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ARTICLE

Impacts of population and fishery spatial structures on fishery stock assessment

Wenjiang Guan, Jie Cao, Yong Chen, and Matthew Cieri

Abstract: Fish populations and fishing efforts in most fisheries exhibit spatial heterogeneity. However, spatial considerations are generally ignored in fishery stock assessment and management because of a lack of spatially explicit data and poor understanding of the spatial dynamics of most fisheries. This study uses a simulation approach to evaluate the consequences of misspecifying spatial structure and migration during the assessment process. We developed an operating model to simulate a fishery using US Atlantic herring (*Clupea harengus*) as our model species. This population consists of two well-defined spawning substocks distributed and mixed in four management areas. Simulations were done for three alternative "true" populations, each having a different spatial structure both biologically and with regard to the geographic distribution of fishing effort. Stock assessments were then performed for the three simulated "true" populations using standard methodologies and assumptions currently used. Management-area-based assessments lead to overestimation of spawning stock biomass and underestimation of fishing mortality because of the interaction within the management area between the spatial structure of the population and that of the spatially heterogeneous fishery removals. In contrast, when fishing is spatially homogeneous, movement across management boundaries may not be relevant to modeling population dynamics. Such an idealized situation does not typically hold, however.

Résumé : Si les populations de poissons et les efforts de pêche associés à la plupart des pêches sont hétérogènes sur le plan spatial, les considérations d'ordre spatial sont généralement laissées de côté dans l'évaluation et la gestion des stocks halieutiques en raison du manque de données spatialement explicites et d'une compréhension limitée de la dynamique spatiale de la plupart des pêches. Cette étude utilise une approche de simulation pour évaluer les conséquences d'une définition incorrecte de la structure spatiale et de la migration dans le cadre du processus d'évaluation. Nous avons mis au point un modèle opératoire pour simuler une pêche en utilisant le hareng (*Clupea harengus*) des États-Unis comme espèce modèle. Cette population comprend deux sous-stocks reproducteurs bien définis répartis et mélangés dans quatre zones de gestion. Des simulations ont été menées pour trois « vraies » populations différentes, chacune présentant sa propre structure spatiale tant sur le plan biologique qu'en ce qui a trait à la répartition géographique de l'effort de pêche. Des évaluations des stocks ont ensuite été effectuées pour les trois « vraies » populations simulées, selon des méthodologies et hypothèses normales en usage courant. Les évaluations basées sur les zones de gestion ont mené à la surestimation de la biomasse des stocks reproducteurs et à la sous-estimation de la mortalité du poisson en raison de l'interaction, à l'intérieur de la zone de gestion, des structures spatiales de la population et des prélèvements liés à la pêche dont la répartition spatiale est hétérogène. Par contre, si la pêche est spatialement homogène, les déplacements entre zones de gestion peuvent n'avoir aucune incidence sur la modélisation de la dynamique des populations. Toutefois, une telle situation théorique ne s'avère généralement pas. [Traduit par la Rédaction]

Introduction

Fisheries stock assessment, providing scientific information to inform fisheries management decisions, is an essential process in developing a sustainable fishery (NRC 1998). Advances in stock assessment methods have been achieved over the last few decades (Quinn and Deriso 1999). These have variously consisted of improvements or enhancements to model structure, complexity, and resolution; better accounting of uncertainty; improved statistical estimators; and increases in data quality and quantity (Punt and Hilborn 1997; Methot 2000; Chen et al. 2003). However, as an abstraction of reality it remains impractical to model fishery population dynamics perfectly. Therefore, simplifying assumptions are still needed, given constraints on data availability and the uncertainty associated with our understanding of fisheries population dynamics. The spatial structure of the fishery population dynamics has recently received more attention, with some suggesting that simplifications that neglect critical aspects of spatial structure lead to erroneous assessment results (Booth 2000; Kerr et al. 2010; Cope and Punt 2011) and subsequently mistaken management actions (Punt et al. 2000; Taylor et al. 2011). Fu and Fanning (2004) used simulation modeling to test the hypothesis that misspecifying spatial structure might be one of the factors contributing to the collapse of Atlantic cod stocks off Nova Scotia. Ying et al. (2011) suggested that misspecifying population spatial structure would result in overexploitation or local depletion of important subcomponents.

The emergence of spatial structuring within a species' range could be driven by many factors, such as biological variation (Begg et al. 1999), environmental variability (Lande et al. 1999), habitat availability (Botsford et al. 2009), or spatially variable fishing pressure (Booth 2000). Through evolution, fish have acquired different dispersal and movement patterns at different life history stages. As a result, spatial heterogeneity is often observed in fish popula-

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tions (Cadrin and Secor 2009). Typically, a stock may consist of several substocks having different movement patterns (e.g., natal homing, reproductive mixing). These substocks may or may not have similar biological characteristics (e.g., spawner–recruitment relationships). Although many complex spatial stock structures have been revealed, they are not typically incorporated into most fisheries stock assessments or considered by the management process (Ying et al. 2011).

Spatial distribution of fishing effort (referred to in this study as fishery spatial structure) usually reflects the spatial distribution of fish as well as fleet economics and so is by its nature also heterogeneous. Ignoring fishery spatial structuring may lead to serious biases in estimates of fishing mortality (*F*) and yield (Hart 2001). Additionally, the targeted deployment of fishing effort makes the interpretation of fishery dependent data difficult (Paloheimo and Dickie 1964) because of hyperstability (Hilborn and Walters 1992). Most stock assessments include, implicitly or explicitly, the assumption of randomly distributed fish populations with respect to fishing effort (Quinn and Deriso 1999). However, complex spatial stock structure and nonrandom distribution of fishing effort do exist in many fisheries, and these can result in large errors (Cadrin and Secor 2009).

Regarding stock assessment options, there are several ways to deal with spatial structure: (A) model a single stock for its entire range, (B) model a separate stock for each management area, (C) model a single stock, with separate fisheries for each management area, (D) model separate biological stocks with known catch, (E) model multiple stocks with movement rates into each management area, but with no biological interaction, or (F) model multiple stocks with movement rates into each management area, also with biological interaction. Some attempts have been made to incorporate movement into assessment models (Punt et al. 2000; Montenegro et al. 2009; Hulson et al. 2011), but these require detailed information on emigration and immigration. Therefore, the first three options (i.e., stock assessment options A, B, and C), which essentially ignore any spatial structure, are the most common approaches used. As such, examining the consequences of misspecified spatial structuring in stock assessment and management has become increasingly important. Cope and Punt (2011) used a simulation approach to demonstrate that single-area stock assessments perform poorly when catch histories differ among subareas, even assuming there are no biological differences or movements among them. Ying et al. (2011) suggested that assessing a metapopulation as several independent populations using a biomass dynamic model without considering movement tends to lead to overexploitation. Nevertheless, there have been few attempts to investigate how the interaction between population and fishery spatial structure impacts the performance of stock assessments.

Simulation testing, using mathematical models to represent systems of interest, allows designed experimentation on systems that cannot easily be manipulated otherwise. Using Atlantic herring (*Clupea harengus*) in the northeastern USA as an example, we developed a simulation to evaluate the impacts of both population and fishery spatial dynamics on stock assessments. We simulated various "true" fisheries with different spatial structures based on the information available for Atlantic herring and its fishery in the northeastern USA. We simulated three "true" fish stocks and fisheries with different spatial structures: (*i*) spatial structure in both stock and fishery; (*ii*) spatial structure in the stock only; and (*iii*) spatial structure only in the fishery. We then conducted an assessment for these three "true" stocks with and without correct spatial structure. The differences in the assessment results among different simulation scenarios were evaluated to identify possible consequences for assessment performance of incorrect assumptions about spatial structure. Specifically, we addressed the following issues: (1) What are the consequences of misspecifying the spatial structures of fish stocks and (or) the fishery in an assessment (e.g., ignoring population spatial structure as if assessing a single stock or failing to account for heterogeneity in fishing effort)? (2) How does the interaction between both population structure and fishery spatial structure additionally affect assessment performance? (3) Under what conditions will spatial structure affect this performance? We chose Atlantic herring as an example in this study because its spatial structure is rather typical in fisheries and sufficient information was available to simulate spatial structures of both the stock and the fishery. This approach and its results, however, have broader implications for other stocks and fisheries, particularly those with similar multiple stock component structures (i.e., inshore–offshore components) and multiple fisheries management areas (e.g., groundfish stocks in the northeastern USA and pelagic fish species in the US South Atlantic and Gulf of Mexico).

Materials and methods

Atlantic herring

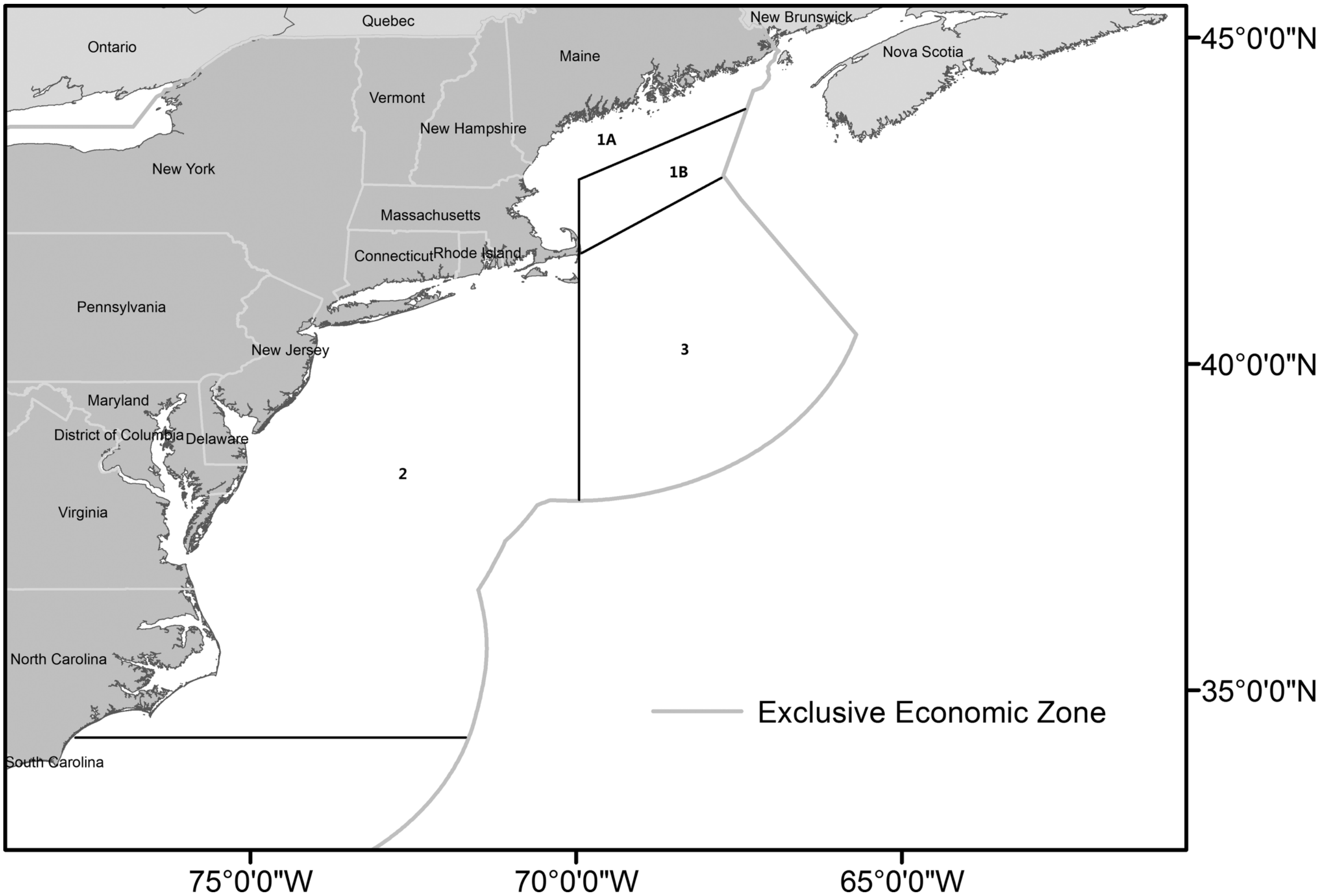
We used Atlantic herring in the northeastern USA as the model species in this study. Atlantic herring is an important pelagic species and fishery in the northeastern USA and also a major prey item for groundfish, marine mammals, large pelagic fishes, and seabirds (Overholtz et al. 2004; Kanwit and Libby 2009). Herring in this region are thought to consist of three spawning components: Nova Scotia (NS), coastal Gulf of Maine (GOM), and Georges Bank – Nantucket Shoals (GB) (Iles 1972; ASMFC 1995; Reid et al. 1999). Each component exhibits different stock structure, and their stock abundances tend to fluctuate independently (Overholtz et al. 2004). However, there is little evidence for distinct genetic differences among the spawning components (Reid et al. 1999). Juvenile and adult herring usually make complex, time-varying north–south and inshore–offshore migrations for feeding, spawning, and overwintering (Reid et al. 1999; Overholtz et al. 2004). Different components intermix throughout most of the year except during spawning seasons (Kanwit and Libby 2009). Four management areas (Fig. 1) are defined for data collection and regulation. Although there is considerable intermixing of the western portion of the NS herring stock, both in the GOM and Southern New England (Kanwit and Libby 2009), herring in USA waters are assumed to have two spawning components: an inshore component that spawns in the GOM and an offshore component that spawns on GB (Overholtz et al. 2004). The mixing rate of each component into each management area tends to change by month (Overholtz et al. 2004) as the herring undergo distinct and overlapping annual migrations.

Landings by management area have changed over time. The landings from GB once accounted for more than 50% of the total catch between 1961 and 1975, except for 1965 (Shepherd et al. 2009). Following the extirpation of herring on GB in 1976, however, landings dropped markedly. There was almost no directed commercial fishery for herring on GB between 1978 and 1995 (Melvin and Stephenson 2007). Instead, the GOM coastal area yielded about 62% of the total landings between 1977 and 2008 (Shepherd et al. 2009). Fishing effort also differed correspondingly among these areas over this period.

During the 1970s, the herring stock components in the GOM–GB region were assessed separately based on the assumption of little intermixing between them (Overholtz et al. 2004). Once it was recognized that catches in some areas were a mixture of fish from both components, the assessment model was reformulated as a single stock complex (Overholtz et al. 2004). This change effectively ignored the existence of any spatial structure and removed the NS stock from the analysis.

The biological and fishery characteristics of this species, such as differential growth rates and heterogeneous fishery removals, make it a good reference for studying the implications of population and fishery spatial structure for the assessment process. This

Fig. 1. Four management areas for Atlantic herring in the northeastern USA.



stock is almost a textbook example in its inshore–offshore population structure and misaligned management units. As such, our methods could be applicable to other similarly situated stocks, and our results could be broadly interpreted.

Operating model development

We developed three spatially explicit simulations to explore the dynamics of herring, including movements of the two sub-stocks (i.e., GOM and GB stocks) among the four management areas (Fig. 1). Each simulation described a different spatially structured scenario with respect to the population and fishery (Table 1). The first simulation (termed PF) was used to examine a case where there was spatial structure in both the fishery and the population (i.e., there were time-varying differences in the relative proportions of GOM and GB fish present in each of the four management areas and also in the way fishing removals occurred proportionally among the different areas). PF was designed to mimic, as closely as possible, the real herring stock and fishery as known today. The second simulation (termed P) was developed to explore a case where there was spatial structure in the population but not in the fishery (i.e., fishing removals were random with respect to the distribution of fish stock). The third simulation (termed F) had spatial structure only in the fishery and not in the population, which was assumed to be randomly distributed.

Simulations were initialized at the beginning of 1967, with a monthly time step, and ran through the end of 2008, thus covering the same time period used in the latest stock assessment. Management areas were defined according to NEFMC (2010), and the spatial distribution of herring in the region was simulated based on proportional mixing in each area (Tables 2 and 3). The GOM and GB herring stocks were distributed across the four management areas at the beginning of each month for all the years based on a mixing probability matrix (Tables 2 and 3). For a given model time step, the GOM stock was first distributed across areas based on a multinomial-based sample with expected month-specific proportions defined in Table 2. The GB stock was then distributed to achieve specified relative proportions of GB and GOM stocks defined in Table 3, starting with area 1A as a first priority and moving progressively to areas 1B, 2, and then 3. The prioritization is needed in case there are not enough GB fish to achieve the desired relative proportions across all areas. This approach used to model the spatial structures of the two herring stocks implies that (*i*) both stocks have the same ability to locate feeding grounds and respond to environmental changes, resulting in strong correlations between the fish abundance of GOM and GB stocks during the months of mixing in the areas where the two stocks mix (i.e., for a given month in an area with mixing if there are few fishes from the GOM stock, few GB fish will be present in the same area); and (*ii*) the sequence of order for distributing fish of GB stock among management areas should reflect the likelihood that GB fish migrate to a given area. Simulations were done to ensure that the two matrices could capture herring migration patterns. GOM and GB stocks spawn in areas 1A and 3, respectively (Reid et al. 1999) and remain segregated during spawning season. Mixing occurs during winter and summer feeding and with movement during nonspawning times of the year (Reid et al. 1999).

Table 1. Simulation (SIM) cases of the "true" herring population and fishery.

SIM	Assumption	Parameters defining spatial structure
PF	Stock has spatial structure: GOM and GB stocks	Stock mixing in four management areas was defined by parameters in Tables 2 and 3
	F differs among management areas and among months	Spatial and temporal distribution of *F* was defined by eqs. A.5 and A.6
P	Stock has spatial structure: GOM and GB	Stock mixing in four management areas was defined by parameters in Tables 2 and 3
	F was equally divided among four management areas and among 12 months (i.e., no spatial structure in *F*)	$\mathrm{FMRM}_{m,r,y}$ = 1/12 in eq. A.7 $\mathrm{FMRA}_{r,y}$ = 1/4 in eq. A.7
F	Stock has no spatial structure: a single stock	Stock is evenly distributed among the four management areas
	F differs among management areas and among months	Spatial and temporal distribution of *F* was defined by eqs. A.5 and A.6

Note: Age-specific fishing selectivity = [0.0, 1.0, 1.0, 1.0, 1.0, 1.0]; natural mortality = 0.2; survey catchability = 0.1; Coef in eq. A.7 = 4.0. Survey selectivity follows double logistic functions, where survey selectivity is defined by a double logistic function with the four parameters [3.0, 0.5, 3.0, 0.5]. F_y is from Shepherd et al. (2009). GOM, Gulf of Maine; GB, Georges Bank; FMRM, a proportional value for dividing an area- and year-specific fishing mortality into area- and month-specific fishing mortality; FMRA, a proportional value for dividing a year-specific fishing mortality into area- and year-specific fishing mortality.

Table 2. The expected distribution of the inshore stock (i.e., Gulf of Maine (GOM) stock) by month and management area.

	Management area			
Month	1A	1B	2	3
January	0.1	0.1	0.8	0
February	0.2	0.2	0.6	0
March	0.4	0.2	0.4	0
April	0.6	0.4	0	0
May	0.65	0.35	0	0
June	0.7	0.3	0	0
July	0.75	0.25	0	0
August	0.8	0.15	0.05	0
September	0.8	0.1	0.1	0
October	0.75	0.1	0.15	0
November	0.4	0.2	0.4	0
December	0.2	0.2	0.6	0

Note: The numbers in the table are the expected proportions of the GOM stock that occur in a given management area for a given month. Variability in the spatial distribution is incorporated by sampling from a multinomial distribution with an effective sample size of 100 to generate the simulated proportions for a given month and year during simulations.

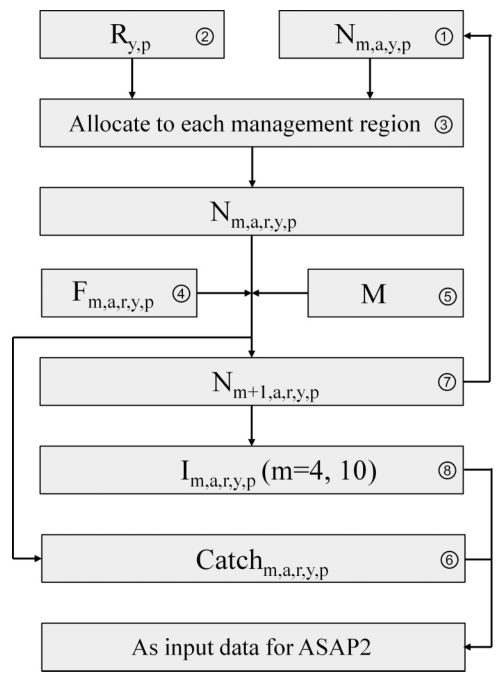
Table 3. The proportion of herring in a management area coming from the offshore stock (i.e., Georges Bank (GB) stock) by month.

	Management area			
Month	1A	1B	2	3
January	0	P_{pm}	P_{pm}	1
February	0	P_{pm}	P_{pm}	1
March	0	P_{pm}	P_{pm}	1
April	P_{sm}	P_{pm}	1 (0.18)	1 (0.82)
May	P_{sm}	P_{pm}	1 (0.17)	1 (0.83)
June	P_{sm}	P_{pm}	1 (0.16)	1 (0.84)
July	P_{sm}	P_{pm}	1 (0.15)	1 (0.85)
August	0	P_{pm}	P_{pm}	1
September	0	P_{pm}	P_{pm}	1
October	0	P_{pm}	P_{pm}	1
November	0	P_{pm}	P_{pm}	1
December	0	P_{pm}	P_{pm}	1

Note: P_{sm} is a random number drawn from uniform distribution [0.2, 0.8] representing the proportion of herring coming from the GB stock. P_{pm} is a random number drawn from triangle distribution with lower limit 0.7, upper limit 0.9, and mode 0.87. For a given month if there is only one area with 100% herring from the GB stock, the proportion of herring distributed in this area was the remaining GB stock after deducting those in the other three areas. For a given month if there are two areas with 100% herring from the GB stock, the proportion of herring in these two areas was decided by the remaining GB stock (after deducting those in other areas of the month) by the proportions shown in parentheses. The priority of distributing GB stock is as follows: 1A > 1B > 2 > 3. The values were assumed based on NEFMC (2010).

Spatial structuring of the fishery was simulated based on historical catch records for each management area. The stock and fishery simulation procedures are summarized in Fig. 2, and details are presented in the Appendix. The stock biomass values

Fig. 2. Flowchart for simulating the population dynamics (annotation numbers (circled in the figure) are listed in Appendix A). *R*, *N*, *F*, *M*, and *I* in the figure denote recruitment, abundance, fishing mortality, natural mortality, and survey index, respectively. The subscripts *m*, *y*, *p*, *a*, and *r* represent month, year, stock, age, and region, respectively. ASAP2 stands for the age-structured assessment program version 2.



used in the fishery simulation were considered the "true" biomasses for the GOM and GB components. The outputs of the fishery simulation included monthly data for fishery removals, fishery catch-at-age, survey catch-at-age, and survey index for the four management areas. These output data were used as input data for stock assessment (see below for stock assessment methods) to yield stock estimates for the GB–GOM components and for all four areas, which were then compared with the corresponding "true" stock parameters built in to the simulation. Uncertainties considered in the simulation included probability distribution matrices (e.g., Tables 2 and 3) and observational errors for simulated catch-at-age and survey index data.

Stock assessment approach

Stock assessments for each simulation were conducted using an age-structured assessment program (ASAP; Legault and Restrepo 1998). ASAP assumes separable annual *F* to estimate population sizes using forward projection, given catch-at-age and an index of

Table 4. Assumptions made in the estimation with respect to stock and fishery spatial structures.

Assessment scenario (AS)	Data	Assumption made
S	A single catch was calculated across all management areas	Fishery was assumed to have no spatial structure (same fishing mortality over four management areas)
	A single survey index was calculated across all management areas	Stock was assumed to have no spatial structure (unit stock)
B	Sources of catch in the four management areas could be identified, and catch could be divided into two groups based on their sources: GOM and GB	Fishery was assumed to have spatial structure, which is consistent with stock spatial structure (two stocks: GOM and GB)
	Survey indices were derived separately for GOM and GB	Stock is assumed to have spatial structure (two stocks: GOM and GB)
M	Catch was grouped by management areas	Fishery spatial structure was assumed to be the same as management areas (four fishing areas with different fishing mortalities)
	Survey indices were grouped by management areas	Separate stock was assumed for each management area, which is consistent with spatial structure of the fishery

Table 5. Parameters in the ASAP model that were assumed in the estimation.

Parameter or function	Assumed values in the estimation
λ for others	1.0 (total catch in mass, index) or 0.0
Catch at age ESS	100
Survey at age ESS	100
Fishing selectivity at age	[0.0, 1.0, 1.0, 1.0, 1.0, 1.0]
Survey catchability	Constant
Catch CV	0.20
Survey index CV	0.25
CV for others	0.5
λ for recruitment	0.005
Survey selectivity	Double logistics
Steepness	1.0 and Beverton–Holt model was turned off

Note: ESS, effective sample size for age composition.

abundance. The ASAP model was used for the most recent herring assessment (Shepherd et al. 2009) and to assess other fish populations (e.g., Atlantic cod; NEFSC 2012). Three assessment scenarios were applied to each simulation, differing in their assumptions with respect to population and fishery spatial structuring (Table 4). Our assessment scenarios were "S", a single stock scenario where spatial structure was ignored, treating the GOM and GB as a single stock with a single set of simulated catch and indices data applied across all four management areas; "B", a scenario based on biological scale where the source of herring in the four management areas (i.e., the proportion belonging to the GOM or GB component) could be identified; and "M", a scenario based on management areas where four components were recognized corresponding to the four management areas and assessed by management area separately. Auxiliary parameters for the ASAP-based stock assessment are listed in Table 5.

Simulation scenarios

Our aim was to explore the range of possible relationships between "true" spatial structure and the assumptions of stock assessment and to compare how management and assessment outcomes varied depending on these. To this end, a total of nine different outcomes (Table 6) were obtained from combining the three simulated cases (PF, P, and F) with the three assessment scenarios (S, B, and M). Thus, for each of the three simulated "true" populations, we conducted the assessment at three distinct spatial scales: single stock scale (i.e., consolidating all management areas and assuming a single stock), biological scale (i.e., discriminating between GOM and GB stocks), and management boundary scale (i.e., separately assessing management areas 1A, 1B, 2, and 3). Of these nine outcomes (Table 6), P–B was the only

Table 6. Simulation outcomes considered in this study with different combinations of simulation cases (SIM) of the "true" stock and fishery spatial structure defined in Table 1 and for spatial structures assumed in the assessment scenarios (AS) defined in Table 4.

			Match (+) or mismatch (–) of spatial structure between data simulation and estimation	
Outcome	SIM (defined in Table 1)	AS (defined in Table 4)	Stock spatial structure	Fishery spatial structure
PF–S	PF	S	–	–
PF–B	PF	B	+	–
PF–M	PF	M	–	+
P–S	P	S	–	+
P–B	P	B	+	+
P–M	P	M	–	+
F–S	F	S	+	–
F–B	F	B	–	–
F–M	F	M	–	+

one in which the simulation and the assessment scenario matched spatially with respect to both biological stock structure and the geographical distribution of fishing pressure. For all other outcomes, there were various mismatches in spatial structure between the simulated fishery and what was assumed in the assessment model (Table 6). One hundred simulation runs were used to generate each outcome. Early testing runs indicated that 100 simulation runs were sufficient to capture the range of outputs and yield stable results.

Performance measures

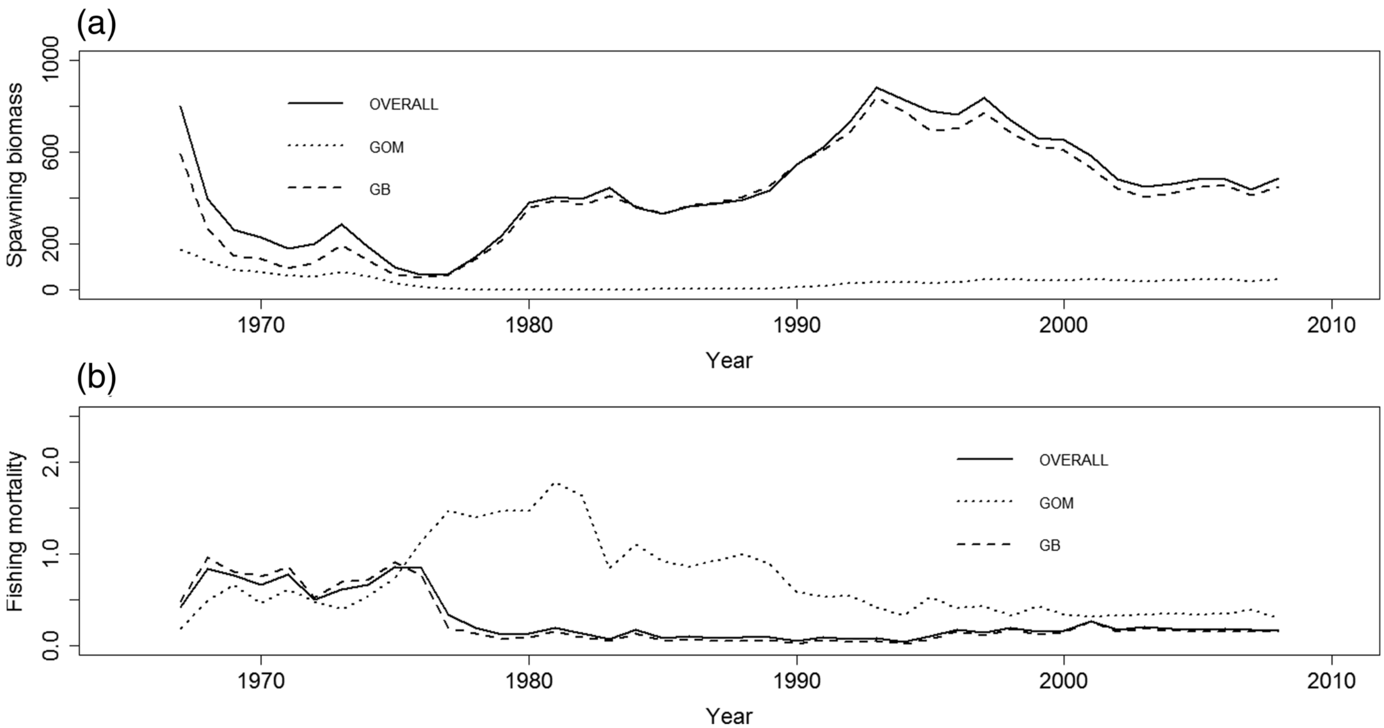
The impacts of spatial misalignment between the simulations and the assessment scenarios were evaluated with respect to their effects on estimates of stock status and fishing removals. Relative error (RE), calculated as follows, was used to measure error associated with spawning stock biomass (SSB) and F:

$$\text{(1)} \qquad \mathrm{RE}_{2008} = \frac{E_{2008} - E_{2008}^{\mathrm{T}}}{E_{2008}^{\mathrm{T}}} \times 100\%$$

$$\text{(2)} \qquad \mathrm{RE}_{\mathrm{a}} = \sum_{y=1967}^{2008} \frac{E_y - E_y^{\mathrm{T}}}{E_y^{\mathrm{T}}} \times 100\%$$

where RE_{2008} measures estimation error in the terminal year (i.e., 2008), while RE_{a} measures the overall estimation error over the stock assessment time period (i.e., 1967–2008). E_{2008} is the param-

Fig. 3. The trajectory of (*a*) spawning biomass and (*b*) fishing mortality in a simulation run.



eter value estimated in the assessment for 2008, E_{2008}^{T} is the simulated "true" value in 2008, E_y is the parameter value for year *y* estimated in the assessment, and E_y^{T} is the simulated "true" value for year *y*. Parameter *E* in the two equations could be either SSB or *F* in this study.

The management-area-specific value of E_y^{T} could not be obtained because of movement among the areas. Therefore, for the scenarios where assessment was based on management area boundaries, E_y values were combined across the areas to facilitate comparisons. Median values of RE (denoted MRE) were used to compare the scenarios. MRE provides the direction of the error (positive or negative) and relates to bias.

For the outcome assuming the two independent stocks (i.e., GOM and GB), performance measures were calculated for both stocks separately and combined. For the assessments assuming four independent stocks, measures were only calculated for the combined stocks.

Results

Simulated population dynamics

SSB and *F* trajectories, both stock-specific and overall, are shown in Fig. 3 for the simulated herring population. The GB stock dominates the population SSB, while the GOM stock persists at a low level (Fig. 3). The GOM stock experienced high *F* from the mid-1970s onward, especially during the late 1970s to late 1980s. The GOM stock is only distributed in management areas 1A, 1B, and 2, mainly overwintering in area 2 and using 1B as a migratory route (Table 2). The GB stock is mainly distributed in management areas 1B, 2, and 3, aggregating in area 3 during late summer and fall for spawning and spread among all three areas during the rest of the year (Table 3).

Evaluating estimation errors

The RE values of estimated SSB and *F* for terminal year and all years combined have similar trends (Figs. 4 and 5). For simulation case PF, where there exists underlying spatial structure in both the population and the fishery, SSB is overestimated and *F* is underestimated when the assessment is done based on the assumption of four independent stocks corresponding to the four management areas (outcome PF–M). In contrast, SSB is underestimated and *F* is overestimated when the assessment misspecifies spatial structure as consisting of only a single stock (outcome PF–S). For outcome PF–B, for which assessment is conducted by assuming two independent spawning stocks (i.e., GOM and GB), the MREs of both SSB and *F* for the combined stocks are each less than 1% (Figs. 4 and 5), suggesting that the overall stock status is well estimated even though fishery spatial structure remains misspecified (Table 6). However, in this case the GOM stock has larger estimation errors than the GB stock (Figs. 4 and 5). For simulation case P, where the "true" population has spatial structure but experiences homogeneous fishing mortality *F*, all assessment scenarios (i.e., S, B, and M; Table 4) yield relatively small estimation errors. Furthermore, the errors in the two scenarios involving mismatched scales (i.e., outcomes P–S and P–M; Table 6) are almost the same as in the scenario where simulation and assessment scales match (i.e., outcome P–B; Table 6). For simulation case F, where the simulated "true" underlying population is a unit stock but fishing effort has built-in spatial structure, assessment scenarios S and B perform well. However, assessment scenario M produces extremely poor estimates with large MRE values (Figs. 4 and 5).

Discussion

It is generally believed that ignoring or misspecifying spatial structure can lead to a biased view of stock status and hence to misleading management advice (Booth 2000; Punt and Donovan 2007; Rothschild 2007; Ying et al. 2011). This study used a simulation approach to identify the nature of these estimation errors and the conditions under which they could occur. We suggest that the impacts of misspecifying population and fishery spatial structure vary. If fishing removals are distributed homogeneously throughout a population, misspecification of its spatial structure in assessment appears not to result in large assessment errors. However, when fishing effort is spatially heterogeneous, a mis-

Fig. 4. Relative error (RE) of estimated fishing mortality (*F*) for (*a*) terminal year and (*b*) all years combined under each outcome listed in Table 6. The values of median relative error (MRE) are also shown. Statistics for the Gulf of Maine (GOM) stock and Georges Bank (GB) stock under assessment scenario B are shown.

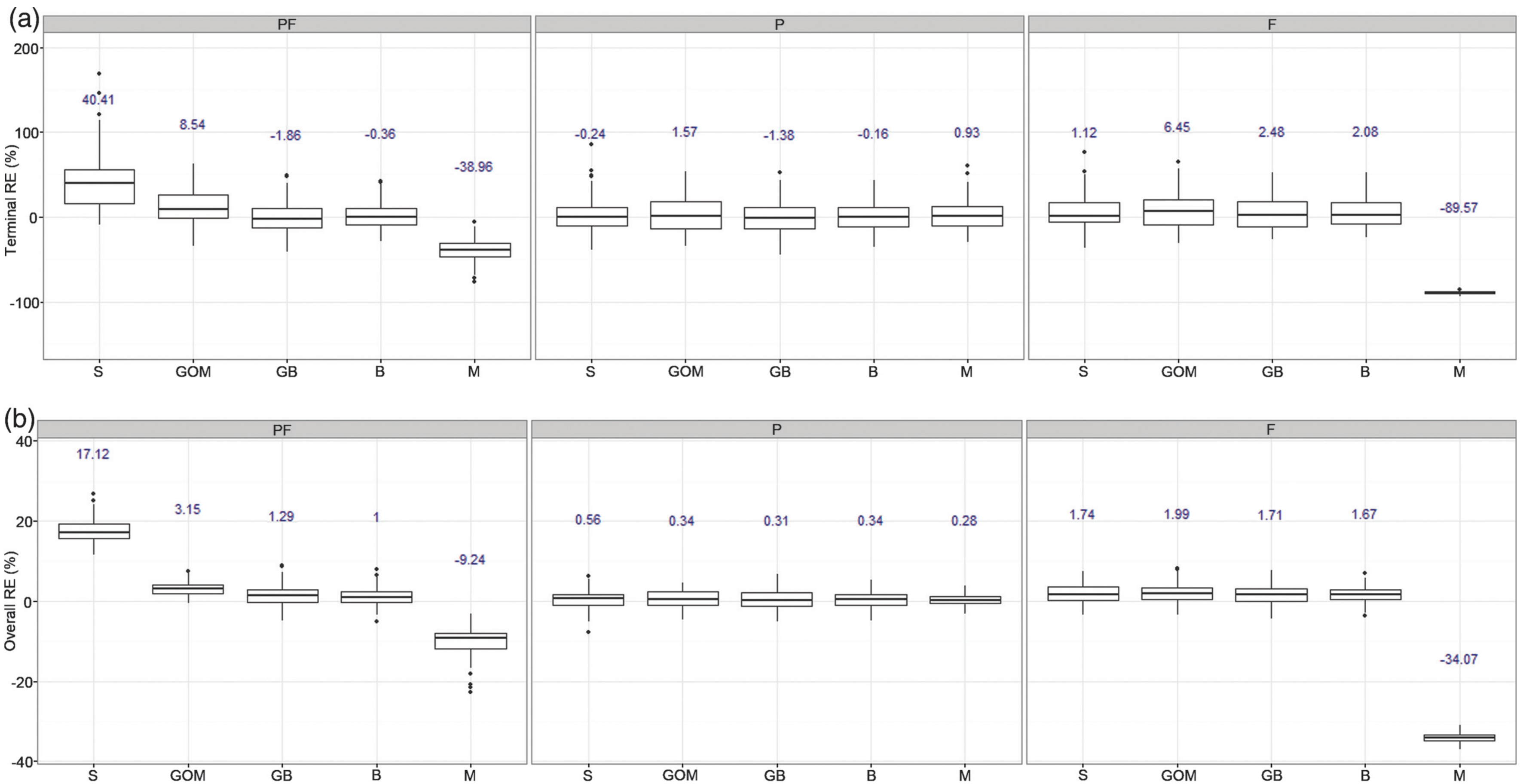


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Fig. 5. Relative error (RE) of estimated spawning stock biomass (SSB) for (*a*) terminal year and (*b*) all years combined under each outcome listed in Table 6. The values of median relative error (MRE) are also shown.

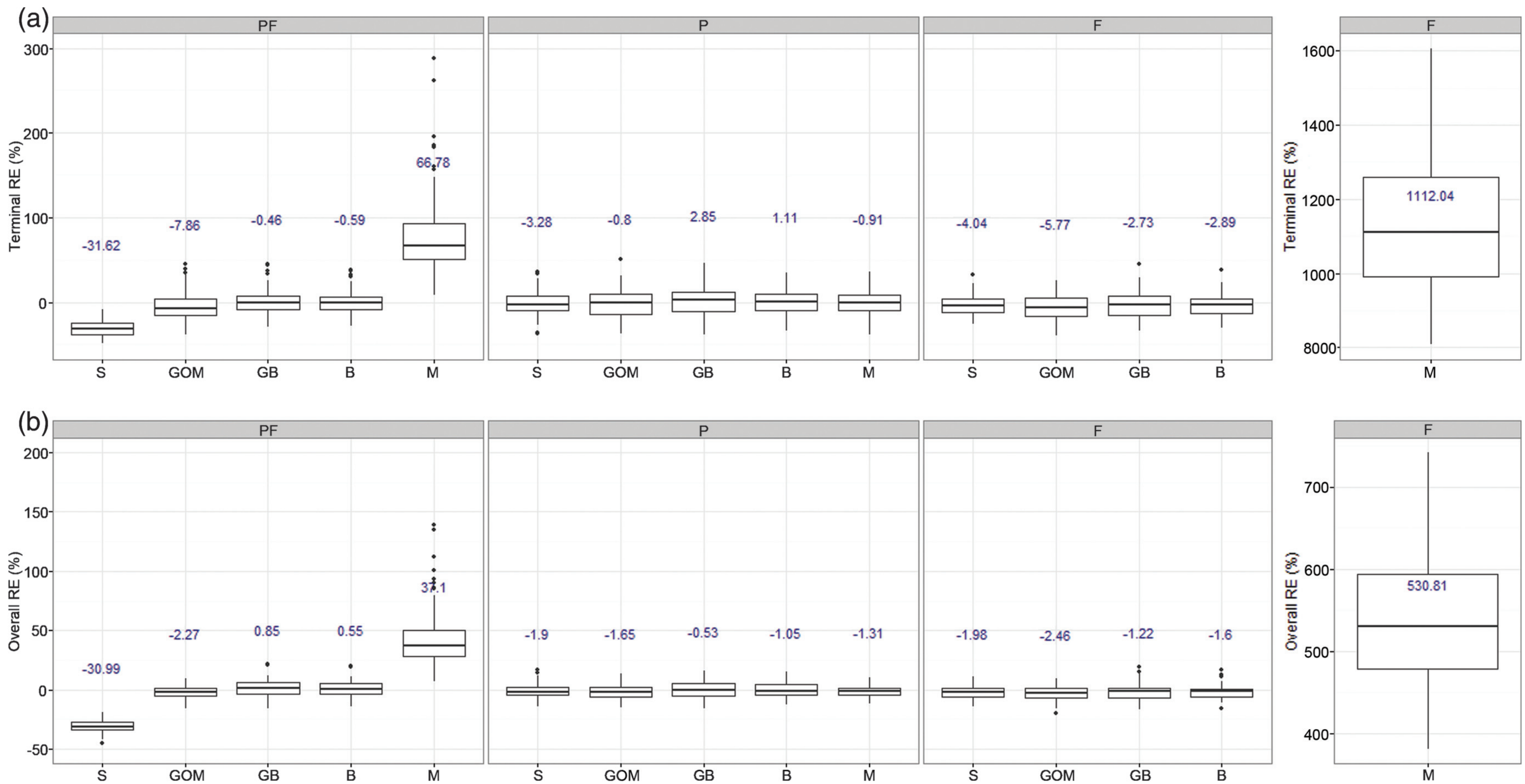

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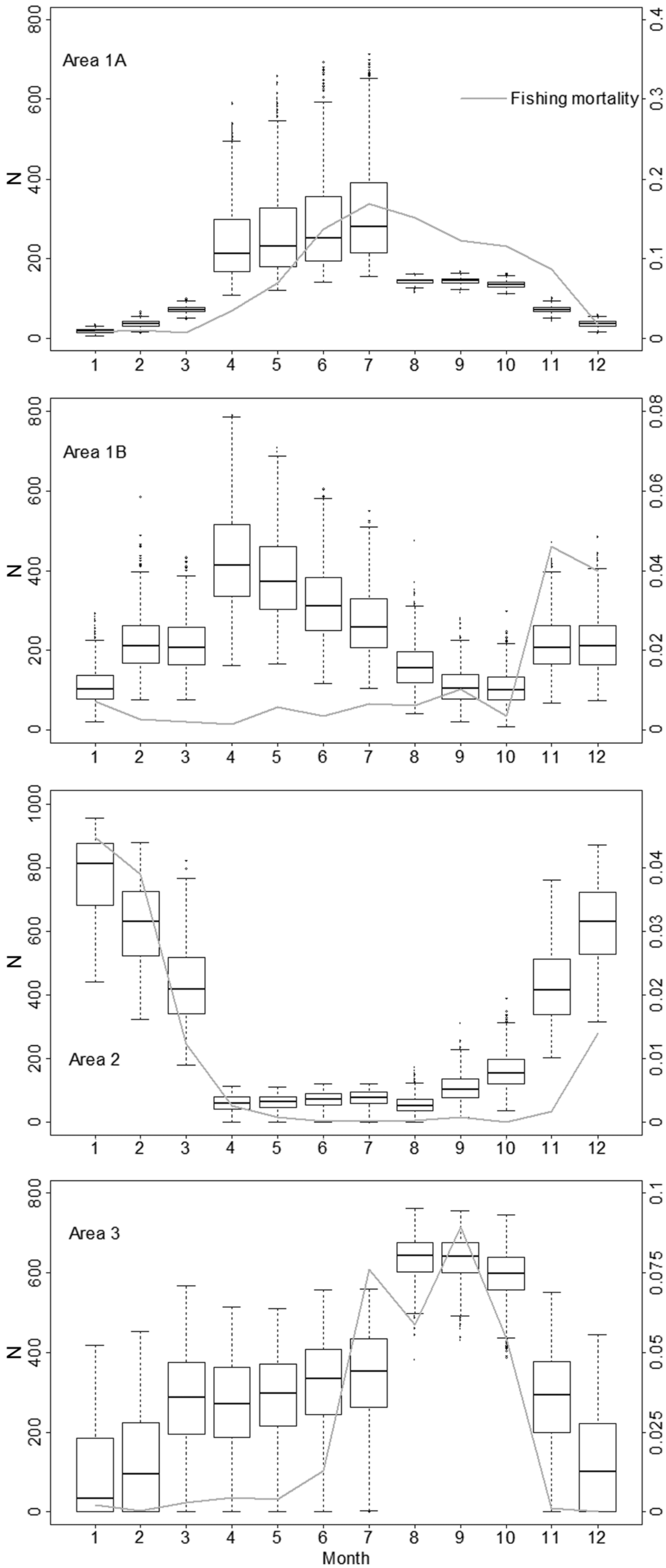
Fig. 6. Temporal coincidence between the spatial distribution of the herring population and the spatial distribution of fishing mortality. Boxplots show the area- and month-specific total abundances (i.e., summation of GOM and GB stocks) derived from 100 simulation runs based on the two mixing matrices defined in Tables 2 and 3 with 1000 fish in each stock; the curves show the averaged fishing mortality in each area for each month.



specification can result in large estimation errors. Most stock assessment models implicitly or explicitly assume random distribution of fishing effort with respect to targeted fish stocks (Ying et al. 2011). However, it is unlikely that fishing effort is random in an actual fishery. Fishing effort usually reflects the spatial distribution of a population (Botsford et al. 2009), as well as regulatory and economic constraints. Fish are unlikely to be spatially homogeneous given life history processes and heterogeneous environmental conditions (Dieckmann et al. 1999). This often results in high spatial variability in fishing removals.

The simulation case PF in this study most closely resembles what are believed to be the real circumstances describing this stock and its fishery (i.e., heterogeneous spatial structure likely exists for both population and fishery simultaneously). As expected, fishing mortality *F* is high in areas 1A, 2, and 3 when fish are aggregated at those locations (Fig. 6). Under these circumstances, conducting the assessment based on current management areas tends to overestimate SSB and underestimate *F*. If fishers have the capability and freedom to follow fish, management-area-based assessment tends to overestimate population abundance, since migration is ignored. Accordingly, it may be risk-prone to conduct assessments based on management areas, which implicitly assumes that each management area contains independent fish stock, when there are movements of fish among these areas. Atlantic bluefin tuna (*Thunnus thynnus*) have a similar spatial regime to that of Atlantic herring, with two spawning stocks and these mix during feeding. These two stocks, western and eastern, are assessed separately based on a jurisdictional boundary that ignores migration and mixing. Taylor et al. (2011) demonstrated that current "rebuilding quotas" could not allow for western stock recovery if mixing were incorporated into the assessment.

Our results suggest that the assumption of a single stock, as made in the most recent assessment, offers a fairly conservative outcome (PF–S) insofar as it tends to underestimate SSB and yield. Kerr et al. (2010) described similar results for GOM cod, so these findings are not surprising. However, the assumption that the GOM–GB stock has no interaction with the adjacent NS stock is more risky given the results of this study. Intermixing and exchange among stocks is well known to occur (Reid et al. 1999; Kanwit 2005), yet is ignored in both the NS and GOM–GB assessments, which are conducted separately by Canada and the USA. Outcome F–M in our results illustrates this point.

Assessing each substock independently produced the most adequate estimate of stock status even in the presence of variable *F* among areas. However, additional information such as tagging and otolith microchemistry is needed to effectively decompose catch and survey data into their proper subcomponents. Punt et al. (2000) developed a spatially explicit population model for assessing shark in which they showed that uncertainty is reduced by incorporating spatial structure based on tag–recapture data.

There are alternative factors that could have influenced the results of this study. The current ASAP used for herring models stock dynamics use an annual time step. However, our simulations employed a monthly time step to more accurately portray the movement of the stock. This inconsistency in temporal scale might have contributed to our estimation errors. Additionally, the actual stock and fishery spatial structures might be more complex than what we simulated. If, for example, the stock in this study understook age- or size-specific homing or spawning activities (McQuinn 1997; Stephenson et al. 2009) that were unaccounted for in our simulation, these could have increased estimation errors.

One possible factor that may have influenced our results is the disparity in size between the GOM and GB stocks. It is generally thought that the GB component is at least twice the size of the GOM component. To explore this possibility, we ran a sensitivity analysis with both substocks at equal abundances, but found no significant effect of stock size on estimation error for SSB and *F*.

In summary, we conclude that management-area-based assessment tends to lead to an overestimation of SSB and an underestimation of *F* (scenario PF–M) because of the presence of spatial structure in both the population and the fishery targeting it. Moreover, even when the population itself has no spatial structure (i.e., it exists as a unit stock), spatial structure in the fishery can still produce large assessment errors when stock assessment is conducted based on management areas (i.e., outcome F–M). However, when fishing removals are homogeneously distributed, misspecifying population spatial structure does not tend to increase error. Given these results, assessment scientists are cautioned against imposing spatial structure during the assessment process unless a supporting rationale is clearly evident.

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Appendix A

Annotations to the simulation procedure (Fig. 2) are given below.

(1) The initial abundance (i.e., January 1967) and age composition were taken from Shepherd et al. (2009). The fractional contribution of the GOM stock to the total population abundance was assumed to be constant at 0.18 from age 1 to age 6+ (Shepherd et al. 2009). Thus, the initial year class abundances for the two substocks were calculated as

$$N_{1,a,1967,\mathrm{GOM}} = 0.18N_{1,a,1967} \tag{A.1}$$

$$N_{1,a,1967,\mathrm{GB}} = 0.82N_{1,a,1967} \tag{A.2}$$

where $N_{1,a,1967,\mathrm{GOM}}$ is the abundance of fish of age a in the GOM stock in January, and $N_{1,a,1967,\mathrm{GB}}$ is the abundance of fish of age a in the GB stock in January. Six age classes were considered (i.e., 1, 2, 3, 4, 5, and 6+). Subsequent age-specific abundances for the two substocks were calculated in the simulation.

(2) The proportion of total annual recruitment (R_{total}) contributed by the GOM stock was assumed to be the same as its initial abundance ratio (0.18) and remained constant over the entire simulation interval. Recruitment, defined for each substock as fish reaching age 1, occurred at the beginning of each year (January) and was calculated as

$$R_{y,\mathrm{GOM}} = 0.18R_y \tag{A.3}$$

$$R_{y,\mathrm{GB}} = 0.82R_y \tag{A.4}$$

where $R_{y,\mathrm{GOM}}$ is recruitment to the GOM stock in year y, $R_{y,\mathrm{GB}}$ is recruitment to the GB stock in year y, and R_y is total recruitment in year y obtained from Shepherd et al. (2009).

(3) For simulation cases PF and P, depicting a stock with spatial and temporal structure, Tables 2 and 3 describe the spatio-temporal patterns of the GOM and GB stocks in the four management areas. At the beginning of each month, the abundance of GOM herring at each age class in each management area ($N_{m,a,y,\mathrm{GOM}}$) was determined based on the proportional figures given in Table 2. Similarly, based on $N_{m,a,y,\mathrm{GOM}}$ and the mixing fractions ($N_{\mathrm{GB}}/N_{\mathrm{total}}$) for each management area described in Table 3, the abundance of the GB stock ($N_{m,a,y,\mathrm{GB}}$) could also be calculated for each age class and each management area. All age classes had the same mixing proportions shown in Tables 2 and 3. Table 2 was developed based on herring life history, and Table 3 was based on NEFMC (2010).

For operating model F, 25% of $N_{m,a,y,\mathrm{GOM}}$ and $N_{m,a,y,\mathrm{GB}}$ was allocated to each management area at the beginning of each month.

(4) For simulation cases PF and F, which incorporate spatial structure in fishing effort, seasonal patterns of fishing mortality F are assumed based on seasonal patterns of catch, ignoring within-season depletion. Fishing mortality for age a in month m, region r, and year y ($F_{m,a,r,y}$) was calculated as

$$\mathrm{FMRA}_{r,y} = \frac{\mathrm{Catch}_{r,y}}{\sum_r \mathrm{Catch}_{r,y}} \tag{A.5}$$

$$\mathrm{FMRM}_{m,r,y} = \frac{\mathrm{Catch}_{m,r,y}}{\sum_m \mathrm{Catch}_{m,r,y}} \tag{A.6}$$

$$F_{m,a,r,y} = F_y \times \mathrm{FMRA}_{r,y} \times \mathrm{FMRM}_{m,r,y} \times \mathrm{SelF}_a \times \mathrm{Coef} \tag{A.7}$$

$\mathrm{Catch}_{r,y}$ is catch in year y in region r from Shepherd et al. (2009); FMRA is a proportional value for dividing a year-specific fishing mortality into area- and year-specific fishing mortality; and FMRM is a proportional value for dividing an area- and year-specific fishing mortality into area- and month-specific fishing mortality. Catches recorded in southern New England, GB, and GOM–NB were allocated to management areas 2, 3, and 1, respectively (Fig. 1). However, there was no breakdown of the catch in area 1 available for the whole time series (i.e., no separate catch data available for areas 1A and 1B). Therefore, we assumed that if catch in area 1A was X times larger than in area 1B, with X being a random number drawn from a uniform distribution U [5, 10], then the catch in area 1 could be divided between areas 1A and 1B. This uniform distribution was defined based on the ratio of catch between areas 1A and 1B provided by NEFMC (2004). $\mathrm{Catch}_{m,r,y}$ was catch in month m, region r, and year y. F_y was drawn from Shepherd et al. (2009). Coef was a constant coefficient and was set at 4 (because F is partitioned among four regions). SelF_a was fishery selectivity and was set at 0.0 for age 1 and 1.0 for other ages, the same as in Shepherd et al. (2009).

For simulation case P, depicting a uniform spatio-temporal distribution of fishing mortality, $\mathrm{FMRM}_{m,r,y}$ and $\mathrm{FMRA}_{r,y}$ were set at 1/12 and 1/4, respectively.

(5) Natural mortality (M) was constant at 0.2·year^{-1}.

(6) For each stock, catch of age a in region r and year y ($\mathrm{Catch}_{m,a,r,y,P}$) was calculated in the simulation as

$$\mathrm{Catch}_{m,a,r,y,P} = N_{m,a,r,y,P}(1 - e^{-F_{m,a,r,y}-M/12})\frac{F_{m,a,r,y}}{F_{m,a,r,y} + M/12} \tag{A.8}$$

Observational error was added to catch and catch-at-age data (CV = 0.2, with an effective sample size of 100). Observed catch, $C_{m,r,y,O}$, was calculated as

$$\mathrm{Catch}_{m,r,y,O} = \mathrm{Catch}_{m,r,y,P}e^{\varepsilon} \tag{A.9}$$

where $\varepsilon \sim N[0, \log(\mathrm{CV}^2 + 1)]$.

Age composition of catch was assumed to follow a multinomial distribution, from which random trials were drawn to simulate the observed age composition (Chen 1996). The number of trials equaled the effective sample size (i.e., 100).

(7) For each substock of age a, the abundance in region r and year y ($N_{m,a,r,y,P}$) was calculated as

$$N_{m+1,a,r,y,P} = N_{m,a,r,y,P}e^{-F_{m,a,r,y}-M/12} \tag{A.10}$$

$$N_{1,a+1,r,y+1,P} = N_{12,a,r,y,P}e^{-F_{12,a,r,y}-M/12} \tag{A.11}$$

$$N_{1,A,r,y+1,P} = N_{12,A-1,r,y,P}e^{-F_{12,A-1,r,y}-M/12} + N_{12,A,r,y,P}e^{-F_{12,A,r,y}-M/12} \tag{A.12}$$

(8) The survey indices were calculated as

$$I_{m,a,r,y,P} = N_{m,a,r,y,P} \times q_y \times \mathrm{SelS}_a \tag{A.13}$$

where q_y is survey catchability and was set to 0.1. SelS_a is survey selectivity, which is formulated as a double logistic function calculated as

$$\mathrm{SelS}_a = \left[\frac{1}{1 + e^{-(a-3)/2}}\right]\left[1 - \frac{1}{1 + e^{-(a-3)/2}}\right]\Big/0.25 \tag{A.14}$$

To make the maximum selectivity equal to 1, we multiplied the double logistic function by 4. This maximum occurred at age 3.

Observational error was added to the survey abundance index (CV = 0.25) and to survey size composition data, with an effective sample size of 100. To generate the observed survey index, we employed the same approach used to generate the observed catch data.

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