

Calculation of population-level fishing mortality for single- versus multi-area models: application to models with spatial structure¹

Brian J. Langseth and Amy M. Schueller

Abstract: Spatial considerations in stock assessment models can be used to account for differences in fish population dynamics and fleet distributions, which, if otherwise unaccounted for, could result in model misspecification leading to bias in model results. Calculating an overall fishing mortality rate (F) across spatial components is not straightforward but is often required for harvest management. We examined effects of spatial assumptions on model results under different approaches for calculating F . We show that (i) F can differ by as much as 50% depending on the spatial structure of the model; (ii) for multi-area models, F changes with size of area for all but one approach; and (iii) results are sensitive to model assumptions about catchability between areas and the spatial distribution of effort and abundance. Findings suggest caution be taken when interpreting results between models with different spatial structures. When comparing single- with multi-area models, we recommend adding F across areas when catchability is the same between areas and either effort or abundance is proportional to area. Otherwise no single approach can be expected to be superior in all cases. We suggest simulation be used to evaluate the best approach to meet particular management objectives.

Résumé : Des considérations spatiales dans les modèles d'évaluation des stocks peuvent être utilisées pour expliquer des variations de la dynamique des populations et des répartitions de flottes qui, si elles n'étaient pas prises en compte, pourraient se traduire par une mauvaise paramétrisation des modèles menant à des biais dans les résultats de ces derniers. Le calcul du taux de mortalité par pêche (F) global sur un ensemble d'éléments spatiaux n'est pas simple, même si ce paramètre est souvent nécessaire pour la gestion des prises. Nous avons examiné les effets d'hypothèses spatiales sur les résultats de modèles pour différentes approches de calcul de F . Nous démontrons que (i) F peut présenter jusqu'à 50 % de variation selon la structure spatiale du modèle, (ii) pour les modèles à zones multiples, F varie en fonction de la taille de la zone pour toutes les approches sauf une et (iii) les résultats sont sensibles aux hypothèses du modèle concernant la capturabilité entre zones et la répartition spatiale de l'effort et de l'abondance. Ces constatations indiquent que la prudence est de mise dans la comparaison des résultats entre modèles caractérisés par différentes structures spatiales. Pour la comparaison de modèles à une seule zone et à zones multiples, nous recommandons d'ajouter le F sur toutes les zones quand la capturabilité est la même d'une zone à l'autre et que l'effort ou l'abondance est proportionnel à la superficie de la zone. Sinon, aucune des approches n'est d'emblée supérieure aux autres dans tous les cas. Nous suggérons d'utiliser la simulation pour déterminer la meilleure approche pour les objectifs de gestion visés. [Traduit par la Rédaction]

Introduction

Spatial considerations in stock assessment models are becoming increasingly common in fisheries management. Incorporating spatially varying components within a stock assessment model allows for inclusion of migratory patterns of a species (Fahrig 1993; SEDAR 2015); differences in growth and natural mortality between areas of residence (Vetter 1988); and differences in fishery catch (Cope and Punt 2011), fishery catchability (Langseth et al. 2016), or fishery selectivity within a population (Hurtado-Ferro et al. 2014). Differences in migration, growth, mortality, and fishery aspects result in potential concerns for management depending upon the goals and objectives for management (Cope and Punt 2011). Consequently, new methods are being developed to account

for spatial differences in fish populations and fleets that were previously assumed to be homogeneous across space.

Spatial dynamics are typically represented in stock assessments through a combination of spatial heterogeneity, movement, and reproductive isolation (Cadrin and Secor 2009). The degree to which these operate can result in multiple configurations for modeling spatial structure (see Punt et al. 2015 for examples). When spatial heterogeneity exists, one approach to account for it has been to model the biological and fishery aspects for each spatial unit separately, thereby introducing spatially explicit population dynamics (Punt et al. 2015; Booth 2000). The spatial units are then linked via migration, recruitment, or the distribution of fishing effort. An alternative approach has been used to include

Received 1 July 2016. Accepted 27 May 2017.

B.J. Langseth. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, 1845 Wasp Boulevard, Building 176, Honolulu, HI 96818, USA.

A.M. Schueller. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, NOAA Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC 28516, USA.

Corresponding author: Brian J. Langseth (email: brian.langseth@noaa.gov).

¹This article is being published as part of the special issue "Space Oddity: Recent Advances Incorporating Spatial Processes in the Fishery Stock Assessment and Management Interface" arising from a related theme session at the 145th Annual Meeting of the American Fisheries Society, Portland, Oregon, USA, August 2015.

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spatial heterogeneity in a model with nonspatial population dynamics by assuming that fishing fleets act as unique areas (Cope and Punt 2011). This “areas-as-fleets” approach has been used to model spatially varying catch-at-age (Waterhouse et al. 2014), spatially varying catch histories (Cope and Punt 2011), and age-dependent dispersal (Berger et al. 2012). The method determines fishing mortality rates for each respective area (fleet), which are then often combined into an overall rate.

Management frequently requires a single overall fishing mortality rate for policy decisions. However, when spatial assessment models are used, the question becomes how to effectively calculate a single rate across all spatial units or fleets. Beverton and Holt (1957) described an approximation to the overall fishing mortality rate using fishing mortality rates and yields across regions. Cordue (2012) developed measures of average fishing mortality over time with a two-fleet model whereby fleets operated in different spatial areas and at different times of the year, but noted that finding one single measure of fishing mortality rate for a population with spatial structure would be difficult. Maury et al. (1997), Sampson and Scott (2011), Methot and Wetzel (2013), and Waterhouse et al. (2014) used different approaches for calculating a single population fishing mortality rate in the face of spatial heterogeneity within a population or fishery. However, we have found that the overall fishing mortality rate differs in recent comparisons among models with varying degrees of spatial structure.

Our objectives were to compare a variety of methods for calculating the population-level fishing mortality rate from models with and without spatial population dynamics under varying degrees of spatial structure and to discuss the potential issues that can arise when using each of the considered methods. We start by describing the published and general approaches for calculating an overall fishing mortality rate. We then show, using a non-age-structured single-year model that overall fishing mortality rates calculated using the described methods were different depending on the spatial structure of the model — whether a single- or multi-area model was used, and if multi-area, the relative sizes of the areas. Using an age-structured multiyear assessment model modified from the Gulf menhaden (*Brevoortia patronus*) stock assessment, we also show that the overall fishing mortality rate for multi-area models changed with the relative size of the areas. Our results were dependent on the specific assumptions about catchability and the distribution of abundance and effort made in our models, and we discuss the implications of these assumptions. This manuscript highlights the difficulties that arise when aggregating fishing mortality rates across spatial units, as a single value is often needed for management, or when comparing single- and multi-area models.

Methods

We use multiple methods for calculating fishing mortality and catch within two types of models under varying degrees of spatial structure and modeling assumptions to show the influence of spatial representation on methods of calculating overall fishing mortality rate and resulting overall catch. We first describe various methods for calculating fishing mortality and catch. We then describe a non-age-structured single-year model and show how alternative methods for calculating overall fishing mortality result in different values as the relative sizes of the spatial areas change. Next, we compare results from the non-age-structured single-year model with an age-structured multiyear model that is based on an existing stock assessment model for Gulf menhaden to further evaluate the properties of aggregating fishing mortality over space. Lastly, we evaluate alternative assumptions about the value of catchability between areas and the distribution of abundance and fishing effort across areas, so as to understand the implications of these assumptions on results.

Calculating population-level fishing mortality and catch

Methods for combining fishing mortality rates have been explored in the literature. Shepherd (1983) combined fishing mortality rates across age, and Cordue (2012) combined fishing mortality rates over time. We focused our application to space and, therefore, used only the methods described in the literature for dealing specifically with spatial combinations.

Beverton and Holt (1957) suggested the concept of an effective overall fishing mortality coefficient (\tilde{F}_t) at time t across specified spatial areas. By assuming a closed whole population and that fishing effort was uniform across the entire area, \tilde{F}_t represented the same total fishing mortality for the entire area as was observed. Beverton and Holt (1957) defined \tilde{F}_t , which we call $F_{BH,t}$, as

$$(1) \quad F_{BH,t} = \frac{Y_{tot,t}}{\sum_r \frac{Y_{r,t}}{F_{r,t}}}$$

where $Y_{r,t}$ and $F_{r,t}$ were yield in numbers and fishing mortality, respectively, in region r at time t , and $Y_{tot,t}$ was yield across all regions at time t .

Maury et al. (1997) described a methodology using Virtual Population Analysis to estimate total fishing mortality, which they called F_t but which we call $F_{M,t}$. They used a conservation of number of fish approach (eq. 2), defined whereby regional abundances ($N_{r,t}$) summed to total abundance (N_t) and by rearranging the Baranov catch equation formed an equation to be solved iteratively for $F_{M,t}$ based on effort ($E_{r,t}$), catch ($C_{r,t}$), spatial area ($S_{r,t}$), fishing mortality ($F_{r,t}$), and natural mortality ($M_{r,t}$) in each region r at time t , and total natural mortality (M_t) at time t . Maury et al. (1997) assumed that catchability per surface unit and fish density were the same between areas and that migration occurred instantaneously at the end of each time step. The equations in the case of two areas were

$$(2) \quad N_{1,t} + N_{2,t} - N_t = \frac{C_{1,t}(M_{1,t} + F_{1,t})}{F_{1,t}[1 - \exp(-F_{1,t} - M_{1,t})]} + \frac{C_{2,t}(M_{2,t} + F_{2,t})}{F_{2,t}[1 - \exp(-F_{2,t} - M_{2,t})]} - \frac{C_t(M_t + F_{M,t})}{F_{M,t}[1 - \exp(-F_{M,t} - M_t)]} = 0$$

where

$$(3) \quad F_{1,t} = \frac{S_{1,t}E_{2,t}}{S_{2,t}E_{1,t}}F_{2,t}$$

The logic was that based on abundance, catch, and mortality rates by region, the overall fishing mortality rate applied to both areas would result in a comparable overall abundance across areas. The authors noted that the equations could be extended to more than two areas. For our application, F_1 and F_2 were calculated initially; thus eq. 2 could be calculated directly, as opposed to iteratively, as was the case for Maury et al. (1997). The value for M_t was not specified in Maury et al. (1997), so we used the same value for natural mortality across all areas.

Waterhouse et al. (2014) extended work done by Sampson and Scott (2011) by developing an areas-as-fleets model to calculate overall fishing mortality rates for a nonspatial population dynamics model based on catches from fleets operating in distinct areas. The authors assumed that differences in catch-at-age between fleets were due to differences in recruitment or fishing mortality and explored how multiple gear types and areas within the fishery led to differences in overall selectivity. Similar to Beverton and Holt (1957), the intent was to have a set of regional age-specific areas-as-fleets fishing mortality rates ($F'_{a,r}$) that if applied over the

Table 1. Summary of the methods used for calculating overall fishing mortality and overall catch for the non-age-structured and age-structured models as described in the text.

Approach	Use	Nonspatial or spatial	Citation
F_{BH}	Non-age	Spatial	Beverton and Holt 1957
F_M	Non-age	Spatial	Mauzy et al. 1997
F_W	Non-age	Nonspatial	Waterhouse et al. 2014
F_A	Both	Nonspatial	
F_{mean}	Both	Nonspatial	
F_T	Both	Spatial	Methot and Wetzel 2013; Sampson and Scott 2011
C_A	Non-age	Nonspatial	
C_{tot}	Non-age	Nonspatial	
C_{mean}	Non-age	Nonspatial	
C_T	Non-age	Spatial	Methot and Wetzel 2013; Sampson and Scott 2011

Note: The second column indicates whether a method was used for the non-age-structured model only (non-age) or if the method was used for both the non-age-structured and age-structured models (both). The third column indicates whether or not the model included spatial or nonspatial population dynamics. The fourth column indicates the citation of the method, if available. Temporal subscripts for fishing mortality and catch were removed for ease of presentation. Equations for each of the methods are described in the text.

entire population would produce the same set of catches-at-age as the original rates ($F_{a,r}$) applied only to the subpopulations within their individual areas (r). The set of equations for determining overall areas-as-fleets rates were solved iteratively for each area and were

$$(4) \quad C_{a,r} = N_{a,r} \frac{F_{a,r}}{M + F_{a,r}} [1 - \exp(-M - F_{a,r})]$$

$$= \left(\sum_r N_{a,r} \right) \frac{F'_{a,r}}{M + \sum_r F'_{a,r}} \left[1 - \exp(-M - \sum_r F'_{a,r}) \right]$$

We summed the $F'_{a,r}$ together to form a single overall rate, which we call F_W . We did not use eq. 4 within an age-structured model and so dropped the age subscripts when calculating F_W .

In addition to the methods described in the literature previously, we also evaluated other general approaches to calculate fishing mortality and catch. For models without spatial population dynamics but with spatial representation (i.e., following the areas-as-fleets concept), we used an addition approach where we added fishing mortality rates from both areas according to

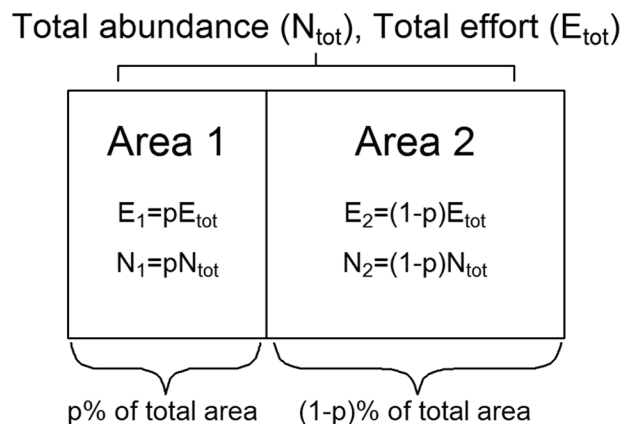
$$(5) \quad F_A = F_1 + F_2$$

Catch was calculated either from the Baranov catch equation using F_A (C_A) or simply summing the region-specific catches according to $C_{tot} = C_1 + C_2$. Because mortality rates are instantaneous, in addition to adding rates together as in eq. 5, we also averaged the total mortality rates from the two areas and subtracted natural mortality to get a single overall fishing mortality rate according to

$$(6) \quad F_{mean} = -\ln[\exp(-F_1 - M)p + \exp(-F_2 - M)(1 - p)] - M$$

where p was the proportion of total area for one area (with the other being $1 - p$). Catch (C_{mean}) was calculated from the Baranov catch equation using F_{mean} . For models with spatial population dynamics, we used a time step approach similar to what is used for Stock Synthesis (Methot and Wetzel 2013) and what was used in Sampson and Scott (2011). We calculated abundance separately in each area and added the regional abundances together to cal-

Fig. 1. Schematic showing effort (E) and abundance (N) for a population divided into two areas, as dependent on the relative size of the two areas (p and $1 - p$) and the total effort (E_{tot}) applied to and the abundance (N_{tot}) of the entire stock.



culate a single overall fishing mortality rate (F_T) based on the relationship that $Z_t = -\ln(N_{t+1}/N_t)$ under equilibrium conditions. The equation for this was

$$(7) \quad F_{T,t} = Z_t - M$$

$$= -\ln \left[\frac{pN_t \exp(-F_{1,t} - M) + (1 - p)N_t \exp(-F_{2,t} - M)}{pN_t + (1 - p)N_t} \right] - M$$

Catch (C_T) was calculated from the Baranov catch equation using $F_{T,t}$. Table 1 summarizes the respective methods and their use in the following non-age-structured and age-structured models.

Non-age-structured single-year model

We first describe a simple thought experiment for catch to illustrate the effects of spatial structure. Assume that a fish stock is divided into two areas with size as some proportion p and $1 - p$ of the total area. If, like that in Fig. 1, the areas are combined, the overall catch could be calculated as $C_{tot}^* = qN_{tot}E_{tot}$, where q is the catchability of the fishery per unit of effort, N_{tot} is the total abundance, and E_{tot} is the total effort. However, if the two areas of the stock are not combined and are modeled with spatial population dynamics, then using a similar formulation

$$(8) \quad C_{tot} = C_1 + C_2 = qE_1N_1 + qE_2N_2$$

$$= q(pE_{tot})(pN_{tot}) + q(1 - p)E_{tot}(1 - p)N_{tot}$$

$$= C_{tot}^*[p^2 + (1 - p)^2]$$

which is most different from the combined-area calculation when the two areas are equally sized ($p = 0.5$).

We then extended that thought experiment to address effects of spatial structure on overall fishing mortality and catch by using the fishing mortality and catch metrics listed in Table 1 in a non-age-structured model for a single year. The initial fishing mortality rate for each area was calculated as the product of catchability ($q = 0.0035$) and effort in each area (Ep or $E(1 - p)$), with total effort assumed as $E = 100$ units. Then the total fishing mortality rate was calculated according to the equations for each method in Table 1. We compared model results when using methods in Table 1 for a model with two fleets operating in separate areas (with size p and $1 - p$), but modeled without spatial population dynamics (similar to an areas-as-fleets model), with results when using one method (F_T) in Table 1 for a model with two fleets operating in separate areas and modeled with spatial population dynamics. Natural mortality was varied and included in the calculations of

fishing mortality and catch. This was done to see if the fishing mortality rate for each of the two models depended on the value of natural mortality. Values for natural mortality were $M = 0.01$, 0.5 , and 1 .

Age-structured multiyear model

An age-structured, multiyear model was used to determine if the differences in results among methods of calculating fishing mortality rate and catch for the non-age-structured model would persist under increased model complexity. The age-structured model was based on the assessment model used for Gulf menhaden (SEDAR 2013) and was considered as a case study for this research. The Gulf menhaden assessment model is a single-area, likelihood-based statistical catch-at-age model, constructed in the Beaufort Assessment Model framework (Williams and Shertzer 2015) and used in spatial simulations previously (Langseth et al. 2016) where catchability was a parameter of interest. We briefly describe the age-structured model below, but detailed equations can be found in Langseth et al. (2016) and so are not repeated here.

An operating model was used to calculate catch, age compositions, and effort in each year, which were then used as data inputs into the age-structured model. Calculations within the operating model were based on area-specific fishing mortality rates calculated as the product of catchability and effort in each year in each of two areas with sizes p and $1 - p$, where p is the proportion of total area. Fishing mortality rates from each area were then combined into a single rate for each year following the calculation methods listed in Table 1. Depending on the method for calculating an overall fishing mortality rate, population dynamics were modeled as either nonspatial or spatial. For nonspatial population dynamics, a single overall rate was calculated first and, along with assumed biological parameters, was used to establish stock dynamics over time across the entire combined area. For spatial population dynamics, each area-specific fishing mortality rate was used to calculate separate stock dynamics in each area before a single overall rate was calculated for each year. We used nonspatial population dynamics for F_A and F_{mean} , following an areas-as-fleets approach, and spatial population dynamics for F_T . We assumed no movement between areas, and recruitment occurred as a single population with new recruits assigned proportional to the size of each area.

The age-structured model used similar equations and assumptions as the operating model, but assumed only nonspatial population dynamics. The age-structured model used catch, age compositions, and effort inputs for each year, as well as assumed biological parameters to estimate fishing mortality at age by year, selectivity at age, catchability, initial recruitment, initial deviations in abundance, and recruitment deviations. Population dynamics within the age-structured model were calculated from a single overall fishing mortality rate and therefore matched the nonspatial population dynamics within the operating model. Additional assumptions of the age-structured model matched those of the operating model, including constant selectivity and catchability across time, fixed natural mortality, and that biological conditions of the fish (growth, catchability, selectivity, etc.) were the same across areas.

Rather than estimate fishing mortality and other parameters in the age-structured model, which could mask differences in model outputs, we fixed model parameters and other estimated quantities at the values used in the operating model. We did this to maintain the importance of the estimated parameters, particularly catchability, as in the original application of the case study (Langseth et al 2016). Consequently, fishing mortality at age by year, selectivity at age, catchability, initial recruitment, initial deviations in abundance, and recruitment deviations were all set at the specific values used in the operating model. The age-structured model calculated the resulting overall catch, biomass, and effort algebraically based on the set equations using the val-

ues of fishing mortality calculated from the operating model. We then compared the overall catch and biomass summed over ages, effort, and fishing mortality at age each year from the operating model with the catch, biomass, and effort each year as calculated in the age-structured model to determine the influence of the value of p on the ability of the model to recreate known deterministic quantities.

We used three relative assumptions for p and $1 - p$ within the operating model to calculate true values of catch, effort, and biomass: a 1–99 split, 31–69 split, and 50–50 split. The 1–99 split represented a scenario similar to the single-area model (0–100) while still being a two-area model. The 31–69 split was based on work by Langseth et al. (2014), which delimited the area of Gulf menhaden fishing grounds impacted by hypoxia during the fishing season. The 50–50 split assumed the two areas were of equal size.

Sensitivity analysis

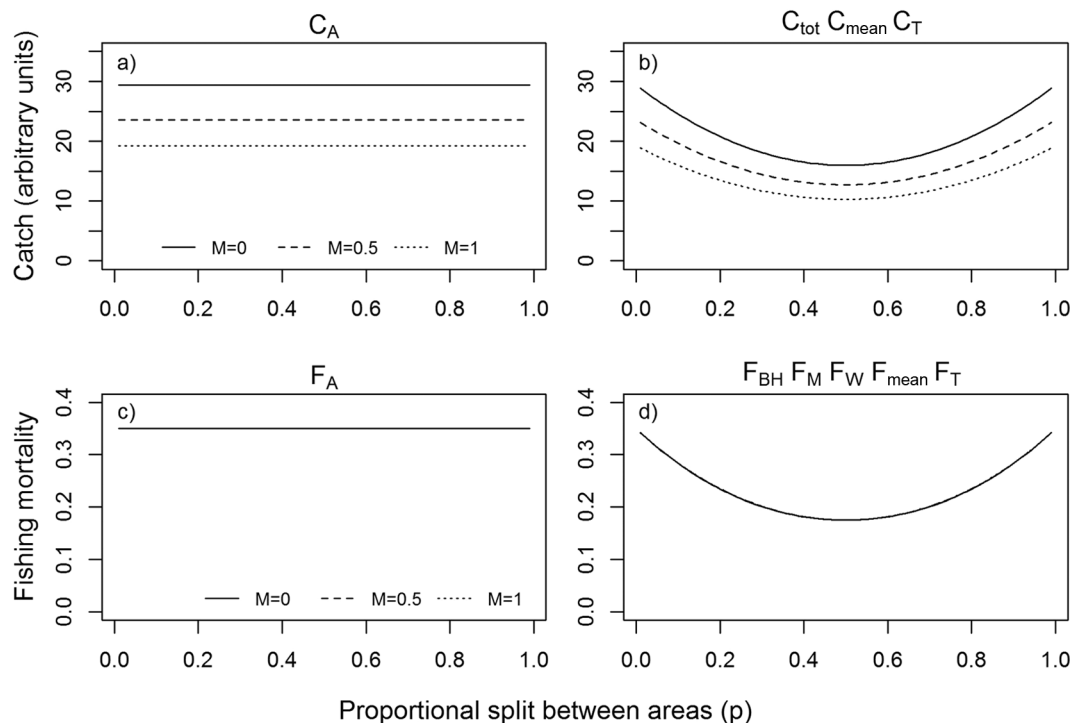
We explored the implications of relaxing several assumptions made in our non-age-structured model and in the age-structured operating model through sensitivity analysis. Specifically, we tested the effects of four sensitivities, including different catchability between areas (base assumption was constant catchability between areas); different allocation of effort across areas (base assumption was proportional to area size); different allocation of abundance across areas (base assumption was proportional to area size); and simultaneous differences in catchability with the alternative allocations of effort and abundance. Catchability was decreased by a factor of 10 in area one (i.e., the area of size p) for the catchability sensitivity. Total abundance and effort were individually allocated with a constant $\frac{2}{3}$ apportionment to area one and $\frac{1}{3}$ apportionment to area two for their sensitivity runs. Finally, for the combined sensitivity run, all of the above described changes were made simultaneously. The results for different allocations of effort and abundance were similar for the non-age-structured model, which was expected given that the chosen allocation values for effort and abundance were the same. For the age-structured model, assumptions about allocating abundance were only applicable for one of the methods used to calculate fishing mortality rate (F_T) and were not comparable across methods. Therefore, alternative assumptions about abundance allocation were not presented for either model. Some of the methods considered for calculating fishing mortality rate had restricting assumptions and therefore were not included in sensitivity runs. Specifically, the $F_{\text{BH},t}$ method assumes uniform effort across the entire area (Beverton and Holt 1957), so sensitivity to alternative effort allocation was not evaluated using this method. Also, the $F_{\text{M},t}$ method assumes the same catchability per unit of area and equal fish density (Maury et al. 1997), so sensitivity to alternative catchability and abundance allocation was not evaluated using this method.

Results

Non-age-structured single-year model

The non-age-structured model with initial population dynamic assumptions showed that the total catch and fishing mortality rate changes depending on the size of the two areas. Total catch (C_A) was constant regardless of the size of areas when fishing mortality rates were added across areas, but depended on the specific size of areas for the other general methods evaluated (Figs. 2a and 2b). For the other general methods, catch for models without spatial population dynamics (C_{mean} , C_{tot}) as well as catch for models with spatial population dynamics (C_T) ranged from 100% (equality) to 54% of the catch when calculated from only one area (i.e., $p = 0$ or 1). The primary change caused by M was changing the overall scale of catches, which was as expected. Catches were

Fig. 2. Overall catch and fishing mortality rate from methods outlined in Table 1 and described in the text for the non-age-structured model across values of the size (p and $1-p$) for each area proportional to the total area and value of natural mortality ($M = 0$, solid line; $M = 0.5$, dashed line; $M = 1$, dotted line).



the same among C_{tot} , C_{mean} , and C_T when M was near zero and differed only slightly among one another as M increased.

Similar patterns as those for catch were also observed for fishing mortality (Figs. 2c and 2d). Fishing mortality was constant across different sizes of areas when rates from each area were added (F_A), but depended on the size of the areas for all other methods of calculations. Fishing mortality rates ranged from equality to 50% of the rate calculated for a single-area model (i.e., $p = 0$ or 1). Methods described in the literature (F_{BH} , F_M , and F_W) differed only slightly and were also minimally affected by the value of M . General approaches for calculating fishing mortality rates (F_{mean} and F_T) were identical to one another and nearly identical to values from methods from the literature. Given the lack of effect of M in the non-age-structured model, different M values were not considered in the age-structured model.

Age structured multiyear model

The age-structured model showed similar results as the non-age-structured model. Calculated values from the age-structured, multiyear model reproduced true values from the operating model when fishing mortality rates from the two areas were added (F_A), regardless of the size of the areas (Fig. 3). If averaging fishing mortality from the two areas (F_{mean}), the age-structured model reproduced catch, biomass, and fishing mortality, but the resulting value of effort did not reproduce the values used in the operating model (Fig. 4). Effort was most different under the 50–50 areal assumption, similar in pattern to the difference in catch and similar in pattern and value (50% of F_A) for fishing mortality as shown in the non-age-structured model (Fig. 2). Calculated effort from the age-structured model was more similar to known effort from the operating model for the 31–69 areal assumption (56% of F_A) and was most similar for the 1–99 areal assumption (97% of F_A).

When F_T was used to calculate an overall fishing mortality rate in the operating model, and thereby spatial population dynamics were assumed, patterns from the age-structured model were sim-

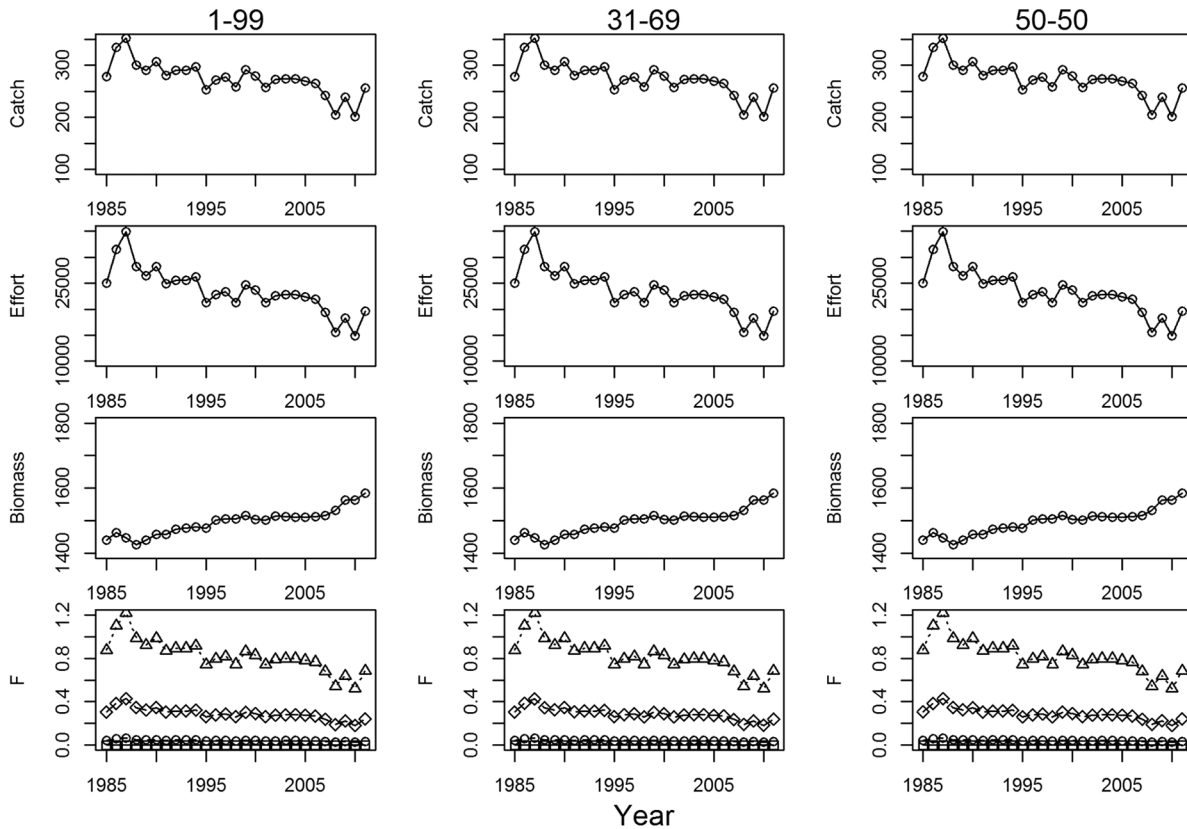
ilar to those when F_{mean} was used. Catch, abundance, and fishing mortality matched well, while effort did not (Fig. 5). The difference in the known and calculated values was slightly less under F_T than F_{mean} , with the exception of the 50–50 areal assumption, which was the same. Similar to the non-age-structured model, results were most different when the relative proportion of areas was 50–50. Differences in the results from the age-structured model were smallest as the operating model approached a single-area assumption (i.e., 0%–100% split), but once a single-area model was used, results under F_T (as well as F_{mean}) became identical to results when using F_A , and all calculated metrics matched known values from the operating model.

Sensitivity analysis for non-age-structured model

Sensitivity analysis on the base assumptions of constant catchability and the allocation of abundance and effort showed that these assumptions influenced results. When catchability differed between the two areas, all calculated catches changed with size of areas (Figs. 6a and 6b). The overall change in catch across different sizes of areas depended on the relative difference in catchability, which was a factor of 10. The patterns in fishing mortality rate were similar to that of catch, but were unaffected by differences in natural mortality (Figs. 6c and 6d). As under base assumptions, the magnitude of catch and fishing mortality rates for the general approaches (F_{mean} and F_T , C_{mean} and C_T) were identical, while differences within the literature methods were negligible.

When effort was allocated as a constant proportion of total effort, catch (C_A) was constant across different sizes of areas when the fishing mortality rates were added across areas, but depended on the assumed size of areas for the other methods (Figs. 7a and 7b). The same pattern occurred for fishing mortality (Figs. 7c and 7d). The changes in catch and fishing mortality across values of p for methods affected by the size of areas were related to our assumed allocation for effort and changed from one-third (for $p = 0$) to two-thirds (for $p = 1$) of the values for C_A and F_A . Differences among those methods affected by the size of areas were negligible.

Fig. 3. Using the F_A method of calculating fishing mortality under the 1%–99%, 31%–69%, and 50%–50% areal assumptions compared with known values of overall catch (first row); overall biomass (third row); and fishing mortality (F) for age 0 (open circle), age 1 (open square), age 2 (open triangle), and age 3+ (open diamond) from the operating model based on observed effort (second row). Lines indicate calculated values of catch, effort, and biomass in the age-structured model using the same parameter estimates as in the observation model while fixing fishing mortality for ages 0, age 1, age 2, and age 3+ for each areal assumption.



When different catchabilities were used and neither effort nor abundance were proportional to the size of the areas, all methods for calculating fishing mortality and corresponding catches were independent of the size of areas (Fig. 8). Therefore, our original assumption of how effort and abundance were allocated influenced the extent to which changes in size of areas affected model results. If effort and abundance were allocated independent of the size of areas, then the relative size of areas had no effect on fishing mortality rates and catch. However, under assumptions of different catchability and allocation of abundance and effort independent of the size of the areas, the magnitude of fishing mortality rates and catch differed between the F_A method and the other methods considered.

Sensitivity analysis for age-structured model

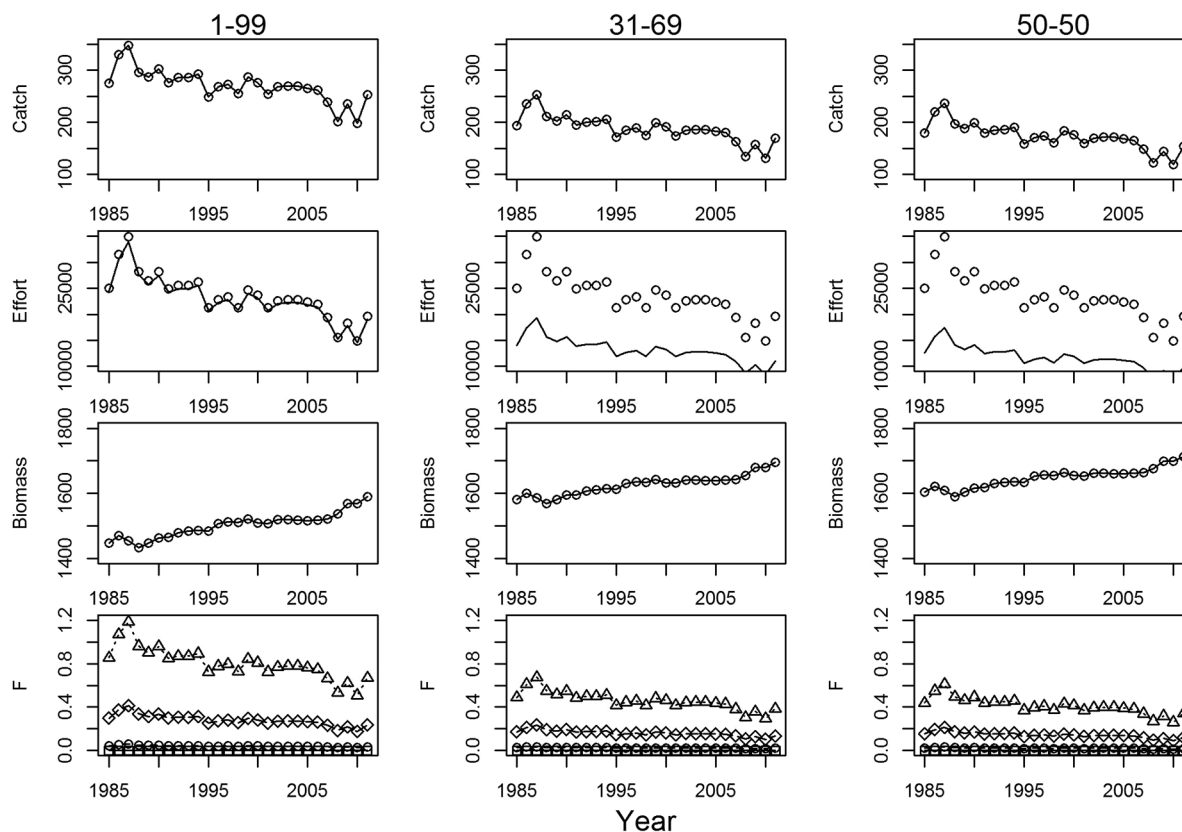
Model assumptions about catchability and the allocation of effort also mattered for the age-structured model. We found that when using the F_A method under alternative assumptions about catchability, contrary to Fig. 3, the age-structured model could not reproduce known values of effort when two areas were present (i.e., p not equal to 0 or 1; Fig. 9). Consequently assumptions about catchability affected model results when using the F_A method, as was found for the non-age-structured model (Fig. 6). Known values of effort were reproduced for the F_A method only when changes in the assumption of effort were allowed. Therefore, assumptions about allocation of effort did not matter for the F_A method, which was also found for the non-age-structured model (Fig. 7). For the other methods of calculating fishing mortality rates, results from the sensitivity analysis for the age-structured model were comparable to results from the sensitivity analysis for the non-age-

structured model. Under all conditions, the model could not reproduce known values of effort for the F_{mean} and F_T methods. Under alternative assumptions about catchability, model results were sensitive to changes in the size of areas, whereas when effort was not proportional to area, the model results were either not sensitive to changes in area (in the case of F_{mean}) or less sensitive (in the case of F_T) to changes in area compared with results under alternative catchability assumptions. Results for F_T were still sensitive to area because we used spatial population dynamics for this method, which assigned new recruits to the populations each year according to the size of the areas.

Discussion

Our findings show that calculating total fishing mortality for a multi-area model can lead to incorrect model estimates when compared with a single-area model. When comparing single-area and multi-area models, or when comparing multi-area models with different sizes for the subareas, analysts and management groups should recognize the effect these choices have on model output. When abundance or effort are distributed based on the size of areas, simulation studies or stock assessments that compare base case single-area models with multi-area models must be cautious about the way in which catch and fishing mortality are combined across space when also calculating effort. If multi-area models use any of the methods described in this manuscript besides F_A to aggregate fishing mortality, then the results are likely influenced by the assumed areal representation. If spatial considerations are to be implemented in stock assessment models to compare single- with multi-area models and effort or abundance

Fig. 4. Using the F_{mean} method of calculating fishing mortality under the 1%–99%, 31%–69%, and 50%–50% areal assumptions compared with known values of overall catch (first row), overall biomass (third row), and fishing mortality (F) for age 0 (open circle), age 1 (open square), age 2 (open triangle), and age 3+ (open diamond) from the operating model based on observed effort (second row). Lines indicate calculated values of catch, effort, and biomass in the age-structured model using the same parameter estimates as in the observation model while fixing fishing mortality for age 0, age 1, age 2, and age 3+ for each areal assumption.



are distributed proportional to the size of the areas, then we recommend that the F_A method be used, as it was shown to provide fishing mortality rates that are comparable across areas. All methods can produce values independent of the size of areas if allocation of effort and abundance is set at fixed proportions that do not change with the size of areas, and thus under these conditions no one method is better than another, although values can differ in magnitude depending on the method. Consequently, careful consideration of the methods and assumptions within models is required, as model results can be dependent on the size of the spatial areas modeled and the method used to calculate total fishing mortality rate.

Caution is warranted when aggregating fishing mortality estimates from spatial assessment models, because the aggregation method can have impacts on perceived stock status and management advice (Guan et al. 2013; Kerr et al. 2014). In instances where fishing mortality is underestimated, harvest over the short term may not greatly impact stock status, but over the long term, harvest could be significantly greater than the sustainable level. For example, fishing mortality estimated within a four-area model was lower than estimates within a single-area model for Atlantic herring (*Clupea harengus*) (Guan et al. 2013); however, Guan et al. did not explore the long-term management consequences. In the future, management strategy evaluations could be used to compare the management implications of using different methods to estimate fishing mortality to determine how well management objectives are being achieved.

Most stock assessment models are currently single-area models and do not account for spatial considerations (Punt et al. 2015). Fish species can have broad spatial distributions, and stock assessment

models should consider differences in parameters across space (Cope and Punt 2011). For those stock assessment models that have already considered spatial differences, there might be unintended consequences in the way that overall fishing mortality rate is being estimated. In this study, the consequence was that calculated effort differed from known values. If catchability were not fixed, calculated effort would have matched known values but catchability would have been biased. Thus, catchability can account for error if it is estimated, but if considering effects on catchability, such as in this study and as was done for Gulf menhaden in Langseth et al. (2016), then results would be affected. Catchability has been shown to vary over time for several species due to density dependence, environmental factors, and biological factors (Wilberg et al. 2009, their table 1 and references therein), which means that results would be affected for many species if catchability were estimated as a way to account for error.

Several assumptions were made in the two models, and the effects of some were explored with sensitivity analysis. One assumption was that there were only two areas in the models. We did not test the effect of using more than two areas to maintain simplicity and to make results comparing single- versus multi-area models as clear as possible. More than two areas would likely lead to complexities in the results and further nonlinearities, such as unique nonlinear relationships that depend on model configuration, and thus inhibit interpretation. We also did not allow movement between spatial units or test an alternative assumption about reproductive isolation, which are both known to influence assessment results such as spawning stock biomass and fishing mortality (Cadurin and Secor 2009). If movement rates were high and multidirectional, thereby blending differences between

Fig. 5. Using the F_T method of calculating fishing mortality under the 1%–99%, 31%–69%, and 50%–50% areal assumptions compared with known values of overall catch (first row), overall biomass (second row), and fishing mortality (F) for age 0 (open circle), age 1 (open square), age 2 (open triangle), and age 3+ (open diamond) from the operating model based on observed effort (second row). Lines indicate calculated values of catch, effort, and biomass in the age-structured model using the same parameter estimates as in the observation model while fixing fishing mortality for age 0, age 1, age 2, and age 3+ for each areal assumption.

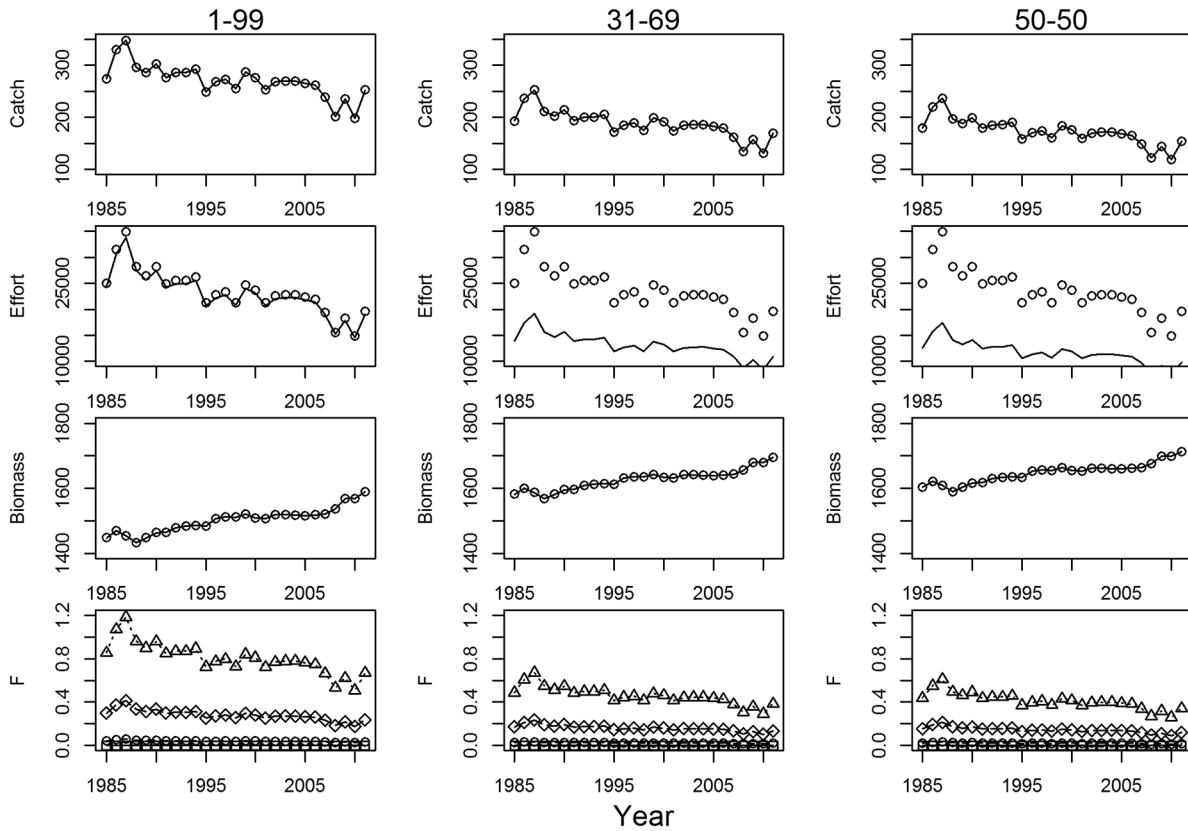


Fig. 6. Assuming catchabilities differed between areas, overall catch and fishing mortality rate are shown, as calculated using the methods outlined in Table 1 and described in the text for the non-age-structured model. Values were calculated across a range of area sizes (with proportion p and $1 - p$ of total area) and a range of natural mortality rates ($M = 0$, solid line; $M = 0.5$, dashed line; $M = 1$, dotted line).

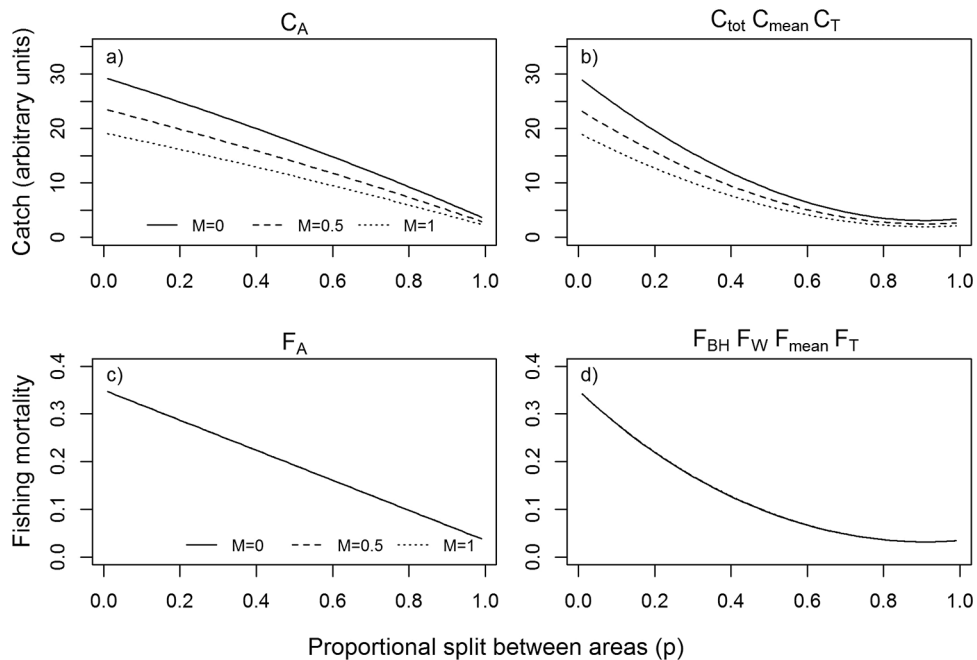


Fig. 7. Assuming effort was allocated as a fixed proportion of total effort rather than proportional to area, overall catch and fishing mortality rate are shown, as calculated using the methods outlined in Table 1 and described in the text for the non-age-structured model. Values were calculated across a range of area sizes (with proportion p and $1 - p$ of total area) and a range of natural mortality rates ($M = 0$, solid line; $M = 0.5$, dashed line; $M = 1$, dotted line).

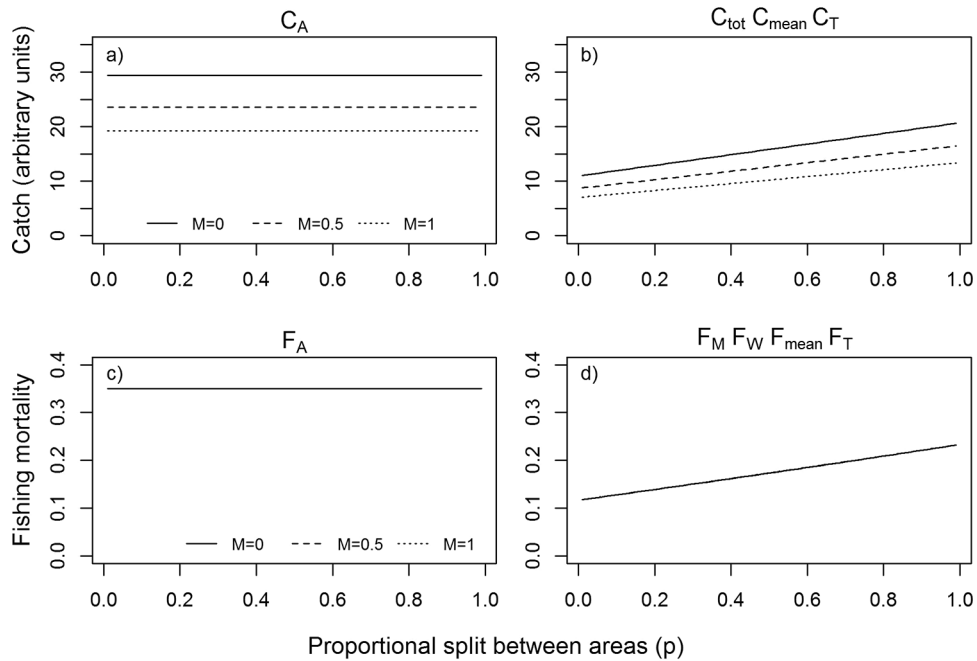
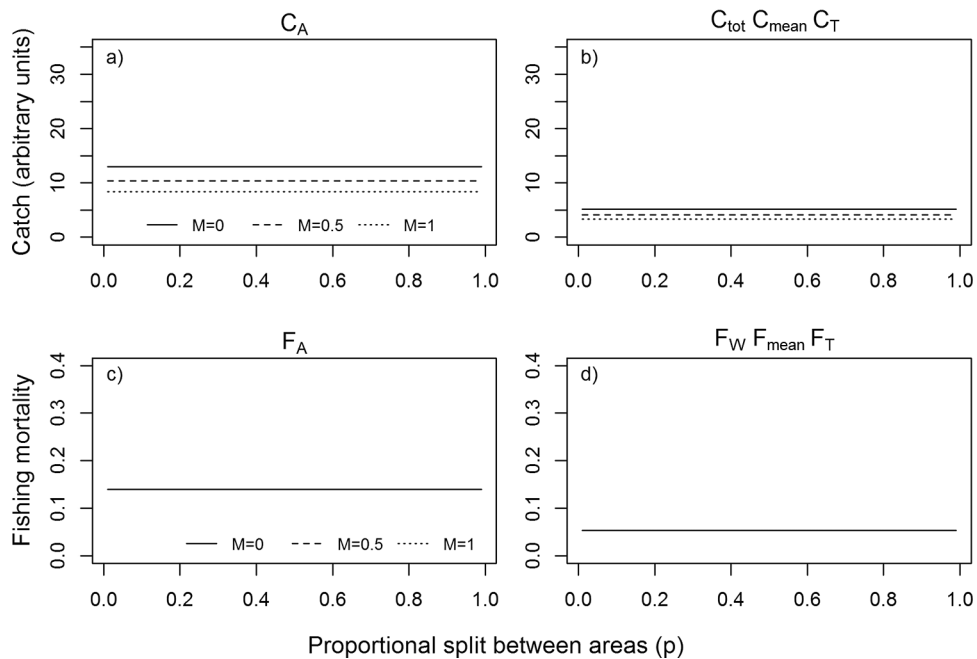


Fig. 8. Assuming catchabilities differed between areas, and abundance and effort were allocated as a fixed proportion of total abundance and effort rather than proportional to area, overall catch and fishing mortality rate are shown, as calculated using the methods outlined in Table 1 and described in the text for the non-age-structured model. Values were calculated across a range of area sizes (with proportion p and $1 - p$ of total area) and a range of natural mortality rates ($M = 0$, solid line; $M = 0.5$, dashed line; $M = 1$, dotted line).

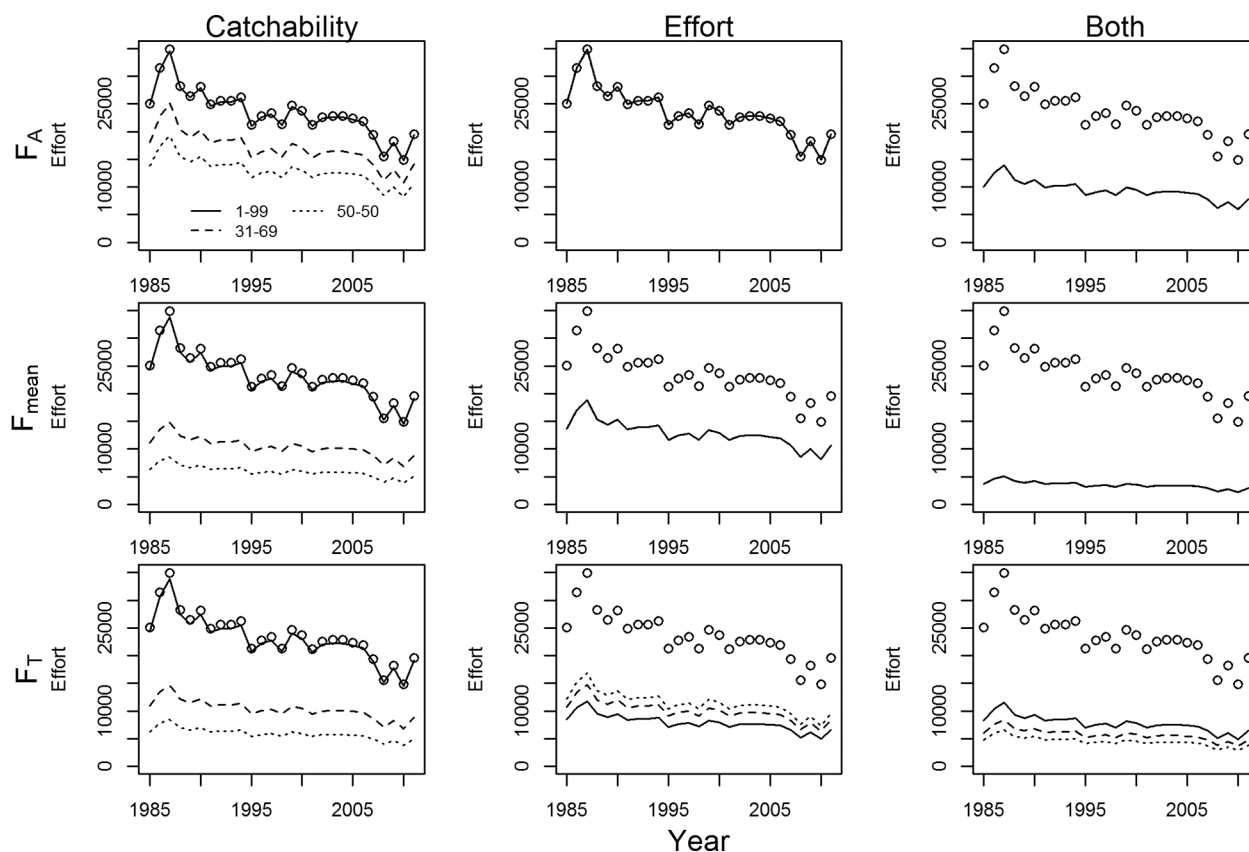


the two areas and causing dynamics to be more similar to that of a single-area population, then results might be similar to or less extreme than those observed in this study. If movement rates were high and unidirectional, then results might be even more affected than that observed in this study. Typically, tagging data are used to estimate movement in spatially explicit assessment models (Goethel et al. 2011).

We examined the sensitivity of results to our base assumptions, which were that abundance and effort were distributed according to the size of the areas and that catchability was the same in all areas. The base assumptions led to the parabolic pattern in catch and fishing mortality with size of area in the non-age-structured model (Fig. 2) at the magnitude of total fishing mortality we considered. The values chosen to increase catchability in area one and

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Fig. 9. Observed (open circles) and calculated (lines) effort from the age-structured model for three methods of calculating fishing mortality rate (F_A , F_{mean} , F_T) under the 1%–99% (solid line), 31%–69% (dashed line), and 50%–50% (dotted line) areal assumptions and three alternative assumptions about catchability and the distribution of fishing effort between areas. Alternative assumptions include (i) catchability in area one set to one-tenth the value of that in area two (Catchability), (ii) effort in areas one and two set to two-thirds and one-third, respectively, of total effort (Effort), and (iii) both assumptions applied together (Both). The methods for calculating fishing mortality rates are outlined in Table 1 and are described in the text. Lines are overlapping when only one appears to be present.



to change the apportionment of effort and abundance for the sensitivity analysis led to different patterns (Figs. 6–9). We acknowledge that fish density and fishing effort are likely to be heterogeneous across space (Swain and Wade 2003). The base assumption of homogeneous fish density between areas was made to follow the approach of Beverton and Holt (1957) and Maury et al. (1997) and to maintain tractability. We also acknowledge there are other ways of allocating effort or abundance that we did not explore here, for example based on distance from a fishing port (Truesdell et al. 2017).

We also assumed values of total mortality up to 1.35 for the non-age-structured model. Higher total mortality rates, due to larger assumed values for effort, catchability, or natural mortality, affected the pattern of fishing mortality rate across areal assumptions and resulted in larger differences in fishing mortality rate among methods. Under the base assumptions about catchability and distribution of abundance and effort, the pattern between fishing mortality rate and p changed as total mortality increased, from a parabolic curve towards a sigmoid pattern to a pyramid with apex at 50–50; however, this change in pattern occurred at much higher mortality rates. Also, when exploring the assumptions about catchability further, a larger scaling factor (e.g., ten times rather than one-tenth) resulted in greater differences in catch and fishing mortality among methods. Although these changes did not influence the primary conclusion that comparisons between models with separate spatial units and those with a single area need careful consideration, resulting patterns

were affected by the overall mortality rate of the species in question as well as the method used to calculate fishing mortality rate.

Changes in selectivity were also not considered in this paper. Waterhouse et al. (2014) incorporated area-specific selectivity in their definition of fishing mortality rate across areas and found that modeling spatial dynamics changed the shape of population selectivity. We did not consider changes to selectivity in the age-structured model because we wanted to determine how well the model could reproduce known quantities based only on differences in spatial structure. It is possible that changes in selectivity parameters could account for the effects shown in our results. While this could lead to differences in outcomes, the real concern is the potential for unintended consequences in estimated fishing mortality rates that are caused by unknowingly incorrect selectivity estimates.

Summary

This manuscript adds to the discussion of best practices for spatial models. As shown herein, several alternative methods of calculating a total fishing mortality rate resulted in different values for multi-area models compared with single-area models. Many of the approaches commonly used for dealing with fishing mortality resulted in rates changing with the size of the spatial areas. Results from our simulations were sensitive to model assumptions, including the specification of catchability and the distribution of effort and abundance. When applying spatial models for use in management, careful consideration should be given to

the selection of the method to calculate fishing mortality rate and ideally would be examined using management strategy evaluation to determine if the approach being applied is suitable given the specific management objectives and procedures in place. We recommend using the F_A approach when comparing between single-area and multi-area spatial model scenarios where catchability is assumed the same between areas and either effort or abundance is assumed proportional to the size of the areas. Any of the tested methods are equivalent if catchability is different between areas and effort and abundance are allocated independent of the size of the areas. Finally, all methods were affected by the relative sizes of the areas if catchability differs by area and both abundance and effort are proportional to the size of the areas. Under those specific circumstances, further consideration of the best method to calculate fishing mortality needs to be undertaken.

Acknowledgements

Authors thank K.W. Shertzer and J.K. Craig for early discussions on this topic and K.W. Shertzer, Y.-J. Chang, and two anonymous reviewers for extensive revisions to earlier drafts of this manuscript. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect the views of NOAA or the US Department of Commerce.

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