



## Incoherent dimensionality in fisheries management: consequences of misaligned stock assessment and population boundaries

Aaron M. Berger <sup>1\*</sup>, Jonathan J. Deroba<sup>2</sup>, Katelyn M. Bosley<sup>1†</sup>, Daniel R. Goethel <sup>3,4</sup>, Brian J. Langseth<sup>5‡</sup>, Amy M. Schueller<sup>6</sup>, and Dana H. Hanselman<sup>4</sup>

<sup>1</sup>Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, NMFS-NOAA, 2032 S.E. OSU Drive, Newport, OR 97365, USA

<sup>2</sup>Population Dynamics Branch, Northeast Fisheries Science Center, NMFS-NOAA, 166 Water St, Woods Hole, MA 02543, USA

<sup>3</sup>Sustainable Fisheries Division, Southeast Fisheries Science Center, NMFS-NOAA, 75 Virginia Beach Drive, Miami, FL 33133, USA

<sup>4</sup>Auke Bay Laboratories, Alaska Fisheries Science Center, NMFS-NOAA, 17109 Point Lena Loop Road, Juneau, AK 99801, USA

<sup>5</sup>Fisheries Research and Monitoring Division, Pacific Islands Fisheries Science Center, NMFS-NOAA, 1845 Wasp Blvd., Bldg. 176, Honolulu, HI 96818, USA

<sup>6</sup>Beaufort Laboratory, Southeast Fisheries Science Center, NMFS-NOAA, 101 Pivers Island Road, Beaufort, NC 28516, USA

\*Corresponding author: tel: +1 541 867 0526; e-mail: [aaron.berger@noaa.gov](mailto:aaron.berger@noaa.gov).

†Present address: Washington Department of Fish and Wildlife, 375 Hudson Street, Port Townsend, WA 98368, USA.

‡Present address: Fishery Resource Analysis and Monitoring Division, Northwest Fisheries Science Center, NMFS-NOAA, 2725 Montlake Blvd E, Seattle, WA 98112, USA.

Berger, A. M., Deroba, J. J., Bosley, K. M., Goethel, D. R., Langseth, B. J., Schueller, A. M., and Hanselman, D. H. Incoherent dimensionality in fisheries management: consequences of misaligned stock assessment and population boundaries. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsaa203.

Received 24 June 2020; revised 24 September 2020; accepted 1 October 2020.

Fisheries policy inherently relies on an explicit definition of management boundaries that delineate the spatial extent over which stocks are assessed and regulations are implemented. However, management boundaries tend to be static and determined by politically negotiated or historically identified population (or multi-species) units, which create a potential disconnect with underlying, dynamic population structure. The consequences of incoherent management and population or stock boundaries were explored through the application of a two-area spatial simulation–estimation framework. Results highlight the importance of aligning management assessment areas with underlying population structure and processes, especially when fishing mortality is disproportionate to vulnerable biomass among management areas, demographic parameters (growth and maturity) are not homogenous within management areas, and connectivity (via recruitment or movement) unknowingly exists among management areas. Bias and risk were greater for assessments that incorrectly span multiple population segments (PSs) compared to assessments that cover a subset of a PS, and these results were exacerbated when there was connectivity between PSs. Directed studies and due consideration of critical PSs, spatially explicit models, and dynamic management options that help align management and population boundaries would likely reduce estimation biases and management risk, as would closely coordinated management that functions across population boundaries.

**Keywords:** ecological boundary, non-stationary dynamics, risk, spatial management, spatial population structure

## Introduction

Spatial structure is a defining feature guiding the population dynamics and sustainable harvest levels of marine resources (Fogarty and Botsford, 2007; Cadrin and Secor, 2009; Goethel *et al.*, 2011). Individual biological responses to variation in oceanographic conditions (Pinsky *et al.*, 2013; Tolimieri *et al.*, 2018; Malick *et al.*, 2020), harvest pressure (Fu and Fanning, 2004; Cope and Punt, 2011, Bosley *et al.*, 2019), regulatory measures (Hilborn *et al.*, 2004; McGilliard *et al.*, 2015), and community dynamics (Holt, 1997; Cottenie, 2005; Thorson *et al.*, 2017) create complex, non-stationary spatiotemporal demographic patterns that can influence management success (e.g. achieving a desired harvest level or ecosystem service). In particular, spatial dimensionality, including the explicit definition and treatment of geographic boundaries, is a key component contributing to the success of spatial management procedures because most stock assessment models rely on panmictic unit stock assumptions (Cadrin, 2020). Therefore, ensuring that assessment and biological boundaries coincide is an implicit and critical assumption of any stock assessment application. Adverse and unintended outcomes have been documented when existing population structure and management unit boundaries have inconsistent spatial dimensions (Cope and Punt, 2011; Hintzen *et al.*, 2015; Kerr *et al.*, 2017). A prudent question that remains is how inconsistent they must be to create consequences for management across different sources and extents of spatial structure (drivers of spatial heterogeneity such as maturity, growth, or selectivity patterns as well as connectivity dynamics). Ultimately, spatial management procedures should consider the population components (e.g. spawning contingents or harvest stock) of societal interest that require management action, given fishery objectives and associated risk profiles. The risks of ignoring spatial population structure, or incorrectly identifying it, can be high when it comes to providing management advice (Hutchinson, 2008; Ying *et al.*, 2011; Ciannelli *et al.*, 2013; Goethel and Berger, 2017).

Incoherence between the scale at which ecological processes function and the domain over which management acts can arise primarily in two ways. First, management boundaries can be defined at broad scales with trivial current or historical ecological relevance such as those based on political borders or boundaries of convenience. Second, demarcations that were originally ecologically driven can become distorted due to dynamic oceanographic conditions and non-stationary demography. Non-stationary patterns in oceanographic conditions can influence stock dynamics through changes in recruitment, growth, and maturity, as well as movement patterns of fish resulting in changes in fishery selectivity (or availability) and catchability (Fulton, 2011; Szuwalski and Hollowed, 2016; Kapur *et al.*, 2020; Malick *et al.*, 2020). In some cases, distributional shifts across existing management boundaries can propagate risk associated with localized depletion, population resilience, and vulnerability to overharvest (Kerr *et al.*, 2010; Ciannelli *et al.*, 2013). Even under the most responsive adaptive management procedures, boundary incoherence can persist due to inherent lag-times with data collection, scientific understanding, and policy implementation (King and McFarlane, 2006; Loehle, 2006).

Methodological advancements in stock assessment continue to provide new pathways for incorporating spatial population dynamics into decision-making procedures (Goethel *et al.*, 2011; Berger *et al.*, 2017a; Punt, 2019; Cao *et al.*, 2020). However,

management unit boundaries that define the spatial extent over which regulations act tend to be static and are often determined by convenient or legacy management unit definitions that may not reflect the current biological population unit (Stephenson, 1999; Smedbol and Stephenson, 2001; Reiss *et al.*, 2009). The growing appreciation for the dynamic nature of marine fish populations (Booth, 2000; Pikitch *et al.*, 2004; Berger *et al.*, 2017b) thus generates concern about the implications of misaligned management boundaries (herein, management boundaries are treated as equivalent to stock assessment boundaries) with existing population structure as well as the utility of static boundaries given the dynamic nature of a stock, especially when forecasted to change (e.g. due to climate). This is particularly true for heavily exploited species because ecological disturbances (e.g. fishing) tend to increase variability in abundance (Hsieh *et al.*, 2006; Shelton and Mangel, 2011) and can produce heterogeneous patterns when applied to patches (e.g. non-uniform fishing effort) across a spatial domain (Turner, 1989; Wiens, 1995; Fraterrigo and Rusak, 2008). Furthermore, management units that split populations into separately assessed stocks can result in biased management quantities (e.g. reference points) when recruitment and movement dynamics are not well understood (Ying *et al.*, 2011; McGilliard *et al.*, 2015; Goethel and Berger, 2017; Bosley *et al.*, 2019).

Recent studies have produced mounting scientific evidence to classify “best practice” approaches to identify and incorporate spatial structure into management procedures (Berger *et al.*, 2017b; Punt, 2019; Cadrin, 2020), resulting in a renewed appreciation of spatiotemporal population dynamics (Berger *et al.*, 2017a) when developing management advice (e.g. Van Beveren *et al.*, 2019; Cadrin *et al.*, 2019; Cao *et al.*, 2020). Studies have also specifically looked at the influence of misaligned biological and management units as a result of genetic structure (Reiss *et al.*, 2009), the amount or type of data available to identify stock structure along with institutional inertia countering management unit boundary change (Kerr *et al.*, 2017), and the interaction between stock assessment and management units when spatially varying catch histories drive stock structure (Fu and Fanning, 2004; Cope and Punt, 2011). Cope and Punt (2011), for example used a simulation experiment to show that regional catch histories were important to track when management required regional resolution, confirming the potential risk for local depletion even when stock-wide terminal biomass estimates are unbiased. However, a study has yet to be undertaken that broadly explores the management implications associated with incoherent population and management boundaries across wide range of factors that generate spatial stock structure.

In this article, the bias and risk of misinformed management caused by boundary incoherence between population segments (PSs) and management unit boundaries were explored for several of the primary biological and fishery pathways that produce spatial stock structure (i.e. unique phenotypic features). Specifically, heterogeneous PSs resulting from spatial differences in maturity, growth, selectivity, recruitment, and movement, as well as interactions among these pathways, were investigated. Three study objectives were evaluated using a coupled operating and estimation model (EM) simulation framework, where EMs (or stock assessments) were informed by data incoherent with the underlying PSs. Simulations evaluated how well EMs captured regional dynamics relative to the (true) spatially heterogeneous PSs (i.e. ecological perspective; objective 1), stock assessment areas (AAs)

(i.e. estimation perspective; objective 2), and stock assessment sub-areas created by incoherent boundaries (harvest management perspective; objective 3). Model performance was enumerated for each simulation scenario in terms of estimation bias and risk profiles relative to coherent boundary (spatial alignment) and incoherent boundary (spatial misalignment) areas. Results provide perspective into the potential consequences of misaligning management boundaries with spatial population structure when panmictic, closed-population stock assessment models are used to provide management advice.

## Methods

A generalized simulation–estimation framework, designed to broadly evaluate and enhance the use of spatial processes in stock assessment (Goethel and Berger, 2017; Bosley et al., 2019; Goethel et al., 2019), was adapted to address study objectives (simulation and data generating code available on github: [https://github.com/KateBoz/SPASAM/tree/master/Management\\_Boundaries](https://github.com/KateBoz/SPASAM/tree/master/Management_Boundaries), last accessed 24 June 2020; see Goethel et al., 2019 for a comprehensive treatment of this framework). An operating model (OM) was developed using key parameter values (Table 1) to represent the “true” population dynamics of a generic fish species with the general characteristics of Atlantic herring *Clupea harengus* in the US Northwest Atlantic Ocean [NEFSC (Northeast Fisheries Science Center), 2018]. Data were generated from the OM for use in an EM that made incorrect assumptions about the spatial boundaries of the population represented in the OM. This framework defined the analytical construct from which alternative stock structure scenarios were examined and summary performance metrics were enumerated.

Specific terms are used throughout the paper to describe processes influencing spatial structure and to define the dimensions of spatial units. The term *spatial heterogeneity* refers to the source of area-specific differences in biological or fishery parameters used in OMs, while *connectivity* refers to the mechanisms governing how area-specific populations interact. The term *boundary incoherence* describes the spatial misalignment of population and management/assessment boundaries between operating and EM areas (see Figure 1). *PS* is a semi-discrete, phenotypic group within the population bounded by one or more sources of spatial heterogeneity and corresponds to the true OM areas. *AAs* are delineated by EMs that are either spatially coherent or incoherent with OM areas. *Assessment sub-areas* are further delineated by the intersection (sensu set theory) between *AAs* and *PSs* (Figure 1).

**Table 1.** Parameter values governing the OM were based on a stock assessment for Atlantic herring *Clupea harengus* in the US Northwest Atlantic Ocean (NEFSC (Northeast Fisheries Science Center), 2018).

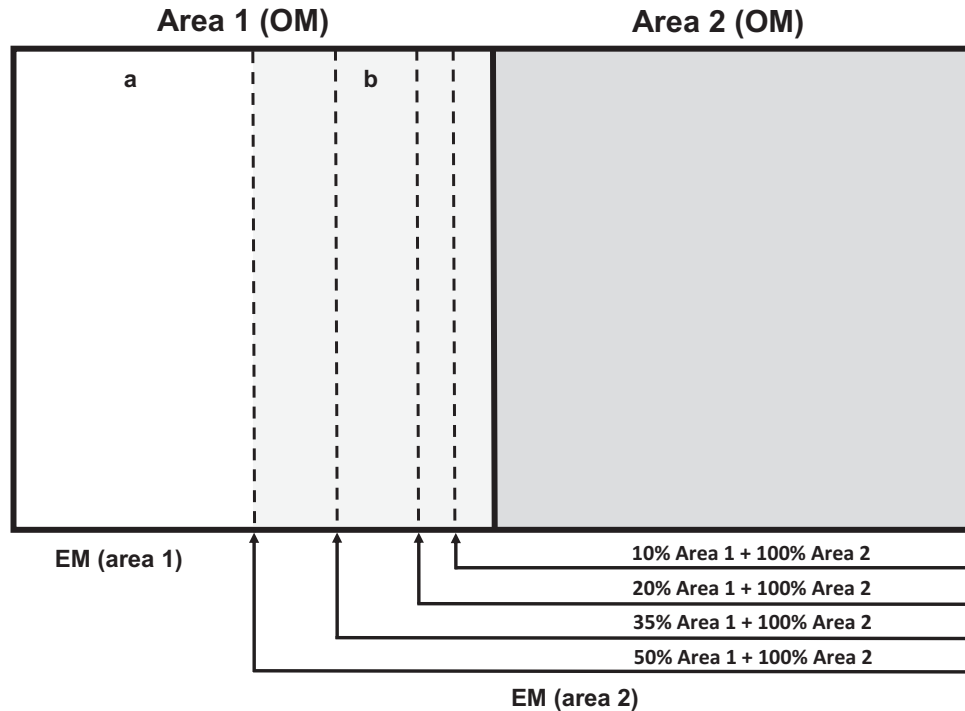
Parameter	Description	Value
$M$	Natural mortality	0.35
$\bar{R}$	Mean recruitment	3 208 750
$\sigma_R$	SD of log recruitment	0.84
$\sigma_F$	SD of log fishing mortality	0.4
$\sigma_Y$	SD of log yield	0.1
$\sigma_I$	SD of log survey index	0.5
$q$	Catchability coefficient for survey	0.0000348

## Study design

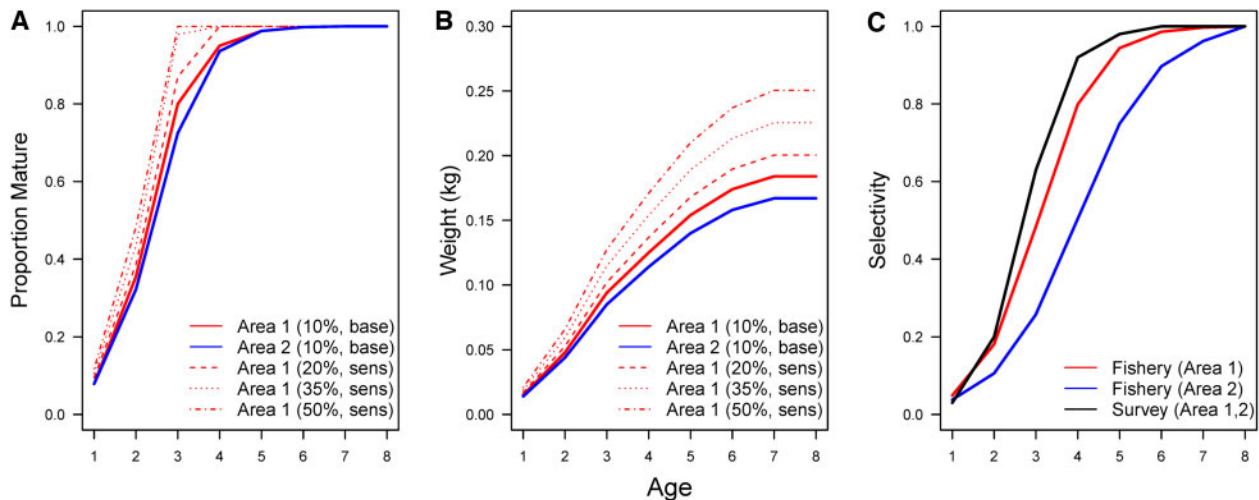
Simulation scenarios were developed that differed by the source of spatial heterogeneity between areas (due to age-specific maturity ogive, scenario  $M$ ; growth,  $G$ ; and selectivity,  $S$ ), connectivity dynamics (recruitment and initial abundance-at-age apportionment,  $Rec$ ; and movement,  $Mov$ ), and the degree of boundary incoherence in the EM with respect to the boundary definition in the OM. The population was defined by two areas (area 1 and area 2) throughout the study to ensure the tractability of results, particularly when spatial heterogeneity was driven by multiple sources. Different sources of spatial heterogeneity were explored either in isolation (i.e. only one source differed between areas) or in combination ( $M$ ,  $G$ , and  $S$ ; or  $MGS$ ), as well as with and without connectivity due to recruitment apportionment ( $Rec$ ) or movement ( $Mov$ ) between areas. When applied in combination, spatial differences were selected so area 1 had larger weights, and higher maturity and selectivity at age than area 2 (i.e. more productive), such that a faster growing fish would likely mature and become selected to fishing gear sooner than a slower growing fish (de Roos et al., 2006). Simulations used a “base” level of heterogeneity (10%) between areas for maturity and growth (i.e. change in area 1 age-specific values relative to area 2) and applied regional trawl fishery selectivity patterns based on herring in the northwest Atlantic (see Figure 2). A set of sensitivity scenarios were also explored that increased the level of spatial heterogeneity (20, 35, and 50%) for maturity and growth.

Scenarios that included connectivity between areas applied different recruitment and initial abundance-at-age apportionment values (hereafter referred to as recruitment apportionment), movement matrices, or both to OM areas. One of the three levels of recruitment apportionment ( $Rec$ ) was examined by area (area 1:area 2): 50:50, 60:40, or 80:20. One of the five levels of unidirectional movement ( $Mov$ ) were examined (emigration rates for area 1:area 2): 0:0, 10:0, 25:0, 0:10, or 0:25. A less than full factorial study design was implemented to reduce the number of scenarios to a tractable number while sacrificing little in terms of inference. As such, each level of recruitment apportionment ( $Rec$ ) and movement rate ( $Mov$ ) was evaluated with all three forms of spatial heterogeneity at once ( $MGS$ ; see Table 2). Furthermore, a complementary set of scenarios where area 2 was more productive than area 1 (the reverse of the default setting) was removed from the study design, effectively halving the total number of simulation scenarios, because initial model runs indicated that this choice had negligible impact on results.

Data were generated from each area of the OM to inform area-specific EMs that assumed single-area, panmictic populations that were either spatially coherent (aligned) or incoherent (misaligned) with the OM (Figure 1). The degree of boundary incoherence in the EM ranged from no boundary misspecification to a relatively high percent of misalignment (i.e. 0, 10, 20, 35, and 50%; see Figure 2). The degree of boundary incoherence between the areas was specified by a fraction,  $p$ , used to assign area-specific data from the OMs to the two misaligned EMs (see *Data Generation* for more details). This amounted to proportionally less data for  $EM_1$  relative to  $OM_1$  by  $p$  (i.e. data from the same *PS* just less data points), and the incorrect inclusion of the remaining  $OM_1$  data with  $OM_2$  data for  $EM_2$  (i.e. weighted average, relative to  $p$ , of data from disparate *PSs*). This design resulted in  $EM_1$  having a boundary that was proportionally too small, and  $EM_2$



**Figure 1.** Stock population boundaries for the OM and alternative EMs (also referred to as “assessment areas”). The OM was specified as two symmetric areas (area 1 and area 2), each representing a different PS defined by governing population dynamics depending on the scenario (see Table 2). The EMs were informed by data that was either spatially coherent with the OM or that was spatially incoherent (misaligned by the degree of boundary incoherence,  $p$ , of 10, 20, 35, or 50%) with the OM. Accordingly, the EM for area 1 (area 2) was always smaller (larger) than the respective OM area, such that area 1a (no shading) represented the area 1 EM and area 1b (light shading) was incorrectly incorporated into the area 2 EM.



**Figure 2.** Differences in (a) maturity, (b) growth, and (c) fishery selectivity between area 1 (red) and area 2 (blue) assumed in the OM. The solid lines represent the level of heterogeneity assumed in simulations (base), which for maturity and growth corresponds to a 10% spatial difference (area 1 relative to area 2) across ages. Sensitivity (sens) to the level of biological heterogeneity (maturity and growth) assumed in OM (non-solid red lines) was examined using spatial differences of 20, 35, and 50% (dashed, dot, and dash-dot lines, respectively). Spatial differences in fishery selectivity were based on regional selectivity patterns for herring in the northwest Atlantic.

with a boundary that was proportionally too big relative to respective OM areas (Figure 1).

The study design resulted in the evaluation of 75 scenarios. For each scenario, a set of 500 simulations spanning 30 years each were conducted to capture variability from process error in

recruitment and fishing mortality and observation error in catch and the survey index of abundance (Table 1). Within each OM area (i.e. PS), fish and fishing effort were assumed to be homogeneously distributed. Movement was assumed to occur instantaneously at the beginning of the year, and local habitat was

**Table 2.** The median relative error (%) in terminal year SSB (top) related to the underlying population segment, PS, (i.e. relative to the true OM spatial areas) is shown by estimation area (A1 = area 1; A2 = area 2) and level of boundary incoherence (none, 10, 20, 35, and 50%) for each spatial heterogeneity and connectivity scenario. The median relative error (%) in TAC (bottom) by assessment estimation sub-areas (A1a, A1b, and A2) and the level of boundary incoherence (none, 10, 20, 35, and 50%) are also shown for each spatial heterogeneity and connectivity scenario (see Figure 1 for further areal descriptions). Scenarios included combinations of spatial heterogeneity from maturity (M), growth (G), selectivity (S), and connectivity via recruitment (Rec) and movement (Mov). The level of spatial heterogeneity assumed for maturity, growth, and selectivity is shown in Figure 2. The proportion of the population recruiting to or moving from areas is identified by the parenthetical (area 1:area 2).

Population segment (SSB)					Degree of boundary incoherence										
Heterogeneity		Connectivity			0%		10%			20%		35%		50%	
M	G	S	Rec	Mov	A1	A2	A1	A2	A1	A2	A1	A2	A1	A2	
×			(50:50)	(0:0)	-0.7	-1.5	-9.8	16.5	-18.9	27.6	-32.3	43.2	-45.8	57.7	
	×		(50:50)	(0:0)	-0.2	-1.5	-9.3	17.2	-18.3	28.9	-32.0	46.1	-45.6	60.7	
		×	(50:50)	(0:0)	-0.6	-1.4	-9.5	14.4	-18.6	24.2	-32.1	40.3	-45.8	55.4	
×	×	×	(50:50)	(0:0)	-1.4	-1.5	-10.2	15.9	-19.2	27.6	-32.6	45.6	-46.2	62.4	
×	×	×	(60:40)	(0:0)	-1.4	-2.3	-10.3	22.3	-19.2	39.9	-32.6	66.1	-46.1	91.7	
×	×	×	(80:20)	(0:0)	-1.5	-2.3	-10.2	51.9	-19.2	97.8	-32.6	162.0	-46.1	229.3	
×	×	×	(50:50)	(10:0)	-19.6	8.0	-26.5	20.7	-33.7	26.8	-44.3	36.1	-55.1	44.9	
×	×	×	(50:50)	(25:0)	-42.8	6.0	-47.6	21.1	-52.4	33.3	-59.6	31.7	-66.8	36.5	
×	×	×	(50:50)	(0:10)	11.2	-18.2	1.1	9.2	-9.1	31.1	-24.4	63.9	-39.8	97.5	
×	×	×	(50:50)	(0:25)	10.3	-43.5	0.3	16.1	-9.8	63.9	-25.0	137.8	-40.2	212.5	
×	×	×	(60:40)	(25:0)	-42.7	7.2	-47.4	24.4	-52.3	29.3	-59.6	35.0	-66.8	39.5	
×	×	×	(60:40)	(0:25)	9.9	-44.0	-0.1	14.8	-10.3	61.4	-25.6	132.4	-40.6	204.1	

Assessment sub-area (TAC)					Degree of boundary incoherence														
M		Connectivity			0%		10%			20%		35%		50%					
M	G	S	Rec	Mov	A1a	A1b	A2	A1a	A1b	A2	A1a	A1b	A2	A1a	A1b	A2			
×			(50:50)	(0:0)	-0.2	-	0.0	-0.4	1.8	2.0	-0.1	2.8	2.8	0.1	3.0	3.0	-0.4	2.6	2.7
	×		(50:50)	(0:0)	0.7	-	0.0	0.2	-5.4	3.2	0.3	-4.0	4.7	0.4	-2.9	6.0	0.2	-2.7	6.2
		×	(50:50)	(0:0)	0.2	-	0.6	-0.1	-8.1	3.1	1.0	-5.3	6.4	0.3	-1.7	10.5	-0.6	-1.1	11.2
×	×	×	(50:50)	(0:0)	0.7	-	0.0	0.6	-15.0	4.5	0.1	-11.7	8.7	0.2	-8.3	12.9	0.6	-6.0	15.8
×	×	×	(60:40)	(0:0)	0.2	-	0.2	0.4	-38.1	12.2	0.1	-34.6	19.5	0.4	-29.9	28.3	0.4	-25.6	36.3
×	×	×	(80:20)	(0:0)	0.9	-	0.0	1.0	-69.4	41.2	0.5	-63.3	72.5	0.7	-55.1	113.9	0.1	-48.9	145.0
×	×	×	(50:50)	(10:0)	-15.4	-	3.0	-16.0	65.6	4.7	-15.4	65.4	2.5	-15.0	61.3	-0.3	-15.7	58.6	-2.0
×	×	×	(50:50)	(25:0)	-35.7	-	1.6	-35.9	264.0	1.3	-35.9	254.4	-2.2	-35.4	238.5	-6.8	-35.7	226.5	-10.1
×	×	×	(50:50)	(0:10)	14.0	-	-16.2	13.2	-57.6	5.5	10.5	-53.4	18.4	11.1	-45.7	38.5	11.1	-40.6	52.2
×	×	×	(50:50)	(0:25)	12.1	-	-39.2	11.3	-77.1	31.0	10.2	-70.1	80.1	10.2	-61.1	139.1	9.3	-54.3	183.3
×	×	×	(60:40)	(25:0)	-36.4	-	2.7	-36.0	273.2	2.7	-35.3	262.0	-0.4	-35.6	248.5	-4.1	-35.1	233.7	-8.1
×	×	×	(60:40)	(0:25)	11.7	-	-38.9	8.6	-77.8	30.3	9.2	-70.4	78.2	8.7	-61.8	134.1	8.3	-54.9	179.1

assumed to govern biology such that fish moving across boundaries adopt area-specific biological parameters.

**Operating model**

The OM defined age-based (8 age-classes with age-8 being a plus group) population dynamics for a single population with heterogeneity between two areas (Figure 1) that operated on an annual time step. Total recruitment at age-1 for each year (y) and simulation (s),  $R_{s,y}$ , for the entire population was assumed to vary around a mean,  $\bar{R}$ :

$$R_{s,y} = \bar{R} e^{\epsilon_{s,y}^R - \frac{\sigma_R^2}{2}}; \epsilon_{s,y}^R \sim N(0, \sigma_R^2). \tag{1}$$

The proportion of the total annual recruitment apportioned to each area differed according to scenario but was invariant across years and simulations within a given scenario. The maturity-at-age ogive, mean stock weight at age, and mean catch weight-at-age values were initially specified based on recently reported values for Atlantic herring in the northwest Atlantic Ocean

[NEFSC (Northeast Fisheries Science Center), 2018], with alterations imposed by spatial area for specific scenarios as part of the study design (Figure 2). Within each scenario, maturities and weights at age were constant.

Fish were subjected to a single fishing fleet with selectivity that was year- and simulation-invariant and followed a logistic shape that differed by area (Figure 2). Asymptotic selectivity at age was used to approximate patterns typical of trawl gear. Fully selected annual instantaneous fishing mortality rates by area (r),  $F_{s,r,y}$ , were specified as a linear increase for the first half of each time series followed by a linear decrease during the second half of each time series, with process error applied across simulations for each scenario, according to:

$$F_{s,r,y} = \bar{F}_y e^{\epsilon_{s,y}^F - \frac{\sigma_F^2}{2}}; \epsilon_{s,y}^F \sim N(0, \sigma_F^2), \tag{2}$$

where  $\bar{F}_y$  describes the year-specific fully selected fishing mortality on the linear increase/decrease time series. The  $\bar{F}_y$  time series began and ended at a minimum value of 0.07 and reached a

maximum value of 0.60 in the middle of the time series. The minimum and maximum fishing mortality rates were similar to extremes estimated for Atlantic herring in the northwest Atlantic Ocean [NEFSC (Northeast Fisheries Science Center), 2018]. The standard deviation (*SD*) of log fishing mortality ( $\sigma_F = 0.4$ ) was consistent with the stock assessment [NEFSC (Northeast Fisheries Science Center), 2018] and ensured that results were not driven by unrealistically low variation in the fishing process. Instantaneous natural mortality,  $\hat{M}$ , was set to 0.35 [NEFSC (Northeast Fisheries Science Center), 2018] for all area, age, year, and simulation combinations. Fish were assumed to die according to an area-, age-, year-, and simulation-specific total instantaneous mortality rate,  $Z_{s,r,a,y}$ :

$$N_{s,r,a+1,y+1} = N_{s,r,a,y} e^{-Z_{s,r,a,y}}, \quad (3)$$

$$Z_{s,r,a,y} = F_{s,r,a,y} + \hat{M}, \quad (4)$$

where  $F_{s,r,a,y}$  equalled the product of  $F_{s,r,y}$  and fishery selectivity at age. For movement scenarios, the above abundance equation was simply adapted by calculating the abundance before movement for a given area, year, age, and simulation from the abundance after movement in the previous year and age because movement was assumed to occur instantaneously at the beginning of each year. Catch,  $C_{s,r,a,y}$ , in each area was a function of abundance and mortality following Baranov's catch equation:

$$C_{s,r,a,y} = \frac{F_{s,r,a,y}}{Z_{s,r,a,y}} N_{s,r,a,y} (1 - e^{-Z_{s,r,a,y}}), \quad (5)$$

where  $N$  was abundance after movement (if movement occurred) and was multiplied by area-specific catch weights at age,  $W_{r,a}$ , to calculate yield ( $t$ ),  $Y_{s,r,y}$ :

$$Y_{s,r,y} = \sum_{a=1}^{8+} C_{s,r,a,y} W_{r,a}. \quad (6)$$

### Data generation

Data generated from each area of the OM were aggregated according to fraction,  $p$  (or the degree of boundary incoherence), for each set of EMs for each scenario. The reorganization of area-specific OM data into disjoint EMs, through the use of  $p$ , was intended to approximate conducting a stock assessment using data from a spatial area that does not align with the "true" spatial boundaries. Equivalently, fraction  $p$  can be considered the proportion of OM<sub>1</sub> data that was excluded from EM<sub>1</sub> (and thus included in EM<sub>2</sub>) for incoherent boundary scenarios. This design necessarily implies that fish in each area were assumed evenly distributed, or equivalently that the degree of incoherence refers to the portion of the well-mixed population rather than portion of area as framed throughout the paper.

A survey index of abundance time series, fishery data, and age compositions were generated for each simulation. An annual survey index of abundance,  $\hat{I}_{s,r,y}$ , was generated assuming area-, year-, and simulation-invariant catchability,  $q$ , and asymptotic selectivity at age,  $S_a$  (Table 1 and Figure 2):

$$\begin{aligned} \hat{I}_{s,r=EM_1,y} &= \sum_{a=1}^{8+} (1-p) N_{s,r=OM_1,a,y} S_{a,r=OM_1} q e^{\epsilon_{s,y}^I - \frac{\sigma_I^2}{2}}; \quad \epsilon_{s,y}^I \sim N(0, \sigma_I^2), \\ \hat{I}_{s,r=EM_2,y} &= \sum_{a=1}^{8+} (p N_{s,r=OM_1,a,y} + N_{s,r=OM_2,a,y}) S_{a,r=OM_2} q e^{\epsilon_{s,y}^I - \frac{\sigma_I^2}{2}}; \quad \epsilon_{s,y}^I \sim N(0, \sigma_I^2), \end{aligned} \quad (7)$$

where  $N$  was abundance after movement and  $p$  was the degree of boundary incoherence to be included in the EM. Annual total yield observed with error,  $\hat{Y}_{s,y}$ , from the fishery was combined among areas in a similar way as for the survey indices:

$$\begin{aligned} \hat{Y}_{s,r=EM_1,y} &= (1-p) Y_{s,r=OM_1,y} e^{\epsilon_{s,y}^Y - \frac{\sigma_Y^2}{2}}; \quad \epsilon_{s,y}^Y \sim N(0, \sigma_Y^2), \\ \hat{Y}_{s,r=EM_2,y} &= (p Y_{s,r=OM_1,y} + Y_{s,r=OM_2,y}) e^{\epsilon_{s,y}^Y - \frac{\sigma_Y^2}{2}}; \quad \epsilon_{s,y}^Y \sim N(0, \sigma_Y^2), \end{aligned} \quad (8)$$

$$\hat{Y}_{s,y} = \sum_{i=1}^2 \hat{Y}_{s,r=EM_i,y}. \quad (9)$$

Observed age compositions for the fishery and survey,  $P_{s,r,a,y}$  were generated by drawing annual samples from a multinomial distribution, with the annual proportions at age equal to true proportions at age, and aggregated by EM area using  $p$  as previously described. Annual effective sample sizes were fixed at 100 to provide relatively informative age-composition data while avoiding unrealistically frequent occurrences of zero observations in the age composition that can be produced with sample sizes derived from iterative reweighting procedures commonly used in stock assessments (Francis, 2011; Deroba *et al.*, 2015).

Biological data included annual input weights at age,  $\hat{W}_{s,r,a,y}$  (i.e. growth), and maturity at age, which were summarized as catch-weighted mean values for each misaligned area in the EM:

$$\begin{aligned} \hat{W}_{s,r=EM_1,a,y} &= W_{s,r=OM_1,a,y}, \\ \hat{W}_{s,r=EM_2,a,y} &= \frac{[(W_{s,r=OM_1,a,y} p Y_{s,r=OM_1,y}) + (W_{s,r=OM_2,a,y} Y_{s,r=OM_2,y})]}{Y_{s,y}}. \end{aligned} \quad (10)$$

The catch-weighted mean maturity-at-age values were calculated as in (10) for weights at age, except with  $W_{s,r,a,y}$  replaced with the area-specific maturity-at-age values. While the true age-specific weight and maturity values were year-invariant, the resulting catch-weighted mean quantities developed as data for each misaligned EM were year-specific due to annual dependence on the proportion of the catch coming from each area. Using a catch-weighted approach to aggregate biological data assumed that fish in each area were randomly distributed spatially and sampled randomly (e.g. as in a portside sampling program randomly sampling landings).

### Estimation models

The EMs matched the population dynamics of the OM except that each EM assumed a single-area, panmictic population, whereas the OM was a single population with spatial heterogeneity. EMs were fit to generated data using maximum likelihood. Standard lognormal likelihood components were used for fits to the survey indices,  $\hat{I}_y$ , and total annual yield,  $\hat{Y}_y$ , with *SDs* set to their respective OM values. A multinomial likelihood was used for fits to fishery and survey age-composition data, with effective

sample sizes set to those used in the OM. Estimated parameters included initial abundance at age in year 1 of the time series, an underlying mean recruitment scalar, annual recruitment deviations around the underlying mean, annual fully selected fishing mortality, fishery and survey selectivity, and survey catchability. All parameters were initialized at their correct (i.e. OM) values. Following from the study design, each EM was fit to 500 generated datasets, each 30 years long, for each of the 75 scenarios. A self-test consistency evaluation (*sensu* Deroba *et al.*, 2015) was performed prior to the evaluation of alternative scenarios using the EM where assumptions and boundary coherence matched that of the OM. All EMs that did not converge were tallied and excluded from further analysis, including summarizing simulation performance metrics.

### Performance metrics

The performance of each scenario was summarized by calculating bias [median relative error (MRE)] and risk (probability thresholds) associated with each set of simulation runs. Specific definitions of bias and risk were developed for each study objective (i.e. relative to PSs, AAs, and assessment sub-areas).

### Population segments

The MRE associated with the terminal year estimate of spawning stock biomass (SSB) was used as a performance measure to describe estimation bias relative to the true heterogeneous PS SSB for each simulation scenario.

$$\text{MRE}_r^{\text{PS}} = \frac{\text{SSB}_r^{\text{EM}} - \text{SSB}_r^{\text{OM}}}{\text{SSB}_r^{\text{OM}}}. \quad (11)$$

The MRE was calculated using the true SSB from area 1 and the estimated value from EM<sub>1</sub>, while the true SSB from area 2 was used with the estimated value from EM<sub>2</sub>. The MRE was also calculated using the sum of the SSB estimates from each EM and the system-wide true SSB (i.e. summed over both areas). The interquartile range of terminal year SSB was used as a summary measure of variability across simulations associated with each scenario. Risk relative to the underlying PSs was characterized as the proportion of spatially incoherent EM simulation runs that exceeded 1 *SD* of the terminal SSB estimate from EM simulation runs with spatially coherent boundaries. In effect, this definition of risk quantified potential management concern related to benefits that individual PSs provide (e.g. ecosystem service). Risk was also quantified for different levels of precision tolerance [i.e. increasing or decreasing the precision threshold, *SD*, using different values for the coefficient of variation (*C.V.*)], as has been done at regional fishery management councils (Ralston *et al.*, 2011; Privitera-Johnson and Punt, 2020) and within scientific advisory bodies (e.g. ICES, 2017) to categorize overall levels of stock assessment uncertainty and specify reference points. For example, the uncertainty associated with terminal year SSB estimates is often used to characterize the precision of stock size information being passed on to management, where more imprecise information leads to larger precautionary buffers (i.e. reduces allowable catch), thereby explicitly incorporating risk into management action.

### Assessment areas

Mean relative error (MRE) in the terminal year estimate of SSB was also used as a performance measure to describe estimation bias relative to the estimation area (or AA) amalgamated OM SSB for each simulation scenario:

$$\begin{aligned} \text{MRE}_{r=1}^{\text{AA}} &= \frac{\text{SSB}_1^{\text{EM}} - (\text{SSB}_1^{\text{OM}} (1 - p))}{\text{SSB}_1^{\text{OM}} (1 - p)}, \\ \text{MRE}_{r=2}^{\text{AA}} &= \frac{\text{SSB}_2^{\text{EM}} - (\text{SSB}_2^{\text{OM}} + (\text{SSB}_1^{\text{OM}} p))}{\text{SSB}_2^{\text{OM}} + (\text{SSB}_1^{\text{OM}} p)}. \end{aligned} \quad (12)$$

The degree of boundary incoherence, fraction *p*, was used to amalgamate OM SSB to match the estimation area. This metric evaluates amalgamated population sizes by area, but it ignores potential localized harvest impacts to misaligned areas.

### Assessment sub-areas

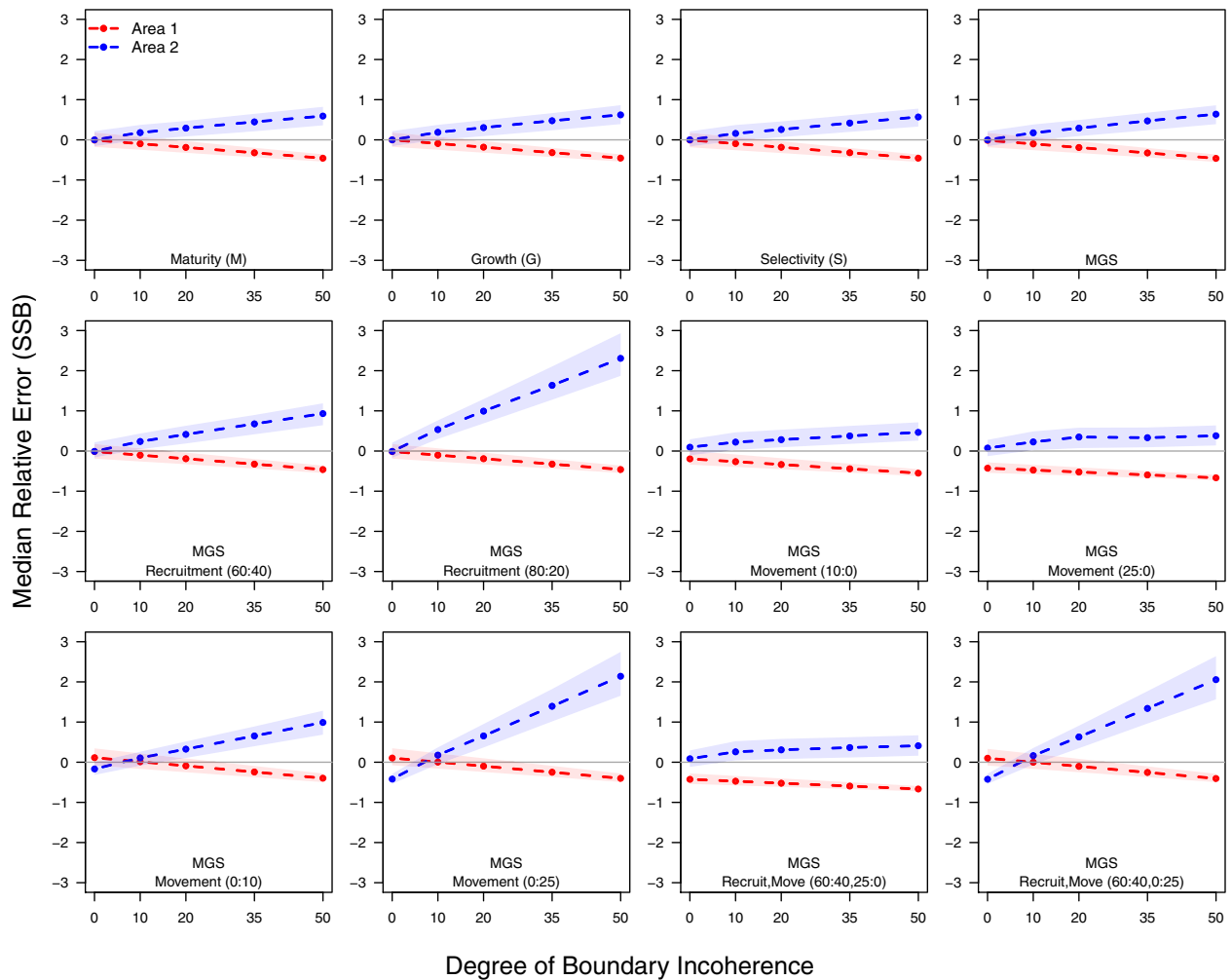
Mean relative error (MRE) in terminal year estimate of total allowable catch (TAC) was used as a performance measure to describe estimation bias relative to the intersection between true and misaligned component sub-areas (area 1a = OM<sub>1</sub> ∩ EM<sub>1</sub>, area 1b = OM<sub>1</sub> ∩ EM<sub>2</sub>, and area 2 = OM<sub>2</sub> ∩ EM<sub>2</sub>; Figure 1) for each simulation scenario. This measure describes assessment-based harvest impacts to PSs by area and sub-area (sAA) created by boundary misalignment.

$$\begin{aligned} \text{MRE}_{r=1a}^{\text{sAA}} &= \frac{\text{TAC}_1^{\text{EM}} - (\text{TAC}_1^{\text{OM}} (1 - p))}{\text{TAC}_1^{\text{OM}} (1 - p)}, \\ \text{MRE}_{r=1b}^{\text{sAA}} &= \frac{\left(\text{TAC}_2^{\text{EM}} \frac{p}{1+p}\right) - (\text{TAC}_1^{\text{OM}} p)}{\text{TAC}_1^{\text{OM}} p}, \\ \text{MRE}_{r=2}^{\text{sAA}} &= \frac{\left(\text{TAC}_2^{\text{EM}} \frac{1}{1+p}\right) - \text{TAC}_2^{\text{OM}}}{\text{TAC}_2^{\text{OM}}}. \end{aligned} \quad (13)$$

The MRE associated with area-specific TAC provides an indication of the potential for over- and under-harvest. Simulation-specific regional selectivity patterns and terminal year biomass at age were used along with a fixed harvest rate (fully selected fishing mortality = 0.25) to calculate area-specific terminal year TAC. The particular value assumed for the fishing mortality rate was effectively a scalar on TAC and, thus, was inconsequential because MRE is a relative measure. Risk relative to sub-area-specific TAC (i.e. assessment-driven management advice) was characterized as the proportion of EM runs that exceeded 1 *SD* of the true area-specific TAC as determined by OM output amalgamated by area and sub-area created by boundary incoherence (eq. 13). This definition of risk was used to quantify potential management concern related to localized harvest specifications.

## Results

Area-specific EMs performed well (MRE at or near zero; Figure 3) when model assumptions matched and spatial boundaries were perfectly aligned with OM areas (i.e. self-test scenario). The mean convergence rate for each set of 500 simulation runs was 99.4% across all 75 simulation scenarios (minimum = 90.0%). For all perfectly aligned scenarios, there was minimal bias in system-wide terminal SSB (MRE ranged from -0.01 to 0.03), as biases for EM<sub>1</sub> (area 1) and EM<sub>2</sub> (area 2) were nearly offsetting



**Figure 3.** The median relative error of terminal year SSB is shown by area (area 1 = red dashed line; area 2 = blue dashed line) as related to the underlying PS (i.e. true OM spatial areas) for each of five levels of boundary incoherence (none, 10, 20, 35, and 50%) per scenario set (panels). The top row represents scenarios without connectivity (combinations of spatial heterogeneity from maturity  $M$ , growth  $G$ , and selectivity  $S$ ), while the second and third rows include scenarios with the addition of connectivity (via recruitment  $Rec$  and movement  $Move$ ). The level of spatial heterogeneity assumed for maturity, growth, and selectivity is shown in Figure 2. The proportion of the population recruiting to or moving from areas is identified by the parenthetical (area 1:area 2). Shading represents the 25th and 75th interquartile ranges of relative error.

in direction and magnitude. Therefore, results focus on mismatched area-specific results.

### Population segments

Spatially incoherent population and management unit boundaries created bias in area-specific estimates of stock (PS) size relative to the true underlying PSs when population structure was due to heterogeneity in maturity ( $M$ ), growth ( $G$ ), and selectivity ( $S$ ). As expected, bias generally increased with the degree of boundary incoherence, averaging  $\pm 12.9\%$  MRE (at 10% boundary incoherence) to  $\pm 52.4\%$  MRE (at 50% boundary incoherence; Table 2 and Figure 3) across all scenarios (i.e. on average, bias was about the same as boundary incoherence). For scenarios with differences attributable to the source of heterogeneity (i.e.  $M$ ,  $G$ ,  $S$ , and the combination of all three sources,  $MGS$ ), the level of boundary incoherence between the OM and EMs was the largest driver of bias (near 20-fold increase in bias across the range of

boundary incoherence examined relative to differences attributable to the source of heterogeneity alone; Table 2). The median bias was smaller for area 1 compared to area 2 because all data used in  $EM_1$  were sampled from area 1, whereas  $EM_2$  used a portion of area 1 ( $p$ ) and area 2 data. In general, bias was negative for area 1, primarily reflecting the loss of SSB relative to  $OM_1$ , and was positive for area 2. The relationship between bias and degree of boundary incoherence was largely linear for both areas, including when all three sources were combined ( $MGS$ ; Figure 3). The interquartile range of SSB across simulation runs suggested SSB for area 2 was about twice as variable on average as SSB for area 1, with variability increasing (decreasing) with the degree of boundary incoherence for area 2 (area 1), and was slightly larger when heterogeneity was due to differences in growth than when formed by differences in maturity or selectivity alone (Supplementary Table S1 and Supplementary Figure S1).

The addition of connectivity dynamics in the OM generally led to larger EM discrepancies relative to underlying PSs.



Independent EMs not accounting for recruitment apportionment (*Rec*) or movement (*Mov*) mostly led to an increase in median bias in one area or the other at each level of boundary incoherence (Table 2 and Figure 3) and more disparity in the variability of terminal SSB between areas (Supplementary Table S1 and Supplementary Figure S1). Unequal recruitment apportionment (*Rec*) mostly affected area 2 (Figure 3), where the MRE was related to the level of disparity between areas and the degree of boundary incoherence. This was a direct result of a larger proportion of biomass being attributed to area 2 from area 1 when boundaries were misaligned. The direction and proportion of the stock moving had the largest effect on MREs across all scenarios, with emigration resulting in negative bias and the rate of movement either reducing (area 1) or exacerbating (area 2) the effect of boundary incoherence (Figures 3). Variability was generally reduced in area 1 and enlarged in area 2 as the degree of boundary incoherence increased (Supplementary Figure S1). The main exception was movement scenarios depicting emigration from area 1 to area 2 where variability was relatively insensitive to boundary incoherence (Supplementary Table S1 and Supplementary Figure S1) due to the underlying mismatch between the independent EMs (no connectivity) and the OM movement dynamics driving population structure (and thus extensively violating EM assumptions of homogeneity). The near concordance between combined recruitment and movement scenarios and movement only scenarios indicate that movement was a stronger driver of bias in terminal year SSB (Figure 3).

Risk associated with misinformed management relative to the underlying true PSs appreciably increased with the degree of boundary incoherence (Table 3). If, for example a 50% C.V. associated with the terminal year biomass estimate was a management decision threshold [e.g. linked to the size of an uncertainty buffer between the overfishing limit (OFL) and the allowable biological catch], the risk of being incorrect by more than one *SD* increases up to 13-fold when boundaries are vastly misaligned (50% incoherence) compared to when slightly misaligned (10% incoherence). Although measures of risk can be related to the level of stochasticity assumed in the OM and parameter uncertainty in the EMs, relative differences provide a robust indication while absolute values should be considered minimums given simplifications inherent with simulations (Punt *et al.*, 2015). For reference, the C.V. associated with terminal year SSB from EM runs with spatially coherent boundaries was 59% for area 1 and 57% for area 2.

Sensitivity runs that increased the level of spatial heterogeneity associated with maturity and growth OM scenarios to levels >10% (i.e. 20, 35, and 50%) led to area-specific characteristics (Figure 4). There was almost no change in bias in area 1 with increasing heterogeneity; however, uncertainty as characterized by the interquartile range (Supplementary Figure S2) increased with increasing heterogeneity and decreased with increasing boundary incoherence. Bias in area 2 increased with increasing boundary incoherence, but the rate of increase steepened with higher levels of spatial heterogeneity, suggesting a multiplicative effect between spatial population structure and management misspecification of boundaries. Uncertainty in area 2 (Supplementary Figure S2) was more similar among levels of heterogeneity than in area 1 and increased with boundary incoherence.

## Assessment areas

Bias relative to AA terminal year SSB was reduced compared to bias associated with the underlying PS SSB (Figure 5) because misaligned AAs effectively averaged over data from separate PSs, thereby reducing the capability to explicitly manage unique components of the population. Across all simulation scenarios, there was generally minor AA bias in area 1, whereas in area 2 there was increasing bias with the degree of boundary incoherence (up to 2–24% depending on scenario when 50% incoherent). Thus, estimation bias is particularly critical for AAs that encapsulate PS boundaries (EM area 2 in this case) because resulting management decisions (e.g. harvest rates) will be applied across different PSs.

## Assessment sub-areas

Incoherent population and management unit boundaries created differing levels of harvest bias relative to sub-areas created by boundary incoherence. In general, MRE trends in TAC across the degree of boundary coherence (Table 2 and Figure 6) were similar in direction and magnitude to MRE associated with true PS SSB (Table 2 and Figure 3). The main exceptions were differences in overall scale (MRE generally reduced for TAC) and increased error associated with area 1b (i.e. the estimation area encapsulating the area of boundary incoherence) relative to area 1a (Figure 6). Specifically, there was near zero bias (heterogeneity scenarios: *M*, *G*, and *S*) or reduced bias relative to other sub-areas (connectivity scenarios: *Rec* and *Mov*) associated with area 1a due to stock assessment data being solely from the correct PS. In contrast, there was considerable bias in estimated TAC associated with area 1b and area 2, suggesting local over- and under-harvest relative to true TAC given intended harvest rates. Bias in these areas was due to the amalgamation of data across differing PSs used in the misaligned EM (stock assessment) for each scenario. Although area-specific bias was related to the level of boundary incoherence, alternative forms of connectivity between PSs resulted in the largest changes to bias among scenarios examined (Figure 6) and increased disparity in the variability of TAC between sub-areas (Supplementary Table S1 and Supplementary Figure S3). Sensitivity runs that increased the level of spatial heterogeneity in maturity and growth in the OM to levels greater than 10% (i.e. 20, 35, and 50%) had no influence on area 1a TAC and had the effect of increasing error in area 1b (negative MRE) and area 2 (positive MRE) with increasing heterogeneity (Figure 4).

Risk associated with misinformed management relative to sub-area-specific assessment-driven management advice was relatively stable across the degree of boundary incoherence for a given level of precision tolerance (C.V.) using scenario *MGS* (Table 3). This insensitivity was a result of a near constant proportional change between the variability in TAC across assessment runs and the degree of boundary incoherence. The main exception was in area 1b where variability proportionally decreased with size of assessment misalignment, implying risk reduction (Table 3). Overall, risk was highest in area 1b, followed by area 1a and area 2.

## Discussion

Spatial structure is a key characteristic defining ecological boundaries (Strayer *et al.*, 2003), yet management boundaries typically do not fully complement important ecological transition points within a stock or population, potentially leading to portions of the same population being unassessed or assessed with incorrect

**Table 3.** Risk associated with using spatially incoherent models to estimate stock status (top) and TAC (bottom) are shown using spatial scenario MGS (maturity, growth, and selectivity; see Figure 2 for details). For all panels, proportions are conditionally shaded (scale: 0–1) so that darker boxes correspond to higher risk.

Population Segment (SSB)								
Area 1					Area 2			
C.V.	Degree of boundary incoherence				Degree of boundary incoherence			
	10%	20%	35%	50%	10%	20%	35%	50%
10%	0.38	0.89	0.98	0.99	0.67	0.91	0.99	0.99
20%	0.05	0.38	0.83	0.94	0.30	0.66	0.91	0.98
30%	0.01	0.14	0.56	0.79	0.16	0.37	0.74	0.90
40%	0.00	0.05	0.29	0.60	0.09	0.21	0.53	0.77
50%	0.00	0.02	0.18	0.38	0.05	0.14	0.36	0.62
60%	0.00	0.01	0.08	0.27	0.04	0.09	0.24	0.46
70%	0.00	0.00	0.05	0.19	0.02	0.06	0.18	0.35
80%	0.00	0.00	0.03	0.12	0.01	0.04	0.13	0.25
90%	0.00	0.00	0.02	0.07	0.01	0.02	0.08	0.20
100%	0.00	0.00	0.01	0.05	0.01	0.01	0.05	0.16

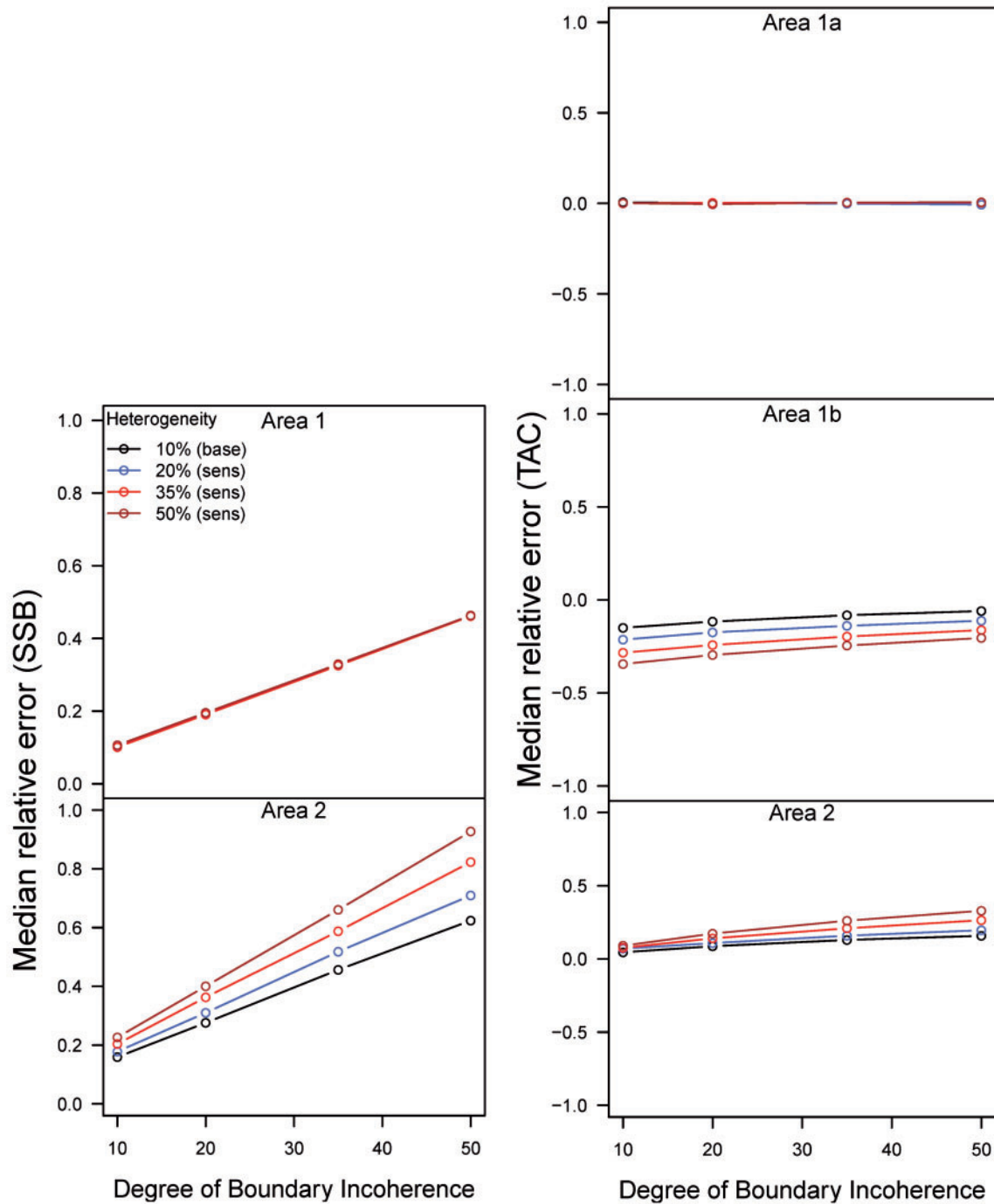
Assessment sub-area (TAC)								
Area 1a					Area 2			
C.V.	Degree of boundary incoherence				Degree of boundary incoherence			
	10%	20%	35%	50%	10%	20%	35%	50%
10%	0.68	0.68	0.68	0.68	0.65	0.63	0.61	0.62
20%	0.44	0.43	0.43	0.43	0.37	0.37	0.39	0.41
30%	0.24	0.24	0.24	0.24	0.22	0.21	0.21	0.24
40%	0.15	0.15	0.15	0.15	0.12	0.12	0.12	0.14
50%	0.09	0.09	0.09	0.10	0.07	0.06	0.07	0.09
60%	0.06	0.06	0.06	0.07	0.05	0.04	0.04	0.05
70%	0.05	0.04	0.04	0.05	0.03	0.02	0.02	0.03
80%	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
90%	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01
100%	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01

Area 1b				
C.V.	Degree of Boundary Incoherence			
	10%	20%	35%	50%
10%	0.71	0.70	0.64	0.63
20%	0.49	0.44	0.39	0.39
30%	0.30	0.30	0.27	0.23
40%	0.21	0.19	0.13	0.11
50%	0.11	0.10	0.07	0.06
60%	0.07	0.06	0.04	0.04
70%	0.03	0.03	0.03	0.02
80%	0.03	0.02	0.01	0.02
90%	0.01	0.01	0.01	0.01
100%	0.01	0.01	0.00	0.00

Risk related to heterogeneous PSs (top) is defined as the proportion of spatially incoherent EM runs that exceed 1 SD of the terminal SSB estimate from EM runs with no boundary incoherence for different levels of precision tolerance (i.e. C.V.). For example, higher values indicate increased risk of specifying stock status incorrectly relative to the true spatial PS due to mismatched areal boundary lines that create non-homogeneity between population units (i.e. boundary incoherence). The mean C.V. associated with EM runs with coherent boundaries was 59% for area 1 and 57% for area 2. Alternative C.V.s are shown to provide a broader risk profile perspective and because measures of precision are related to simulation experiment specifications about observation and process errors.

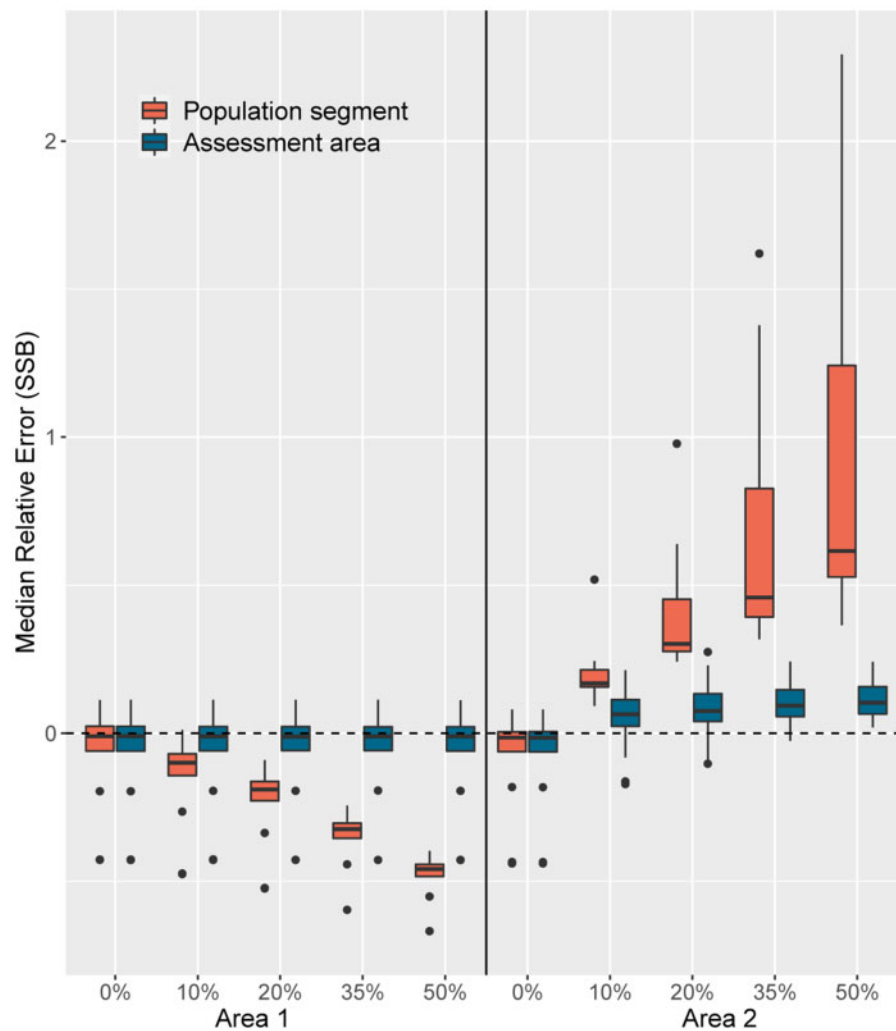
Risk related to area-specific assessment-driven management advice (TAC; bottom) is defined as the proportion of EMs that exceed 1 SD of the true assessment sub-area-specific TAC as determined by OMs.



**Figure 4.** Simulation sensitivity to the underlying level of biological heterogeneity assumed between OM areas. Spatial differences in the maturity and growth of 10% (base) were assumed in the main set of simulations. Sensitivity (sens) in the median relative error for SSB is shown relative to area 1 and area 2 PSs (true OM spatial areas; left panels) and for TAC relative to assessment sub-areas (1a, 1b, and 2) formed by the intersection of assessment and population areas (where the true OM TAC was amalgamated by sub-areas; right panels) for 20, 35, and 50% spatial differences in maturity and growth. Sensitivity evaluations were performed using scenario MGS.

assumptions (e.g. homogenous unit). Furthermore, non-stationary environmental processes that impact habitat suitability for growth, survival, and reproduction can alter spatial structuring of population units such that these portions increase or decrease over time leading to stock assessment bias (Szuwalski and Hollowed, 2016; Kerr *et al.*, 2017). Multi-species fisheries can

reinforce the use of misaligned assessment boundaries when accompanied by common management boundaries for a suite of species that are not closely linked to stock boundaries for any of them. Management procedures inherently include an explicit treatment of boundaries that define the resource units that regulations act upon, and research evaluating the effects of incorrectly



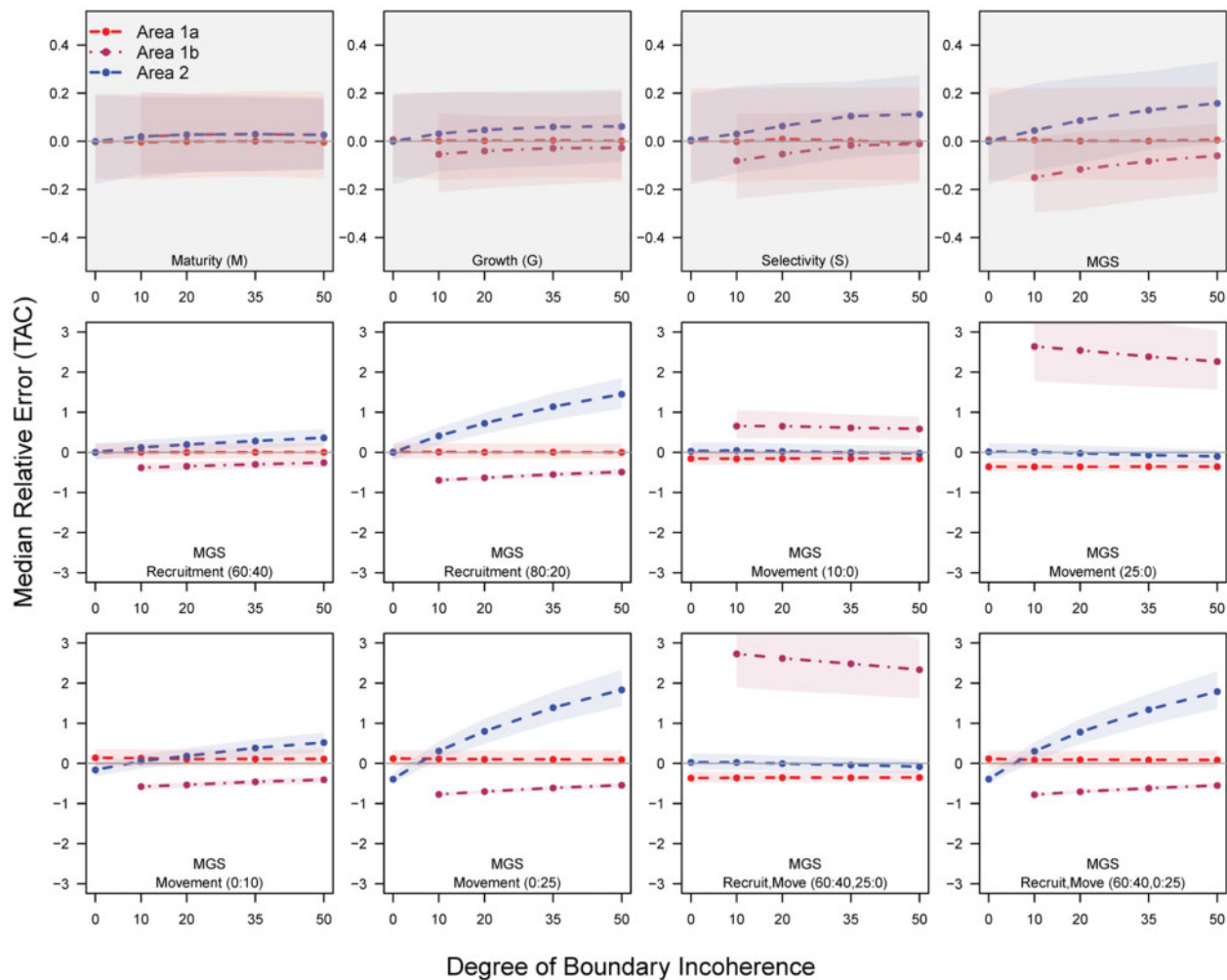
**Figure 5.** The median relative error of estimated terminal year spawning biomass is shown relative to PS (true OM spatial areas; red) and by AA (true OM amalgamated by estimation area; blue) for each of five levels of boundary incoherence (none, 10, 20, 35, and 50%) and areas (1 and 2). Box plots represent the consolidation of MREs across all heterogeneity and connectivity scenarios (see Table 2 for further scenario details). Box plots are configured with a within box bold line (median), box height (25th and 75th percentiles), whisker length (1.5 times the interquartile range between the median and the upper or lower box height), and outliers beyond the whisker length (points).

delineated boundaries for spatially structured populations is essential to fully understand the implications of spatial fisheries management plans (Punt *et al.*, 2015).

In this study, a spatial simulation–estimation framework was used to evaluate biases and associated risks with boundary incoherence between areas that define population structure and management units when assessing a resource. Results highlight the importance of regional management considerations, especially when fishing mortality is disproportionate to vulnerable biomass among management areas, demographic data (e.g. growth and maturity) are not homogenous within management areas, or connectivity (via recruitment or movement) exists among management areas. Smaller, though not inconsequential, differences in bias occurred across levels of boundary incoherence for scenarios that used growth, maturity, and selectivity as sources of spatial heterogeneity compared to scenarios that additionally included connectivity between areas. There was less contrast in results across heterogeneous patterns of movement, growth, and

selectivity, given the designed spatial concordance among life history parameters and selectivity. For example, fish from area 1 grew faster, matured earlier, and thus were selected by the fishery sooner than fish from area 2, and therefore, these traits by definition had synergistic effects on the population even when applied independently. Nonetheless, management advice in the form of TAC specifications was biased, with the level of bias dependent on assessment sub-area (i.e. local depletion or local underutilization) and the degree of boundary incoherence between assessments and spatial structures.

From a stock assessment perspective, misaligned boundaries effectively cause an averaging of potentially important population processes across the management domain, and bias can be exacerbated if there is “demographic leakage” between AAs due to the unknown presence of unidirectional movement or high-/low-productivity areas. These situations create barriers to successful management such as increased risk for local depletion, inappropriate allocations of catch, loss of sustainable yield, and overall



**Figure 6.** The median relative error for TAC is shown by assessment sub-area (area 1a = red dashed line; area 1b = maroon dash-dot line; area 2 = blue dashed line) for each of five levels of boundary incoherence (none, 10, 20, 35, and 50%) per scenario set (panels). The top row represents scenarios without connectivity (combinations of spatial heterogeneity from maturity *M*, growth *G*, and selectivity *S*), while the second and third rows include scenarios with the addition of connectivity (via recruitment *Rec* and movement *Mov*). The level of spatial heterogeneity assumed for maturity, growth, and selectivity is shown in Figure 2. The proportion of the population recruiting to or moving from areas is identified by the parenthetical (area 1:area 2). Shaded plots (grey; top row) indicate a different y-axis scale. Time series shading represents the 25th and 75th interquartile ranges of relative error. Assessment sub-areas are delineated by the intersection of stock assessment and PS areas, where the true OM TAC was amalgamated by sub-areas.

biased estimates informing decisions. There are a growing number of examples, such as Bluefin tuna (*Thunnus thynnus*; Kerr et al., 2017), Pacific hake (*Merluccius productus*; Malick et al., 2020), rockfishes (McGilliard et al., 2015), and northeastern Pacific sablefish (*Anoplopoma fimbria*; Kapur et al., 2020), that suggest situations similar to those evaluated in this study are not uncommon and where boundary incoherence has the potential to deleteriously affect management procedures. For example, Cadrin et al. (2019) showed that naive, closed-population assessment models conforming to geographic management areas for Atlantic Bluefin tuna result in biased estimates of recruitment relative to stock biological-unit assessment models. The latter approach reassigned data collected from mixed-stock fisheries according to stock composition, rather than by management area that can contain multiple populations (e.g. Hintzen et al., 2015).

Risk, defined in this study as the probability of exceeding bias thresholds, relative to individual PS stock size given different

levels of risk tolerance (see Table 3), increased with the degree of boundary incoherence to levels that substantially biased area-specific harvest management decisions (e.g. TACs). Operationally, increased risk can translate into management decisions that expand precautionary harvest buffers. For example, the US Pacific Fishery Management Council increases the buffer between the OFL estimated by the stock assessment and the allowable biological catch as a result of scientific uncertainty in the OFL, where the buffer size is often related to the C.V. associated with the terminal year SSB estimate. Related, many US regional fishery management councils apply a “p-star” approach that additionally incorporates management risk tolerance into the buffer size (Prager et al., 2003; Shertzer et al., 2008). Several other management procedures have been developed worldwide to induce precautionary harvest measures as a result of scientific uncertainty (see, for example Punt et al., 2012). Risk was exemplified in this paper using a representative scenario (MGS) without

connectivity. However, estimating stock status when connectivity dynamics are unknown or ignored would predominantly (though perhaps not exclusively given the context of the situation) increase the risk associated with using spatially incoherent models (Goethel and Berger, 2017).

The fact that the system-wide results were effectively unbiased coincides with recent work with stock structure defined as a single population with spatial heterogeneity (Goethel and Berger, 2017; Bosley *et al.*, 2019) and suggests that even complete ignorance of spatial structure needs not necessarily result in biased assessment outcomes and poor catch advice; “two wrong assessments can make a right”, if maintaining population heterogeneity and avoiding localized depletion are not of concern. Reaping the benefits of this result, however, has several requirements that are seemingly unlikely to be met. For example, the catch of fish from each area would have to be proportional to their frequency of occurrence within the area defined for the EM. Otherwise, the disproportionate mortality would not be accounted for in a panmictic EM, nor would the demographic data (e.g. weights and maturities at age) be reflective of the fish within the EM boundary. This requirement might be achieved if fish from each area are randomly mixed when they are harvested, or if fishing occurs randomly in space, but this is rarely the case (Guan *et al.*, 2013). The very existence of spatial structure or heterogeneity suggests that fish from different areas are unlikely to be randomly mixed, and catch is unlikely to be random in space for a variety of reasons, such as distance from port or management measures that allocate quotas spatially [NEFSC (Northeast Fisheries Science Center), 2018; Bosley *et al.*, 2019; Hanselman *et al.*, 2019]. The chances of achieving unbiased system-wide results, however, could be improved through thoughtful catch allocation schemes that do not increase the chance of disproportionately harvesting fish from one area or another. Likewise, sampling designs that sample harvested fish in a spatially representative fashion will improve the chances that demographic data reflect that of the EM boundary. Also, assessments conducted separately on multiple areas of the same population are often handled by different agencies (e.g. countries). In such transboundary cases, cooperative agreements among regional assessment and management bodies can help ensure proper sampling and the aggregation of fishery data (e.g. in mixed-stock fisheries), catch distribution, and the development of EMs with non-overlapping boundaries that cover the entire population [NEFSC (Northeast Fisheries Science Center), 2017; Song *et al.*, 2017; TRAC (Transboundary Resources Assessment Committee), 2018; Cadrin *et al.*, 2019].

Despite a growing number of studies highlighting how specific spatial stock assessment procedures impact management (e.g. Punt *et al.*, 2015; Berger *et al.*, 2017b; Cadrin, 2020), none have explicitly evaluated how disconnected management and ecological boundaries need to be in order to adversely affect management advice (e.g. bias due to boundary incoherence  $\gg$  variance of estimate). Punt *et al.* (2015) investigated how different stock assessment configurations performed when presented with spatially heterogeneous fishing and biological patterns, and they indicated that estimation performance would have been further degraded if unit boundaries would have been misaligned with simulated patterns. The use of EMs that did not account for unequal recruitment apportionment or movement in this study led to biased results and increased risk for local depletion (also see, for example Ying *et al.*, 2011); however, the level of bias considerably worsened as a result of boundary incoherence (up to a

twofold change in SSB MRE and a onefold change in TAC MRE for every 1% increase in boundary incoherence between areas). Undoubtedly, some degree of boundary incoherence will always be present given transitioning environmental and oceanographic gradients and the resulting dynamic nature of marine fish populations. The challenge will be to optimize ongoing collection of ecosystem monitoring data to minimize risk and adapt to change for single-species management plans, while concomitantly being cognizant that units defined for the management of multi-species fisheries or stock complexes may require additional measures if drivers of spatial heterogeneity are not congruent.

Dynamic ocean management (DOM) is an emerging paradigm that attempts to address such challenges by calling for rapid, adaptive management action in space and time in response to current ocean and fishing conditions using real-time monitoring data (Maxwell *et al.*, 2015). The ability to produce reliable short-term species distribution (Kaplan *et al.*, 2016) and productivity (Tolimieri *et al.*, 2018; Haltuch *et al.*, 2020) forecasts using regional oceanographic modelling systems is improving. Such forecasts can act as predictive components to DOM, which is advantageous when management processes that are required to shift management-unit boundaries (or reallocate harvest between areas) impose time lags on adaptive change. Furthermore, DOM can be a catalyst for implementing ecosystem-based fisheries management and understanding connections among ecosystem components. Toonen *et al.* (2011) suggest that generalized ecosystem boundaries based on geographic proximity, taxonomy, or life history characteristics do not improve understanding of connectivity and thus help little with defining spatial management areas (e.g. marine protected areas; McGilliard *et al.*, 2015). As technological advances in monitoring improve and data assimilation and throughput are further streamlined, we predict that the principles supporting DOM will be further examined (e.g. through management strategy evaluation) and transition from research to operational pathways to develop regulatory measures at spatial scales in tune with changing ocean conditions (e.g. climate change) and ecosystem-level objectives.

Several assumptions and simulation scenario refinements were made to ensure the study design remained tractable, while still targeting study objectives. For example, we limited our scope to one type of population structure: a single population with heterogeneity. Although perhaps the most commonly acknowledged form of population structure in applied stock assessments, results are likely sensitive to other forms of population structure such as metapopulation (Ying *et al.*, 2011; Kerr *et al.*, 2017; Bosley *et al.*, 2019) or natal homing (Goethel and Berger, 2017) that are characterized by different recruitment and movement dynamics. The assumption of population-specific productivity ( $OM_1$  more productive than  $OM_2$ ) when combined with the direction of boundary incoherence (i.e. misaligned  $EM_2$  was always supplemented with data from the more productive area,  $OM_1$ ) used in this study resulted in slightly higher absolute levels of bias as compared to the opposite case ( $OM_1$  less productive than  $OM_2$ ) but was generally inconsequential for overall trends and relative scenario comparisons. Risk profiles (as shown in Table 3) are related to the level of process and observation error assumed in the simulation-EM framework. Even though these assumptions influenced absolute levels of risk, relative changes in risk across scenarios remained comparatively robust. Future work should consider the addition of spatiotemporal boundary incoherence, such as would result from changing environmental conditions or population

dynamic regimes, to complement the stationary levels of boundary incoherence examined in this study. Individual-based models could also prove useful to examine the consequences of simulating spatially discrete weight-at-age and maturity-at-age observations as was done in this study, rather than modelling these as continuous processes linked across space through movement. Simulations also assumed that the distribution of fish was homogenous within each PS (i.e. OM area), and fully selected fishing mortality was homogenous across areas with random annual deviations. Although these assumptions are common in population or stock unit assessments, the impact on results if substantively violated could be dramatic and is a topic for future research.

Understanding spatial population structure is a precondition for sustainable management (Cadrin, 2020). Ultimately, spatial management procedures need to consider the population components (e.g. spawning or harvestable portions of the stock) of societal interest that require management action given fishery objectives and associated risk profiles. Fishing pressure, biological constraints, and environmental gradients are never static through time, which necessitates adaptive management procedures (including the definition of management unit boundaries themselves) to tactically address shifting distributions and altered population dynamics through best practices (Kerr *et al.*, 2017). When large-scale shifts are likely to occur (e.g. climate change), transboundary approaches that include DOM concepts to reconstruct boundaries in an adaptive way (i.e. dealing with the “boundary paradox”; Song *et al.*, 2017) warrant more attention, as do fine-scale species distribution modelling approaches that may reduce the burden of incorrect boundary assumptions between PSs (Cao *et al.*, 2020). Directed studies and due consideration of critical PSs, fishing patterns, political boundaries, spatially explicit models, and transboundary dynamic management options would undoubtedly reduce boundary-related bias and risk, as would closely coordinated management among neighbouring management units that function across stock or population-segment boundaries. Ultimately, the establishment and periodic re-examination of fisheries management units needs to consider the spatial scales of concern as reflected by management objectives, followed by performance testing management strategies of which include the development of stock assessment models that sufficiently reflect key spatial components of the population and fishery (Cadrin, 2020).

The data underlying this article were computer generated using open source programming code available on github at [https://github.com/KateBoz/SPASAM/tree/master/Management\\_Boundaries](https://github.com/KateBoz/SPASAM/tree/master/Management_Boundaries), last accessed 24 June 2020. Many of the population dynamic and fishery parameters governing generated datasets were based on a recent Atlantic herring stock assessment for the northwest Atlantic Ocean [NEFSC (Northeast Fisheries Science Center), 2018].

### Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

### Acknowledgements

The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect those of NOAA or the Department of Commerce. Funding for this project was provided by the Office of Science and Technology, NOAA-National Marine Fisheries

Service under the Stock Assessment Analytical Methods grant and the National Research Council Research Associate Program (NRC-RAP). We thank Jason Cope, Owen Hamel, Jim Hastie, and two anonymous reviewers for thoughtful reviews that improved earlier versions of this article.

### References

- Berger, A. M., Goethel, D. R., and Lynch, P. D. 2017a. Introduction to “Space oddity: recent advances incorporating spatial processes in the fishery stock assessment and management interface”. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 1693–1697.
- Berger, A. M., Goethel, D. R., Lynch, P. D., Quinn, I. I. T., Mormede, S., McKenzie, J., and Dunn, A. 2017b. Space oddity: the mission for spatial integration. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 1698–1716.
- Booth, A. J. 2000. Incorporating the spatial component of fisheries data into stock assessment models. *ICES Journal of Marine Science*, 57: 858–865.
- Bosley, K. M., Goethel, D. R., Berger, A. M., Deroba, J. J., Fenske, K. H., Hanselman, D. H., Langseth, B. J., *et al.* 2019. Overcoming challenges of harvest quota allocation in spatially structured populations. *Fisheries Research*, 220: 105344.
- Cadrin, S. X. 2020. Defining spatial structure for fishery stock assessment. *Fisheries Research*, 221: 105397.
- Cadrin, S. X., Goethel, D. R., Morse, M. R., Fay, G., and Kerr, L. A. 2019. “So, where do you come from?” The impact of assumed spatial population structure on estimates of recruitment. *Fisheries Research*, 217: 156–168.
- Cadrin, S. X., and Secor, D. H. 2009. Accounting for spatial population structure in stock assessment: past, present and future. *In The Future of Fisheries Science in North America*, pp. 405–425. Ed. by R. J. Beamish and B. J. Rothschild. Springer, New York, NY, USA.
- Cao, J., Thorson, J. T., Punt, A. E., and Szuwalski, C. 2020. A novel spatiotemporal stock assessment framework to better address fine-scale species distributions: development and simulation testing. *Fish and Fisheries*, 21: 350–367.
- Ciannelli, L., Fisher, J. A. D., Skern-Mauritzen, M., Hunsicker, M. E., Hidalgo, M., Frank, K. T., and Bailey, K. M. 2013. Theory, consequences, and evidence of eroding population spatial structure in harvested marine fishes: a review. *Marine Ecology Progress Series*, 480: 227–243.
- Cope, J. M., and Punt, A. E. 2011. Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fisheries Research*, 107: 22–38.
- Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, 8: 1175–1182.
- de Roos, A. M., Boukal, D. S., and Persson, L. 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proceedings of the Royal Society B*, 273: 1873–1880.
- Deroba, J. J., Butterworth, D. S., Methot, R. D., Jr., De Oliveira, J. A. A., Fernandez, C., Nielsen, A., Cadrin, S. X., *et al.* 2015. Simulation testing the robustness of stock assessment models to error: some results from the ICES strategic initiative on stock assessment methods. *ICES Journal of Marine Science*, 72: 19–30.
- Fogarty, M. J., and Botsford, L. W. 2007. Population connectivity and spatial management of marine fisheries. *Oceanography*, 20: 112–123.
- Francis, R. I. C. C. 2011. Data weighting in statistical fisheries stock assessment models. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 1124–1138.
- Fraterrigo, J. M., and Rusak, J. A. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters*, 11: 756–770.

- Fu, C., and Fanning, L. P. 2004. Spatial considerations in the management of Atlantic cod off Nova Scotia, Canada. *North American Journal of Fisheries Management*, 24: 775–784.
- Fulton, E. A. 2011. Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES Journal of Marine Science*, 68: 1329–1343.
- Goethel, D. R., and Berger, A. M. 2017. Accounting for spatial complexities in the calculation of biological reference points: effects of misdiagnosing population structure for stock status indicators. *Canadian Journal of Fisheries and Aquatic Sciences*, 74: 1878–1894.
- Goethel, D. R., Bosley, K. M., Hanselman, D. H., Berger, A. M., Deroba, J. J., Langseth, B. J., and Schueller, A. M. 2019. Exploring the utility of different tag-recovery experimental designs for use in spatially explicit, tag-integrated stock assessment models. *Fisheries Research*, 219: 105320.
- Goethel, D. R., Quinn, I. I. T. J., and Cadrin, S. X. 2011. Incorporating spatial structure in stock assessment: movement modeling in marine fish population dynamics. *Reviews in Fisheries Science*, 19: 119–136.
- Guan, W., Cao, J., Chen, Y., and Cieri, M. 2013. Impacts of population and fishery spatial structures on fishery stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 1178–1189.
- Haltuch, M. A., Tolimieri, N., Lee, Q., and Jacox, M. G. 2020. Oceanographic drivers of petrale sole recruitment in the California Current Ecosystem. *Fisheries Oceanography*, 29: 122–136.
- Hanselman, D. H., Rodgveller, C. J., Fenske, K. H., Shotwell, S. K., Echave, K. B., Malecha, P. W., and Lunsford, C. R. 2019. Assessment of the Sablefish Stock in Alaska. North Pacific Fishery Management Council, Anchorage, AK. 263 pp. Available at: <https://archive.afsc.noaa.gov/refm/docs/2019/sablefish.pdf> (last accessed 10 April 2020).
- Hilborn, R., Stokes, K., Maguire, J. J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., *et al.* 2004. When can marine reserves improve fisheries management? *Ocean & Coastal Management*, 47: 197–205.
- Hintzen, N. T., Roel, B., Benden, D., Clarke, M., Egan, A., Nash, R. D. M., Rohlf, N., *et al.* 2015. Managing a complex population structure: exploring the importance of information from fisheries-independent sources. *ICES Journal of Marine Science*, 72: 528–542.
- Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. *In* *Metapopulation Biology: Ecology, Genetics, and Evolution*, pp. 149–164. Ed. by I. Hanski and M.E. Academic Press, San Diego, CA. Gilpin
- Hsieh, C.-H., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., and Sugihara, G. 2006. Fishing elevates variability in the abundance of exploited species. *Nature*, 443: 859–862.
- Hutchinson, W. F. 2008. The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. *Biology Letters*, 4: 693–695.
- ICES. 2017. Technical Guidelines - ICES fisheries management reference points for category 1 and 2 stocks. <http://www.ices.dk/sites/pub/Publication%20Reports/Forms/DispForm.aspx?ID=32751> (last accessed 24 June 2020).
- Kaplan, I. C., Williams, G. D., Bond, N. A., Hermann, A. J., and Siedlecki, S. A. 2016. Cloudy with a chance of sardines: forecasting sardine distributions using regional climate models. *Fisheries Oceanography*, 25: 15–27.
- Kapur, M. S., Haltuch, M., Connors, B., Rogers, L., Berger, A., Koontz, E., Cope, J., *et al.* 2020. Oceanographic features delineate growth zonation in Northeast Pacific sablefish. *Fisheries Research*, 222: 105414.
- Kerr, L. A., Cadrin, S. X., and Secor, D. H. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecological Applications*, 20: 497–507.
- Kerr, L. A., Hintzen, N. T., Cadrin, S. X., Clausen, L. W., Dickey-Collas, M., Goethel, D. R., Hatfield, E. M. C., *et al.* 2017. Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES Journal of Marine Science*, 74: 1708–1722.
- King, J. R., and McFarlane, G. A. 2006. A framework for incorporating climate regime shifts into the management of marine resources. *Fisheries Management and Ecology*, 13: 93–102.
- Loehle, C. 2006. Control theory and the management of ecosystems. *Journal of Applied Ecology*, 43: 957–966.
- Malick, M., Hunsicker, M., Haltuch, M., Parker-Stetter, S., Berger, A., and Marshall, K. 2020. Relationships between temperature and Pacific hake distribution vary across latitude and life-history stage. *Marine Ecology Progress Series*, 639: 185–197.
- Maxwell, S. M., Hazen, E. L., Lewison, R. L., Dunn, D. C., Bailey, H., Bograd, S. J., Briscoe, D. K., *et al.* 2015. Dynamic ocean management: defining and conceptualizing real-time management of the ocean. *Marine Policy*, 58: 42–50.
- McGilliard, C. R., Punt, A. E., Methot, R. D., and Hilborn, R. 2015. Accounting for marine reserves using spatial stock assessments. *Canadian Journal of Fisheries and Aquatic Sciences*, 72: 262–280.
- NEFSC (Northeast Fisheries Science Center). 2017. 62nd Northeast Regional Stock Assessment Workshop (62nd SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document 17-03. 822 pp.
- NEFSC (Northeast Fisheries Science Center). 2018. 65th Northeast Regional Stock Assessment Workshop (65th SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document 18-11. 659 pp.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakum, A., Bonfil, R., Conover, D. O., Dayton, P., *et al.* 2004. Ecosystem-based fishery management. *Science*, 305: 346–347.
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., and Levin, S. A. 2013. Marine taxa track local climate velocities. *Science*, 341: 1239–1242.
- Prager, M. H., Porch, C. E., Shertzer, K. W., and Caddy, J. F. 2003. Targets and limits for management of fisheries: a simple probability-based approach. *North American Journal of Fisheries Management*, 23: 349–361.
- Privitera-Johnson, K. M., and Punt, A. E. 2020. Leveraging scientific uncertainty in fisheries management for estimating among-assessment variation in overfishing limits. *ICES Journal of Marine Science*, 77: 515–526.
- Punt, A. E. 2019. Spatial stock assessment methods: a viewpoint on current issues and assumptions. *Fisheries Research*, 213: 132–143.
- Punt, A. E., Haddon, M., and Tuck, G. N. 2015. Which assessment configurations perform best in the face of spatial heterogeneity in fishing mortality, growth and recruitment? A case study based on pink ling in Australia. *Fisheries Research*, 168: 85–99.
- Punt, A. E., Siddeek, M. S. M., Garber-Yonts, B., Dalton, M., Rugolo, L., Stram, D., Turnock, B. J., *et al.* 2012. Evaluating the impact of buffers to account for scientific uncertainty when setting TACs: application to red king crab in Bristol Bay, Alaska. *ICES Journal of Marine Science*, 69: 624–634.
- Ralston, S., Punt, A. E., Hamel, O. S., Devore, J. D., and Conser, R. 2011. A meta-analytic approach to quantifying scientific uncertainty in stock assessments. *Fishery Bulletin*, 109: 217–231.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. J. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, 10: 361–395.
- Shelton, A. O., and Mangel, M. 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National*



- Academy of Sciences of the United States of America, 108: 7075–7080.
- Shertzer, K. W., Prager, M. H., and Williams, E. H. 2008. A probability based approach to setting annual catch levels. *Fishery Bulletin*, 106: 225–232.
- Smedbol, R. K., and Stephenson, R. L. 2001. The importance of managing within-species diversity in cod and herring fisheries of the North-Western Atlantic. *Journal of Fish Biology*, 59: 109–128.
- Song, A. M., Scholtens, J., Stephen, J., Bavinck, M., and Chuenpagdee, R. 2017. Transboundary research in fisheries. *Marine Policy*, 76: 8–18.
- Stephenson, R. L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. *Fisheries Research*, 43: 247–249.
- Strayer, D. L., Power, M. E., Fagan, W. F., Pickett, S. T. A., and Belnap, J. 2003. A classification of ecological boundaries. *BioScience*, 53: 723–729.
- Szuwalski, C. S., and Hollowed, A. B. 2016. Climate change and non-stationary population processes in fisheries management. *ICES Journal of Marine Science*, 73: 1297–1305.
- Thorson, J. T., Munch, S. B., and Swain, D. P. 2017. Estimating partial regulation in spatiotemporal models of community dynamics. *Ecology*, 98: 1277–1289.
- Tolimieri, N., Haltuch, M. A., Lee, Q., Jacox, M. G., and Bograd, S. J. 2018. Oceanographic drivers of sablefish recruitment in the California Current. *Fisheries Oceanography*, 27: 458–474.
- Toonen, R. J., Andrews, K. R., Baums, I. B., Bird, C. E., Concepcion, G. T., Daly-Engel, T. S., Eble, J. A., *et al.* 2011. Defining boundaries for ecosystem-based management: a multispecies case study of marine connectivity across the Hawaiian archipelago. *Journal of Marine Sciences*, 2011: 1–13. pp.
- TRAC (Transboundary Resources Assessment Committee). 2018. Eastern Georges Bank Cod Status Report. TRAC Status Report 2018/01. 14 pp. <https://repository.library.noaa.gov/view/noaa/23026> (last accessed 24 June 2020).
- Turner, M. G. 1989. Landscape ecology: the effect of pattern and process. *Annual Review of Ecology, Evolution, and Systematics*, 20: 171–197.
- Van Beveren, E., Duplisea, D. E., Brosset, P., and Castonguay, M. 2019. Assessment modelling approaches for stocks with spawning components, seasonal and spatial dynamics, and limited resources for data collection. *PLoS One*, 14: e0222472.
- Wiens, J. A. 1995. Landscape mosaics and ecological theory. *In* *Mosaic Landscapes and Ecological Processes*. Ed. by L. Hansson, L. Fahrig, and G. Merriam. Springer, Dordrecht. pp. 1–26.
- Ying, Y., Chen, Y., Lin, L., and Gao, T. 2011. Risks of ignoring fish population spatial structure in fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 2101–2120.

*Handling editor: Valerio Bartolino*