both metapopulation and single population, two area scenarios, but were less pronounced (area-specific u_{MSY} ranged from 0.15 to 0.23) for the natal homing scenarios (Fig. 3). The resulting system-wide SSB_{MSY} was the lowest for the source–sink metapopulation dynamics due to the constant loss of SSB (and consequent recruitment) from the source population. Adult connectivity was a more important factor than larval connectivity in driving the lower SSB_{MSY} for source–sink dynamics (scenarios 13 and 15 versus 12 and 14 in Fig. 3), because losses due to movement occurred at every adult age instead of just the youngest age of the cohort (i.e., when only larval connectivity was considered).

Similarly, differential recruitment exacerbated the relative differences in management quantities across areas. Because fish always added to the SSB of their current resident area for the non-natal homing scenarios, it was intuitive that the area receiving a subsidy (i.e., the sink) would be able to sustain a higher fishing pressure. Interestingly, the results for bidirectional movement began to mimic source–sink dynamics when productivity differed among populations (e.g., scenarios 17 and 19, Fig. 3). When there was a metapopulation with bidirectional movement and differential productivity, the more productive population needed to be protected, while harvest on the less productive population could be much higher. However, with bidirectional movement, the loss of individuals to the less productive population could be offset by immigration from the de facto sink population (i.e., SSB_{MSY} was higher than for the true source–sink scenarios).

For natal homing scenarios, system-wide SSB tended to be lower, but fluctuations in area-specific harvesting rates (range of 0.15–0.25) were not as strong as for metapopulation structure (range of 0.05–0.45; Fig. 3). When no spawning migrations were assumed to occur with unidirectional movement, system-wide SSB_{MSY} and associated u_{MSY} declined by about 15% resulting in a 5% decline in MSY compared with the same scenarios with spawning migrations. These results were more pronounced for bidirectional movement (declines around 25% for SSB_{MSY} and u_{MSY} with a 10% reduction in MSY). Because fewer fish moved under source–sink dynamics than with bidirectional movement, it was not surprising that SSB_{MSY} was lower for the latter because more fish resided outside their natal area and contributed less to natal SSB.

Application of incorrect harvest levels (HL_App)

The risk of depleting certain areas (within or among populations) while underutilizing others differed across the scenarios examined, but tended to be greatest when the true population structure involved metapopulation dynamics (results are qualitatively summarized in Table 5). Ignoring spatial population structure (i.e., assuming panmictic structure) was not as detrimental as might otherwise be expected for system-wide status (in terms of terminal SSB compared with the true SSB_{MSY}), but it could lead to significant depletion of individual areas (Fig. 4; Table 5). When the underlying dynamics involved source–sink connectivity, as-

Fig. 3. Results from the Move+Prod subset of BRP_Dev models illustrating MSY-based reference points. MSY and spawning stock biomass that achieved MSY (SSB_{MSY}) are in 1000s of metric tons, while u_{MSY} is the harvest rate (yield/biomass). Scenarios are grouped by the general type of spatial population structure used in the simulation model (specifics of each scenario are shown in Table 3). Values are provided by individual area and system-wide (i.e., total summed across areas).
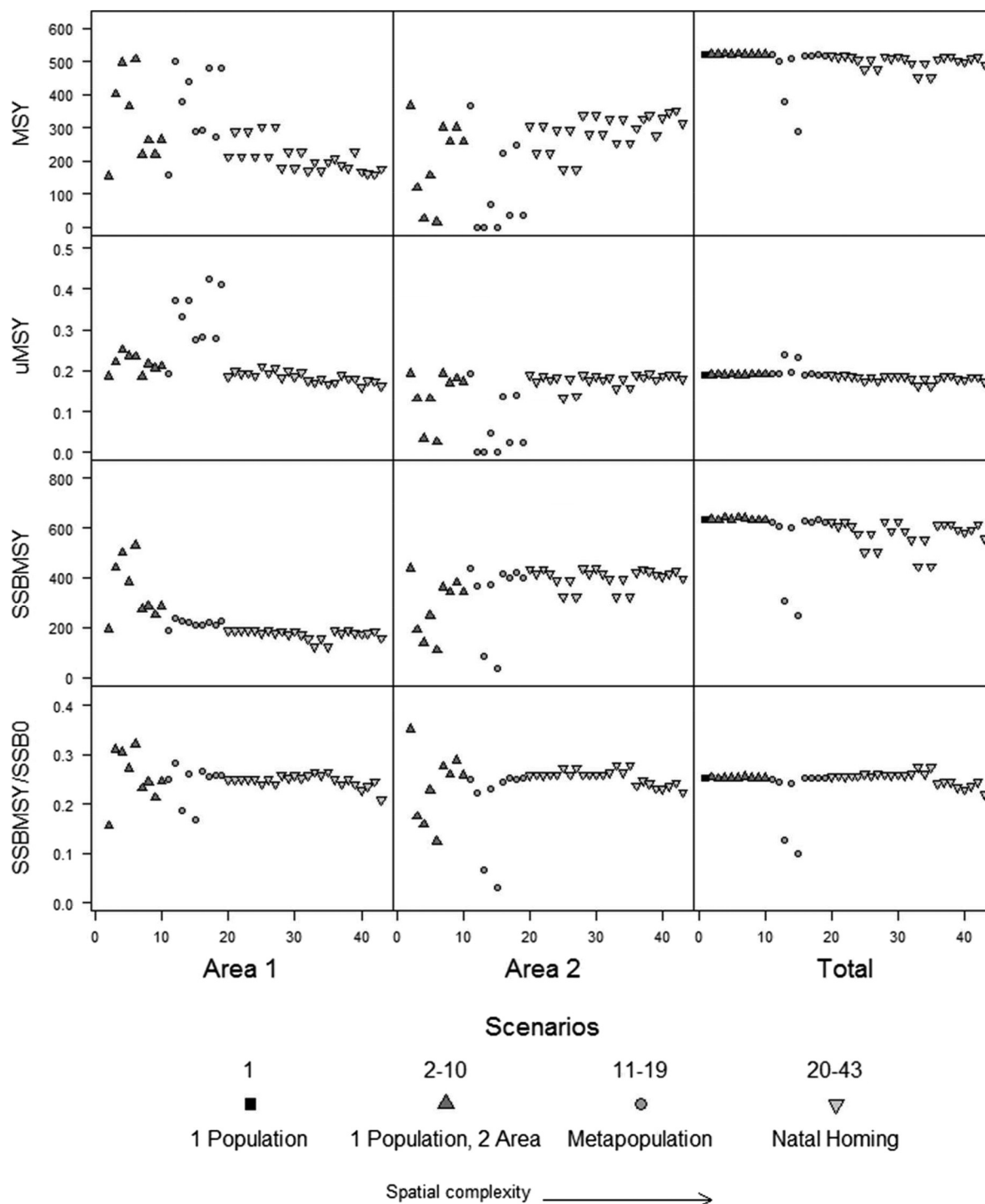
suming no spatial structure led to the source area being severely overharvested (SSB less than 40% of SSB_{MSY} for metapopulation structure) with the sink area being underharvested (SSB over 150% of SSB_{MSY} for metapopulation structure). Moreover, for metapopulation structure with source–sink dynamics, a 25% loss of yield resulted due to misdiagnosing stock structure (Supplemental Fig. S5[2]). The main problem with assuming no structure was that managers would only be provided stock status on a system-wide basis, which could indicate that the system was doing well regardless of area-specific depletion (Fig. 4 and Supplemental Fig. S4[2]).

Interestingly, assuming metapopulation structure when it was not occurring or simply misdiagnosing the connectivity dynamics when metapopulation dynamics were correctly assumed resulted in the most frequent occurrence of depleting an area (Fig. 5; Table 5). When metapopulation structure with source–sink dynamics were assumed, the first area was consistently depleted to

Table 5. Qualitative summary of HL_App results describing the relative rate of occurrence (compared with results of other spatial structure scenarios) for each factor (i.e., depletion, foregone yield, or underutilization) and each of the true and assumed population structure combinations.

Assumed population structure	Factor	True population structure			
		1 population, panmictic	1 population, 2 areas	Metapopulation	Natal homing
1 population, panmictic	Depletion	—	Moderate	Moderate–high	Low
	Foregone yield	—	Low	High	Low
	Underutilization	—	Low	High	Low
1 population, 2 areas	Depletion	Low	Low	Moderate	Low
	Foregone yield	Low	Low	Moderate	Low
	Underutilization	Low	Low	High	Low
Metapopulation	Depletion	Low	Moderate–high	Moderate	High
	Foregone yield	Low	High	High	Moderate
	Underutilization	Low	High	Moderate	High
Natal homing	Depletion	Low	Low–moderate	Moderate	Low
	Foregone yield	Low	Low	Moderate	Low
	Underutilization	Low	Low	High	Low

Note: Results are averaged across movement types and geographic areas within any given assumed to true population structure comparison to provide a qualitative overview of results. When true and assumed spatial structures are identical, results compare different movement assumptions (e.g., unidirectional versus bidirectional movement) for the given population structure.

low levels (SSB ranged from 15% to 50% of SSB_{MSY}), while the second area was underfished (SSB was 120%–140% of SSB_{MSY}) regardless of the true spatial structure. The system-wide SSB tended to be maintained around the true SSB_{MSY}, a notable exception being for a single population with two areas and unidirectional movement (terminal SSB was at 60% of SSB_{MSY}). The biggest detriment occurred for area 1 (i.e., SSB around 15% of SSB_{MSY}) when the true spatial structure involved natal homing. When metapopulation structure with bidirectional movement was assumed, the implications were not as severe (minimum area-specific SSB ~50% of SSB_{MSY}). In certain situations when metapopulation structure was assumed, especially when the true spatial structure involved natal homing, there was considerable foregone yield (5%–25%; Supplemental Fig. S10[2]).

The risk associated with assuming natal homing when in fact it was not occurring was relatively low in most cases. Overharvesting an area by more than 10% occurred in only four scenarios (Fig. 6; Table 5), while there was mostly little foregone yield (Supplemental Fig. S12[2]). The largest impacts were seen when the true underlying structure involved source–sink dynamics (SSB in area 2 was around 30%–70% of SSB_{MSY} for metapopulation or single population, two area-true structures), though this result was pronounced for all true metapopulation structures examined regardless of assumed natal homing movement dynamics. Misdiagnosing connectivity dynamics when natal homing was correctly assumed had limited negative impact.

Red snapper-like application (Snapper_App)

Given the relatively limited level of larval and adult movement examined (Supplemental Table S5[2]), it was not surprising that the system-wide reference points only differed slightly (Supplemental Fig. S13[2]). Misdiagnosing spatial structure had limited impact on the resource (area-specific terminal SSB was within 85% of true SSB_{MSY} for all scenarios tested; Supplemental Fig. S14[2]) when effort was evenly allocated (Snapper_Even_Eff scenarios). However, when panmictic structure was assumed and harvest effort was allowed to aggregate on the more productive area (Snapper_Uneven_Eff scenarios), the potential for overharvesting increased drastically (system-wide SSB was 75%–90% of SSB_{MSY} for all scenarios tested; Fig. 7). The western area (area 2) was often depleted with the terminal SSB usually dropping to less than 50% of SSB_{MSY} and a minimum value around 15%. However, the eastern area (area 1) was consistently well above its SSB_{MSY} (range of 125%–200% of SSB_{MSY}). For most of the true population structures examined, there was ~25% loss in yield from the system when spatial struc-

ture was disregarded and effort was not homogenously distributed (Supplemental Fig. S15[2]).

Discussion

Over the last three decades, there has been increasing awareness that spatial population structure is an important facet of resilience for marine species (e.g., Sinclair 1988; Pelletier and Mahévas 2005; Kerr et al. 2010*a*, 2010*b*; Ciannelli et al. 2013). However, little research has been devoted to describing how ignorance of spatial dynamics may impact biological reference points or the reliability of management strategies (e.g., Ying et al. 2011; Hoshino et al. 2014). Our results demonstrate that management benchmarks and the harvest levels required to attain them are strongly influenced by the underlying population structure and connectivity dynamics. For instance, with metapopulation structure, system-wide harvest rates could be maintained at higher levels compared with other population structures, particularly when source–sink dynamics were present, because movement did not hinder reproduction and area-specific fishing mortality occurred only on a single population at any given time. Yet, it is important to carefully monitor area-specific harvest rates to avoid overharvesting more productive units, which generally act to maintain resource abundance. Alternatively, for natal homing, harvesting within a given area occurs on multiple populations with different productivities, so obtaining MSY-based BRPs necessitated moderate harvest rates in all areas. Unlike with metapopulation structure, area-specific harvest rates were generally independent of movement types and were relatively constant across areas for natal homing scenarios.

Previous studies have suggested that ignoring spatial structure can lead to overharvesting and localized depletion of subpopulation components (e.g., Fu and Fanning 2004; Ying et al. 2011; Hoshino et al. 2014). Our findings further support the general concept that ignoring spatial structure and connectivity dynamics can lead to unintended consequences and expands upon the types of spatial scenarios for which that applies. For the set of spatial scenarios examined for this study, systems that demonstrate source–sink dynamics have the highest potential to introduce problematic management performance when spatial connectivity is not accurately understood. Localized depletion was common when source–sink dynamics were misdiagnosed even though the underlying population structure may be correct. Incorrect assumptions regarding connectivity or mixing dynamics (even when spatial structure is properly defined) can lead to similar, and

Fig. 4. Results from HL_App models demonstrating stock status relative to the true SSB_{MSY} (i.e., $SSB_{Terminal}/SSB_{MSYTrue}$) assuming panmictic population structure. The true spatial population structure for each scenario is described by the *x*-axis tabular labels. Values are provided by individual area and system-wide (i.e., total summed across areas).

Assume No Spatial Structure (1 Population Panmictic) Model
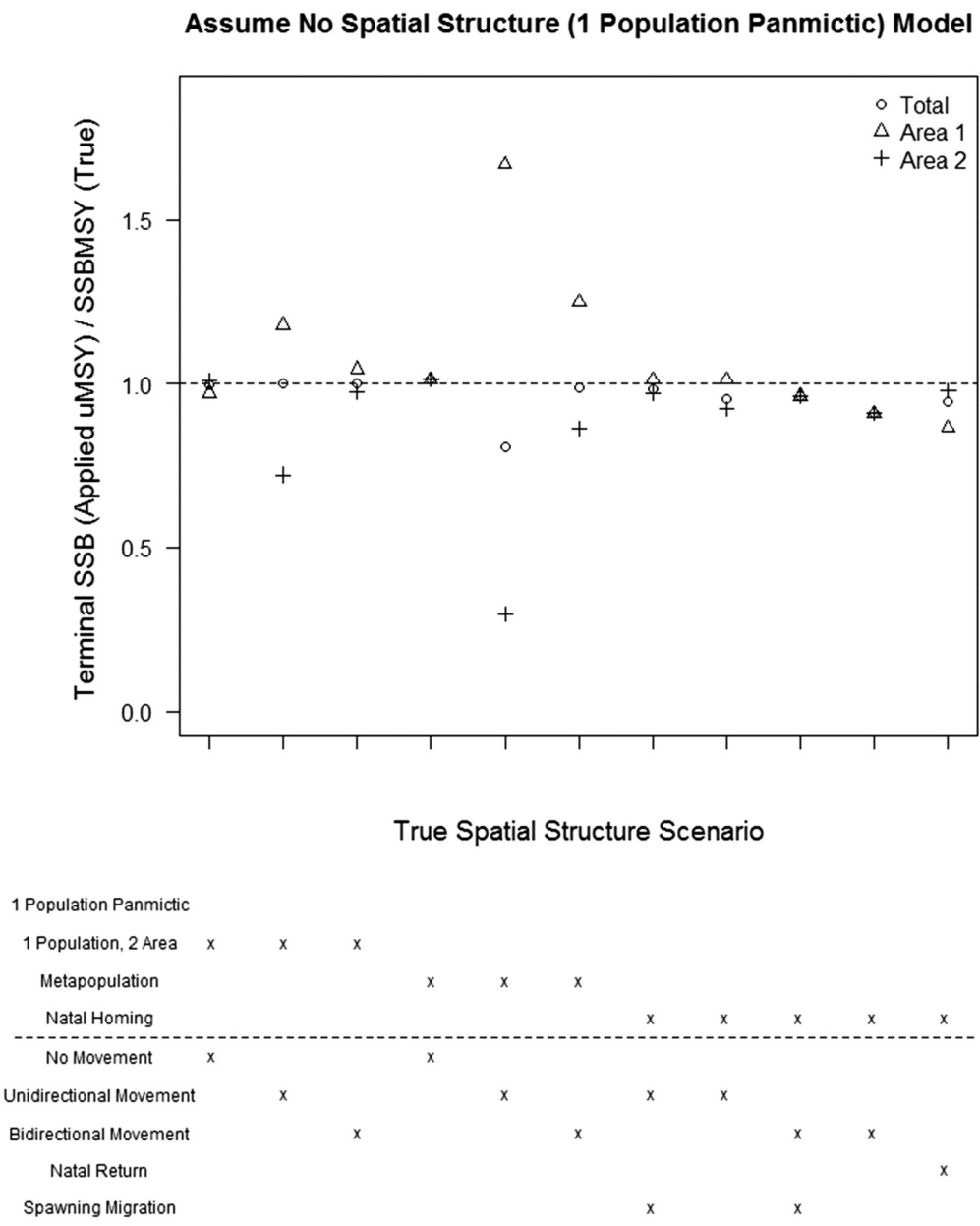
sometimes worse, outcomes compared with incorrectly assuming no spatial structure exists. This is problematic for stock assessment and resource management because connectivity dynamics are rarely well understood (e.g., Porch et al. 1998; Goethel et al. 2015), yet there is no good solution for dealing with this source of uncertainty in spatial population dynamics. Further research on the integration of multiple models (e.g., ensemble modeling utilizing a variety of plausible spatial hypotheses) into the stock assessment–management interface along with explorations with spatially explicit management strategy evaluations should help improve understanding of the robustness of various management procedures to these and other uncertainties.

It was somewhat surprising that when ignoring population structure (i.e., assuming a panmictic population), a metapopulation with source–sink dynamics was the only true spatial structure scenario that resulted in significant system-wide bias (>20%) in terms of stock status and yield. One important factor related to

this finding was that assumed and true connectivity dynamics only included high residency, low movement simulations for the HL_APP scenarios. A comparative analysis using low residency, high movement scenarios demonstrated more pronounced impacts. The low movement scenarios were thought to provide a broader representation of typical connectivity dynamics, but clearly the spectrum of results further illustrates the importance of movement and population structure assumptions on the choice of harvest strategies for marine resources.

A number of generalities and caveats exist with this work, and to better understand the role of these, further consideration and research is warranted. There were many area-specific factors and assumptions (both within a single population and among populations) that could influence results (e.g., degree of movement by age, size, area, and life stage; areal productivity; maturity; growth; fishing effort allocation; and fleet selectivity). To keep the analysis tractable, many of these factors, and the interactions among them,

Fig. 5. Results from HL_App models demonstrating stock status relative to the true SSB_{MSY} (i.e., $SSB_{Terminal}/SSB_{MSYTrue}$) assuming metapopulation structure with source–sink dynamics (i.e., unidirectional movement; left side, upper panel) and bidirectional movement (right side, upper panel). The true spatial population structure for each scenario is described by the x-axis tabular labels. Values are provided by individual area and system-wide (i.e., total summed across areas).

could not be explicitly investigated. The assumed population and connectivity dynamics in the simulations conducted were reasonable, yet simplified compared with real-world applications. Additionally, as with most reference point models, time-invariant model parameters were assumed during the deterministic projection period. Given the flexibility of the modeling approach, it is relatively straightforward to evaluate alternative scenarios, allow for stochasticity in the projection period, and incorporate time-varying parameters and seasonal time increments. Similarly, more complex connectivity dynamics could be included (e.g., density dependence and other functional forms). Further research is needed that closely examines the interplay between specific connectivity assumptions and the copious spatiotemporal biological, fleet, and management processes. By further developing the general framework for new and alternate assumptions regarding spatial, recruitment, and fishery dynamics, we expect that the basic understanding of how spatial processes impact fisheries management will be continually refined.
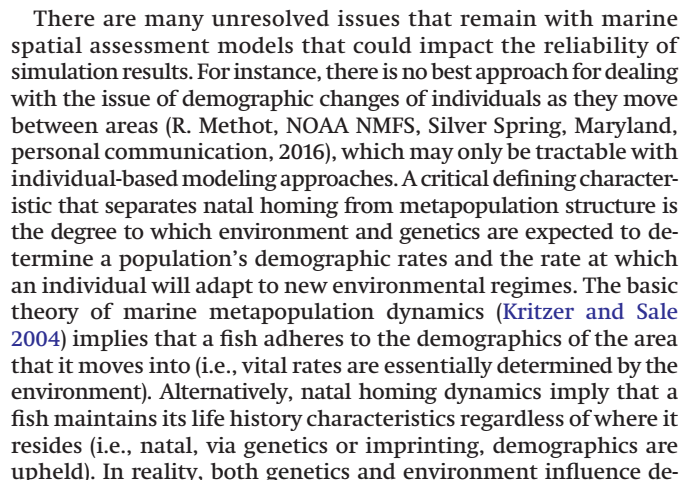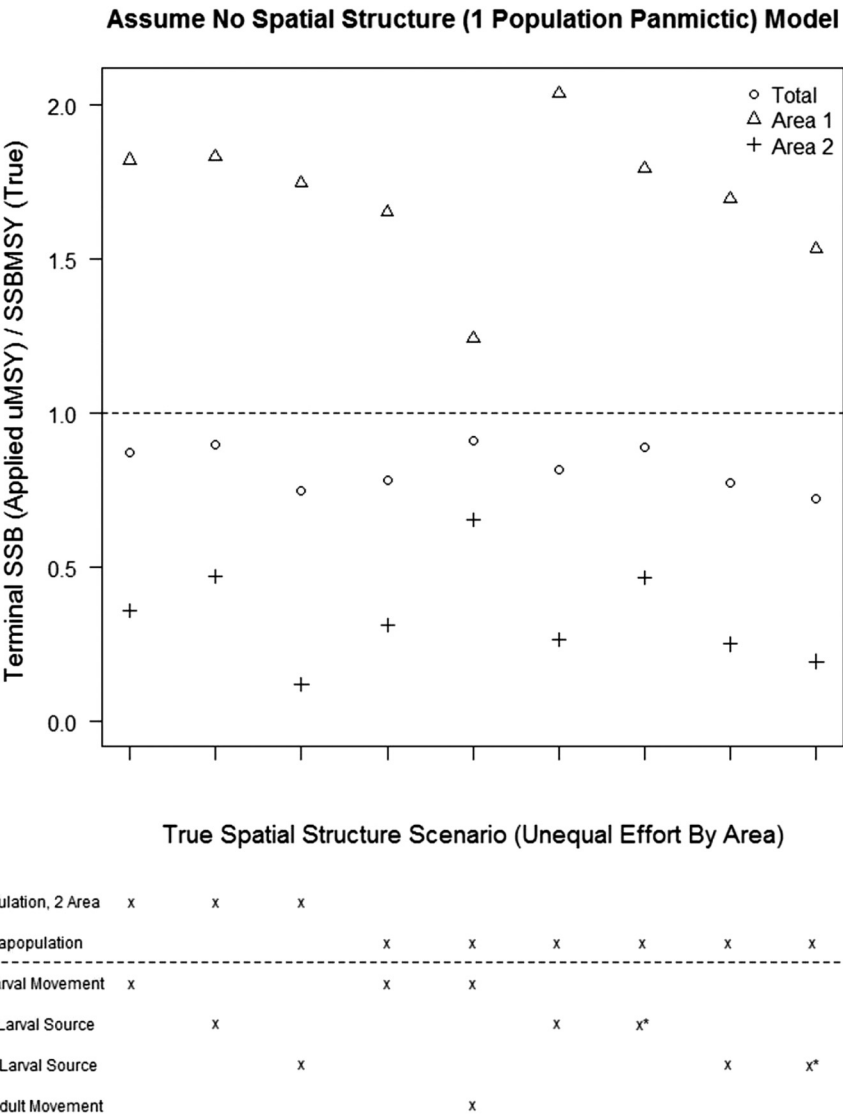
There are many unresolved issues that remain with marine spatial assessment models that could impact the reliability of simulation results. For instance, there is no best approach for dealing with the issue of demographic changes of individuals as they move between areas (R. Methot, NOAA NMFS, Silver Spring, Maryland, personal communication, 2016), which may only be tractable with individual-based modeling approaches. A critical defining characteristic that separates natal homing from metapopulation structure is the degree to which environment and genetics are expected to determine a population's demographic rates and the rate at which an individual will adapt to new environmental regimes. The basic theory of marine metapopulation dynamics (Kritzer and Sale 2004) implies that a fish adheres to the demographics of the area that it moves into (i.e., vital rates are essentially determined by the environment). Alternatively, natal homing dynamics imply that a fish maintains its life history characteristics regardless of where it resides (i.e., natal, via genetics or imprinting, demographics are upheld). In reality, both genetics and environment influence de-

Fig. 6. Results from HL_App models demonstrating stock status relative to the true SSB_{MSY} (i.e., $SSB_{Terminal}/SSB_{MSYTrue}$) assuming natal homing population structure. The upper panel left side illustrates results assuming bidirectional movement and spawning migrations (except the last two scenarios, which assume no spawning migration), while the upper panel right side displays results assuming natal return. The true spatial population structure for each scenario is described by the *x*-axis tabular labels. Values are provided by individual area and system-wide (i.e., total summed across areas).
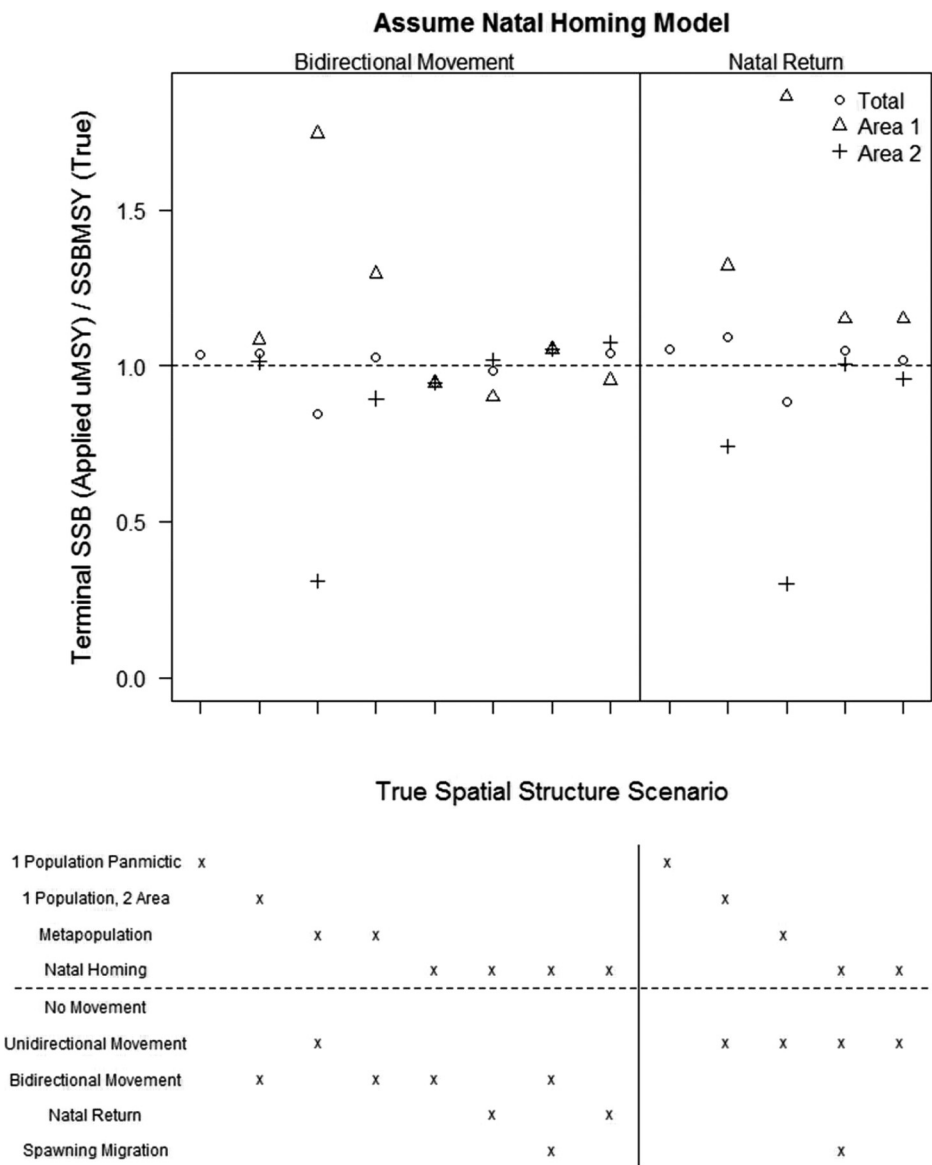
mographic and vital rates to some degree, and both modeling approaches have important limitations. When life history parameters differ by area, assuming that a fish instantaneously adopts the demographics of a new area may result in a reduction in the average size, mass, or maturity of a fish as it moves throughout the spatial domain (i.e., rates could be lower at older ages for different populations). Of course, assuming demographics are purely genetic (as with natal homing) is also incomplete. Stock assessment software exists that attempts to deal with these limitations by assigning vital rates to "growth morphs" or "platoons" of fish that are assumed to have the same demographics (e.g., recruitment year classes; Methot and Wetzel 2013), but no fully satisfactory solution currently exists for spatial models.

Further, the instantaneous movement assumption continues to be an over-simplification in spatial population models, because fish movement occurs across a continuum of physical, biological, and chemical gradients (Turchin 1998). Miller and Andersen (2008)

suggest that estimating continuous time movement parameters (analogous to continuous fishing and natural mortality rates) may be more appropriate for fisheries models. It might be worthwhile to test within the current framework to illustrate the differences that result when fish are able to continuously move from one mortality regime to another. However, until the causal mechanisms that lead to continuous movement are better understood, it may be difficult to apply reference points utilizing this assumption.

Developing more complex evaluations that include multi-component spatial dynamics like the addition of differential selectivity, multiple fleets, and effort aggregation in areas of high biomass concentration are appropriate next steps. The red snapper-like application with uneven fishing effort demonstrated that as more complex, multi-component dynamics are included, the potential pitfalls of ignoring spatial structure could be magnified. Spatial heterogeneity exists in both the distribution of fishery

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Fig. 7. Results from Snapper_Uneven_Eff scenarios demonstrating stock status relative to the true SSB_{MSY} (i.e., $SSB_{Terminal}/SSB_{MSYTrue}$) assuming panmictic stock structure and allowing a nonhomogeneous distribution of effort (i.e., harvest rate in area 1 is halved and harvest rate in area 2 is increased until the total system-wide harvest rate reaches the desired panmictic u_{MSY}). The true spatial population structure for each scenario is described by the *x*-axis tabular labels, where an asterisk represents the lowest residency rate (i.e., 80%) scenario. Values are provided by individual area and system-wide (i.e., total summed across areas).

Assume No Spatial Structure (1 Population Panmictic) Model

1 Population, 2 Area	x	x	x					
Metapopulation				x	x	x	x	x	x
Avg. Larval Movement	x			x	x			
East Larval Source		x			x	x*		
West Larval Source			x				x	x*
10% Adult Movement				x				

resources and fishing effort (Fahrig 1993; Guan et al. 2013), and these are often not proportional to each other across space. Accounting for only the biological aspects of spatial structure does not provide a complete overview of how spatial heterogeneity can impact estimation of biological reference points and related harvest strategies. The snapper-like results provide an indication of the increased complexities that result from spatial effort dynamics, which supports the findings of Hoshino et al. (2014). A wide body of literature on MPAs has demonstrated the importance of spatial harvest displacement for the determination of stock status indicators and achievement of conservation goals (e.g., Punt and Methot 2004; Pincin and Wilberg 2012; McGilliard et al. 2015). Further work is needed to identify and understand the combined impact of both biological connectivity and spatial fleet dynamics (Fahrig 1993; McGilliard et al. 2015).

Our analysis represents a first step towards better understanding the role that population structure has in defining management benchmarks and subsequent harvest levels. Despite the use of simplifying assumptions, the modeling approach highlighted

important patterns and opportunities for investigation (i.e., types of spatial dynamics) that warrant further exploration. Next steps include broadening the generalized simulation model to include increased complexity in the spatiotemporal, population, and fishery dynamics and to more fully account for system uncertainties. An evaluation of data requirements and the associated parameter bias–variance trade-off that must be confronted when moving to multidimensional spatial models, where sample size can become limiting, would also be beneficial. Although the results of this work provide a basic understanding of the interplay between complex spatial dynamics and estimates of management benchmarks for marine resources, we acknowledge that it only represents a first step towards fully integrating spatial biological and fishery dynamics into fisheries policy. There is a clear need for fisheries scientists and managers to be aware of spatial population structure, because it can have strong implications for how to best manage a fishery to meet management objectives (Fahrig 1993; Benson et al. 2015; Hoshino et al. 2014). In addition, spatial heterogeneity due to fleet dynamics and regulatory measures (e.g., MPAs)

only increases the importance of accounting for spatial processes across the assessment–management interface (Guan et al. 2013; McGilliard et al. 2015).

With the increasing recognition of the extensive interactions among time-varying spatial, environmental, population, and fishery processes (Ciannelli et al. 2013), the reliance on static equilibrium models such as those traditionally used to calculate many biological reference points should be reduced (Hilborn 2002; Hoshino et al. 2014). Developing management strategy evaluations where the operating model is generalized to include many hypothesized spatial and environmental complexities (similar to the model developed here) will allow testing the robustness of management procedures to a variety of interacting dynamics and will help managers move away from harvest control rules based on BRPs developed with incomplete assumptions (Butterworth and Punt 1999; Geromont and Butterworth 2015). Of particular interest has been the exploration of empirically driven, spatially explicit reference points that could be used in lieu of or in tandem with conventional BRPs (Reuchlin-Hugenholtz et al. 2015, 2016). No matter how BRPs or harvest strategies are developed, it remains paramount that data collection programs that elucidate migration pathways, connectivity dynamics, and spatiotemporal population structure (e.g., genetic analyses, tagging data, larval transport, and fine-scale life history data) continue to be funded and expanded to support development of more realistic spatial models that can help guide sustainable fisheries management.

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