Estimating Natural Mortality for Atlantic Sea Scallops (*Placopecten magellenicus*) Using a Size-Based Stock Assessment Model

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June 26, 2022

Abstract

We estimate temporally varying natural mortality within a size-based stock assessment model for U.S. sea scallops in three different regions, and compare the results to corresponding models where natural mortality is not estimated, and (in one case) where only the mean natural mortality is estimated. In one model, for the Georges Bank Closed Areas, natural mortality was estimated by year for all sizes, whereas in the other two models (for the Georges Bank Open Areas and the Mid-Atlantic Bight), annual variation in natural mortality was estimated for juveniles only. Estimating natural mortality by year improved the performance over fixed natural mortality in all three models, as measured by improved model fit, Akaike's information criterion (AIC), and reduced retrospective patterns. There was evidence that natural mortality is density-dependent. Large recruitment events were associated with substantial increases in juvenile natural mortality, and natural mortality in the Georges Bank Closed Areas tended to increase at high biomass. Estimation of natural mortality was facilitated by survey data that gave estimates of absolute abundance together with low fishing mortality that minimized the confounding between natural and fishing mortality. Natural mortality is an important process that should be estimated when there is sufficient information to do so.

1 Introduction

Natural mortality (M) is one of the most important parameters in fisheries stock assessments. It is typically directly used to estimate fishing mortality from total mortality, and its value strongly influences estimates of abundance and reference points (Maunder and Piner 2015, Punt et al. 2021). Despite this, natural mortality is frequently not estimated in stock assessment models, and is often assumed constant in time and age or size, even though this is unlikely to be true. The problem is that M is difficult to estimate since it can be confounded by errors in catch estimates, or assumptions regarding fishery and survey selectivity, steepness or stock-recruit relationships, age or growth, length to weight conversions, and survey efficiency (Punt et al. 2021). Erroneous estimates of any of these factors can bias estimates of M (Lee et al. 2011, Johnson et al. 2015), possibly as much or more than a fixed estimate.

The natural mortality of Atlantic sea scallops (*Placopecten magellanicus*) has been estimated by a number of methods. Merrill and Posgay (1964) used the "clapper ratio" method, $M = \dfrac{1}{S}\dfrac{C}{L}$, where C is the density of "clappers", i.e., dead shells with the hinge ligament attached, L is the density of live scallops, and S is the (mean) time for a clapper to separate into two valves after death, to estimate $M = 0.1$ for the Georges Bank sea scallops. There are a number of uncertainties surrounding this method, however, including its equilibrium assumption, the estimate of S, which is likely size specific, and the assumption of equal catchability of clappers and live scallops in survey gear. Additionally, as a ratio estimator, the clapper ratio is biased, which is of particular concern given the high uncertainty in the S term in the denominator (Hart 2013). Applying a bias-correction factor gave a revised estimate of $M = 0.12$ for Georges Bank sea scallops. Estimates of M for Mid-Atlantic sea scallops can be obtained from those from Georges Bank using the idea that M/K, where K is the Brody growth coefficient, should be invariant among populations of the same species (Beverton and Holt 1959, Hart 2013).

In this article, we present a method to estimate size-specific and temporally variable natural mortality in stock assessment models. This method is applied to the U.S. stock assessments of Atlantic sea scallops, and the results are compared these to models where

M is fixed. Sea scallops offer an ideal opportunity to estimate M for a number of reasons. First, there have been areas that have been closed to scallop fishing for a number of years, thereby reducing the confounding of natural and fishing mortality. Similarly, estimation of juvenile M is facilitated because surveys reliably detect juvenile scallops two years before the are currently vulnerable to the commercial fishery. Finally, sea scallops are tracked by a number of dedicated, relatively precise surveys, each of which has its own external estimate of gear efficiency. Such surveys can be used to directly estimate absolute abundance which in turn can be combined with estimates of catch and total mortality to estimate natural mortality.

2   Methods

A size-based stock assessment model (CASA [Catch At Size Analysis], Sullivan et al. 1990, Hart et al. 2013) was used that tracked sea scallop numbers at shell height, i.e., the distance from the base (umbo) to the tip of the shell . Growth was modeled using stochastic growth matrices based on growth increment data from shell ring analysis (Hart and Chute 2009); these growth matrices were fixed and not estimated within the stock assessment model. Three separate models for different regions were used: Mid-Atlantic, Georges Bank Open and Georges Bank Closed (Figure 1). The Georges Bank region was split into two models because of the different management history of the two areas; the Georges Bank Closed Areas have experienced much lower fishing mortality than the Georges Bank Open Areas since 1994, including a number of years that they were completely closed to scallop fishing (Hart and Rago 2006). Splitting the region into two models gives more stable and precise model results than using a single model with domed selectivity for the periods where portions of the region were closed (Hart et al. 2013). Technical details regarding the stock assessment model can be found in Jacobson and Chang (2018).

The models were fitted by maximum likelihood to abundance trends and size data obtained from sea scallop dredge surveys during 1975–2019 (Serchuk and Wigley, 1986, Hart and Rago, 2006), drop camera surveys conducted in most years since 2003 (Stokesbury et

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75 al., 2004, Bethoney and Stokesbury 2018), towed camera (Habcam) surveys during 2011-

76 2019 (Howland et al. 2006, Chang et al. 2017) as well as commercial landings and shell

77 height data from port samples and at-sea observers. Model estimates of survey efficiency

78 were constrained by priors (likelihood penalties); the priors from the two optical surveys

79 had an expected efficiency of one, whereas the expected efficiency of the survey dredge was

80 based on paired tow experiments with Habcam (Miller et al. 2019). Standard deviations

81 of the priors were set at 0.1. The drop camera survey was separated into two time series:

82 one prior to 2015, when standard definition video cameras were used, and since 2015, when

83 high definition digital cameras were used. In 2019, neither the drop camera nor the Habcam

84 surveys were complete on Georges Bank, but at least one of these optical surveys covered all

85 portions of this region. These surveys were therefore combined on Georges Bank in 2019; the

86 combined survey was considered part of the Habcam time series for Georges Bank Closed

87 and the drop camera survey for Georges Bank Open.

88   In the Georges Bank Closed model, natural mortality was assumed to not vary with size

89 since there was no evidence otherwise. For that model, we estimated mean natural mortality

90 (over time), $\bar{M}$, as well as the annual deviations of M from this mean $\gamma(y)$ (except the first

91 year):

$$M(y) = \bar{M} + \gamma(y) \tag{1}$$

92 In the other two models, we varied M by shell height h, using a weighted average of juvenile

93 and adult natural mortality, M_{juv} and M_{ad}:

$$M(h) = \alpha(h)M_{\text{juv}} + [1 - \alpha(h)]M_{\text{ad}} \tag{2}$$

94 where $\alpha(h) = 1 - \dfrac{1}{1 + \exp(-h_0[h - a])}$ is a decreasing logistic function, with left asymptote

95 equal to one and right asymptote equal to zero, h_0 is fixed at the shell height at about

96 age 2.5 (70mm for Georges Back Open and 65mm for Mid-Atlantic), and a is fixed at 0.1

97 (Figure 2). As in equation (1), juvenile and adult natural mortality can be decomposed

98 into their mean values and deviations from the mean: $M_{\text{juv}}(y) = \bar{M}_{\text{juv}} + \theta(y)$ and $M_{\text{ad}}(y) =$

99 $\bar{M}_{\text{ad}} + \omega(y)$. However, the values of the adult natural mortality parameters $\bar{M}_{\text{ad}}$ and $\omega(y)$

100 were not estimable in these two models due to confounding with fishing mortality. They

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were fixed at a value of $\bar{M}_{\text{ad}} = 0.2$ and $\omega(y) = 0$ in the Georges Bank Open model, based on a similar estimate in Georges Bank Closed. The Brody growth coefficient K for Mid-Atlantic scallops is about 25% higher than for those on Georges Bank (Hart and Chute 2009), and hence life history theory suggests that M_{ad} in the Mid-Atlantic should also be 25% higher (Beverton and Holt 1959). Thus, we fixed $\bar{M}_{\text{ad}} = 0.25$ for Mid-Atlantic sea scallops and $\omega(y) = 0$. Mean juvenile natural mortality $\bar{M}_{\text{juv}}$ was also set to those values, but the deviations in juvenile M, $\theta(y)$, were estimated for each year except for the first year.

We evaluated model performance using likelihood and Akaike's information criterion (AIC) as a measure of model fit to the data. We also used retrospective analysis (6 peels) to measure model stability, with Mohn's ρ as a summary statistic (Mohn 1999). It is of interest to examine whether density dependence plays a role in natural mortality. To this end, for each year in the Mid-Atlantic and Georges Bank Open models, we related the model estimates of two year old recruits to juvenile natural mortality. For the Georges Bank Closed Model, estimates of overall natural mortality were compared to biomass for each year. In all three cases, the relationships between natural mortality and log(recruitment) or biomass were fit to GAM models, using the mgcv R package with a Gaussian distribution and for the Georges Bank Open and Mid-Atlantic models, a log link.

Results

Estimation of natural mortality improved fits for all three models and decreased retrospective patterns (Table 1; Figures 3-4). Mean standard errors for natural mortality ranged from 0.044 to 0.049 in the models that temporally estimated M and 0.009 in the Georges Bank closed model that estimated the mean M only (Table 1). In the Georges Bank Closed model, temporal estimation of M was substantially superior in terms of both AIC and Mohn's ρ than just estimating the mean M, which in turn decreased AIC and slightly decreased Mohn's ρ compared to the fixed M run. In the terminal year in Georges Bank Closed, both the fixed M and estimated mean M runs considerably overestimated biomass compared to surveys, whereas the run that estimated M for all years was able to match the declines in survey

biomass observed in 2018 and 2019 (Figure 3a). For Georges Bank Open and the Mid-Atlantic models, estimating juvenile M improved AIC and reduced the retrospective pattern (especially in Georges Bank Open) compared to using a fixed M, although the differences in estimated biomass between these runs were modest.

In the Georges Bank Closed Areas, the three years with the highest natural mortalities all occurred at high biomasses (> 75000 t, Figure 5ab). The one other year with substantially increased natural mortality ($M > 0.3$) occurred at a moderate biomass. In both Georges Bank Open and the Mid-Atlantic, high juvenile natural mortality only occurred after strong recruitment events; there was no evidence of elevated juvenile natural mortality at low or moderate levels of recruitment (< 1500 million, Figure 5c-f). The GAM fits predicted substantial increases in M at high recruitment in these areas.

Discussion

Like many marine fish and invertebrates, natural mortality in sea scallops can be characterized by periods where natural mortality is near constant, punctuated by spikes in M. These increases in natural mortality may be due to high temperatures, disease and/or predation (Dickie and Metcof 1963, Gulka et al., 1983, Belvin et al., 2008, Hart and Shank 2011, Levesque et al. 2016, Siemann et al. 2019). Episodic natural mortality has been noted elsewhere for sea scallops such as in Narragansett Bay (Gulka et al., 1983) and the Bay of Fundy (Smith and Lundy 2002), and is commonly associated with high densities.

Estimation of natural mortality by year is one method to account for variable natural mortality, and in all three models, it substantially improved model performance, as measured both by model fits and reduced retrospective patterns. However, in doing so, we estimated a parameter for every year (45 extra parameters in our case), most of which were similar to the baseline M and contributed little to model fit. For this reason, AIC values for the Mid-Atlantic model with M estimated for each year were only slightly less than using a fixed value for natural mortality. Future work should consider ways to reduce the number of estimated parameters (e.g., using smoothing splines or likelihood penalties on the M deviations), while

still allowing estimates of high natural mortality for the years that it occurs.

Estimation of natural mortality in the Georges Bank Closed model was facilitated by the zero or low fishing mortality in many years ($F < 0.01$ in eight years, and $F < 0.1$ in 19 of the 45 years of the time series). Indeed, we could not obtain a reliable estimate of the mean M in either of the other two models. Even in the Georges Bank Closed model, some uncertainties remain. In particular, some illegal fishing did occur in these areas, as evidenced by a number of enforcement actions. However, vessel monitoring systems that were required on most scallops boats since 1997 show very limited incursions into these areas, so that the levels of illegal fishing were likely much lower than natural mortality, and any bias introduced by illegal fishing was therefore small.

Stokesbury et al. (2007) claimed that there was a "mass mortality", i.e., very high natural mortality, in Nantucket Lightship Closed Area, a portion of the Georges Bank Closed Areas, between 2004 and 2005, based on a large decline observed in their drop camera survey between those years. Our Georges Bank Closed model does not show evidence of increased natural mortality during that time, and there was only a modest decline observed in the scallop dredge survey. The drop camera survey employed a fixed grid design, where the station locations in 2005 repeated those from 2004. Maps showing densities from the 2004 drop camera survey were distributed to fishermen, and the area was reopened to limited fishing in late 2004. It is likely that the large decline in the drop camera survey in 2005 was an artifact due to heavy fishing around the drop camera stations that showed high density in the 2004 survey (as evidenced by vessel monitoring system data), rather than a large increase in natural mortality.

Elevated natural mortality in the Georges Bank Closed Areas tended to occur when its biomass was high. However, in many of the years with high biomass, natural mortality was near its baseline level. The increases in natural mortality in the Georges Bank Closed Areas during 2010-12 were associated with elevated levels of "gray meat" disease (Levesque et al. 2016, Siemann et al. 2019). Diseases are more likely to spread at high densities or biomass. Similarly, predation by *Asterias* spp. sea stars are also contributors to adult natural mortality, and high scallop densities may tend to attract these predators. However, it

appears that while high (adult) biomass may be conducive to disease or predation processes, these processes are not always elevated when the biomass is high.

By contrast, the three large recruitment events in the Georges Bank open and Mid-Atlantic areas were all associated with very high juvenile natural mortality rates. This phenomenon has also been frequently observed in seeding and tank experiments, where juvenile scallops at high densities have experienced high mortality (e.g., Barbeau et al. 1998, Wong et al. 2005, Fréchette et al. 2013). In most cases, the increased mortality was ascribed to predation by *Cancer* spp. crabs, which appear to act as agents of density dependence (Barbeau et al. 1998, Wong and Barbeau 2005, 2006, Hart and Shank 2011), although Fréchette et al. (2013) reported self-thinning due to interference or competition between the scallops themselves. These crabs are not predators of larger scallops (Elner and Jamieson 1979), which may explain why density-dependent mortality of adults is not as strong.

High juvenile mortality on large year classes induced a retrospective pattern in models with fixed M, where biomass (and abundance) estimates declined as more years are added. The conflict between the initial estimate of the large year class and subsequent reduced estimates is eventually resolved in the model by decreasing the estimated size of the large year class, so that the initial high recruitment estimate is (incorrectly) attributed to observation error. Even the variable juvenile M models display a similar retrospective pattern, since it is only after several years of observations of the large year class that the decline can be attributed in the model to increased natural morality rather than observation error. After a sufficient number of years since the recruitment event, abundance and biomass estimates in the fixed and estimated M models will be similar, although the models arrive at the estimate in different ways. The fixed M models reduce the estimated size of the large year classes to well below that indicated by the surveys, whereas when M is estimated, the size of these year classes is reduced in subsequent years by increasing juvenile natural mortality. This distinction becomes important when projecting into the future the fate of a large year class; a fixed M model may substantially overestimate future biomass and landings. A variable M projection model can be constructed by building in density-dependence, based on the relationships between biomass or recruitment and natural mortality (Fig. 4).

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Like many other U.S. fisheries, fishing mortality has declined considerably in the sea scallop fishery since the mid-1990s (Hart and Rago 2006). During the years near the peak of fishing mortality, the effects of natural mortality on population dynamics was limited since fishing mortality was many times greater than natural mortality. Thus, for fisheries where such substantial overfishing is occurring, it would be very difficult to estimate (adult) natural mortality, but the consequences of a misspecified M would be limited. On the other hand, when fishing mortality is reduced below F_{MSY}, fishing and natural mortality are commensurate quantities, so obtaining good estimates of natural mortality is important for understanding stock dynamics. The Georges Bank Closed Areas represent an extreme example of this, since natural mortality has been greater than fishing mortality (and often much greater) for most years since 1994.

We have presented a case study where both overall and juvenile natural mortality can be estimated by year for a data rich stock with surveys of absolute abundance, and where potentially confounding fishing mortality is relatively low. Estimation of natural mortality not only improved model performance, but it gave important biological insights into the role of density-dependence in regulating sea scallop populations.

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Table

Table 1: Summary of model runs: Number of parameters, log likelihood, AIC, Mohn's ρ, and the mean standard error of the M estimates. In the "Est M" runs, natural mortality is being estimated by year, either for all sizes (GB Closed) or juvenile M only (GB Open and MA). In the Mean M run (GB Closed only), the mean M is being estimated, but M is assumed constant over time. In the other runs, M is assumed fixed at the specified value.

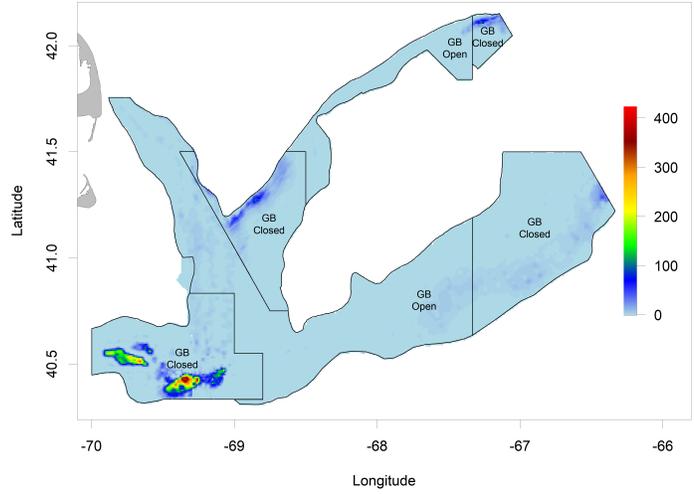| Region	Model	NParam	ln(Likelihood)	AIC	ρ	Mean M SE
GBCl	Est M	145	8735	17760	0.22	0.044
GBCl	Mean M	100	8818	17836	0.34	0.009
GBCl	$M = 0.16$	99	8852	17902	0.37	NA
GBOp	Est M	144	9208	18704	0.33	0.049
GBOp	$M = 0.2$	100	9300	18800	0.56	NA
MA	Est M	150	-7208	-14114	0.33	0.048
MA	$M = 0.25$	106	-7116	-14020	0.41	NA

Figures

Figure 1

Figure 2

(a)

(b)

(c)

Figure 3

18

(a)

(b)

(c)

(d)

(e)

(f)

(g)

Figure 4

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(a)   (b)   (c)   (d)   (e)   (f)
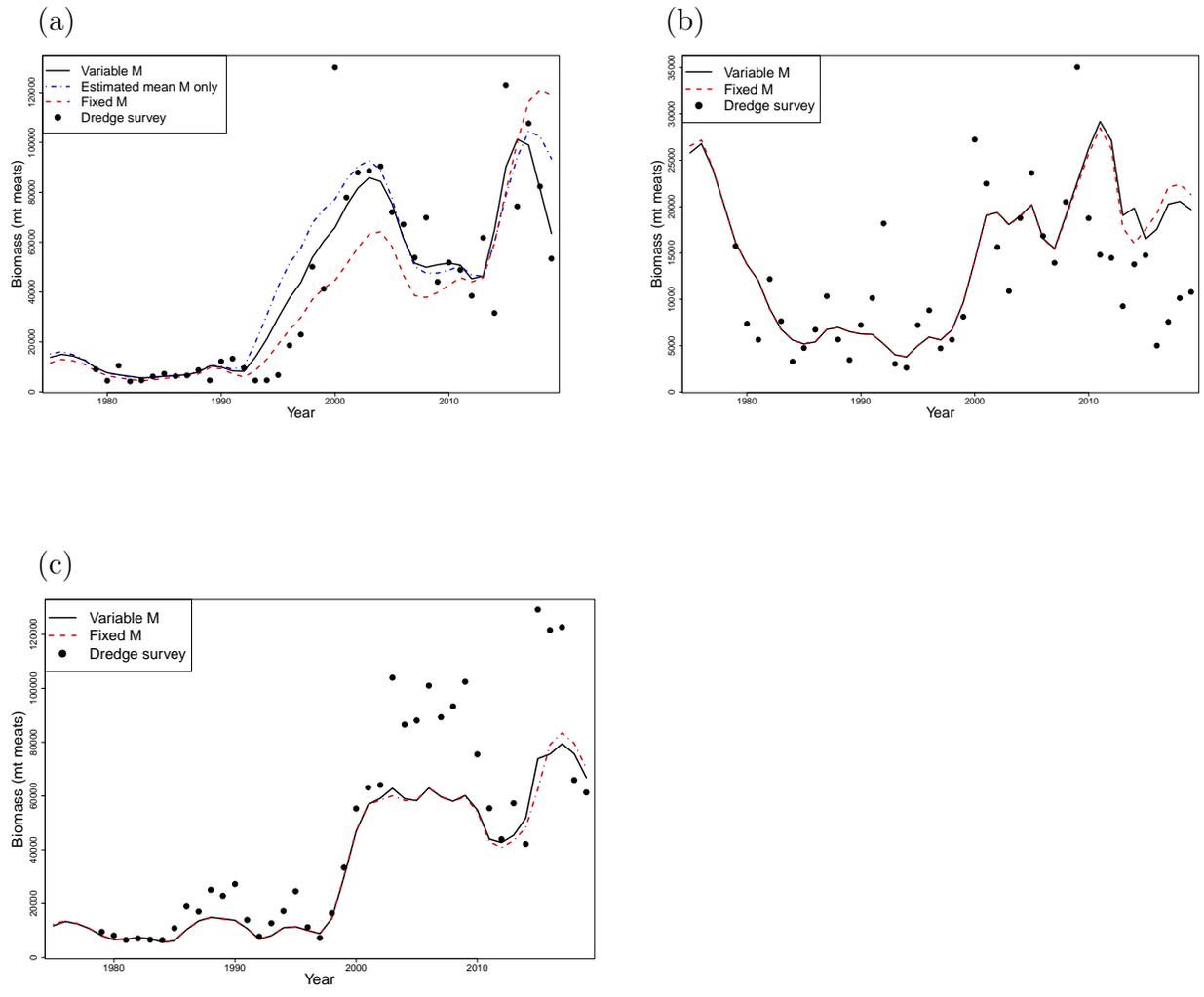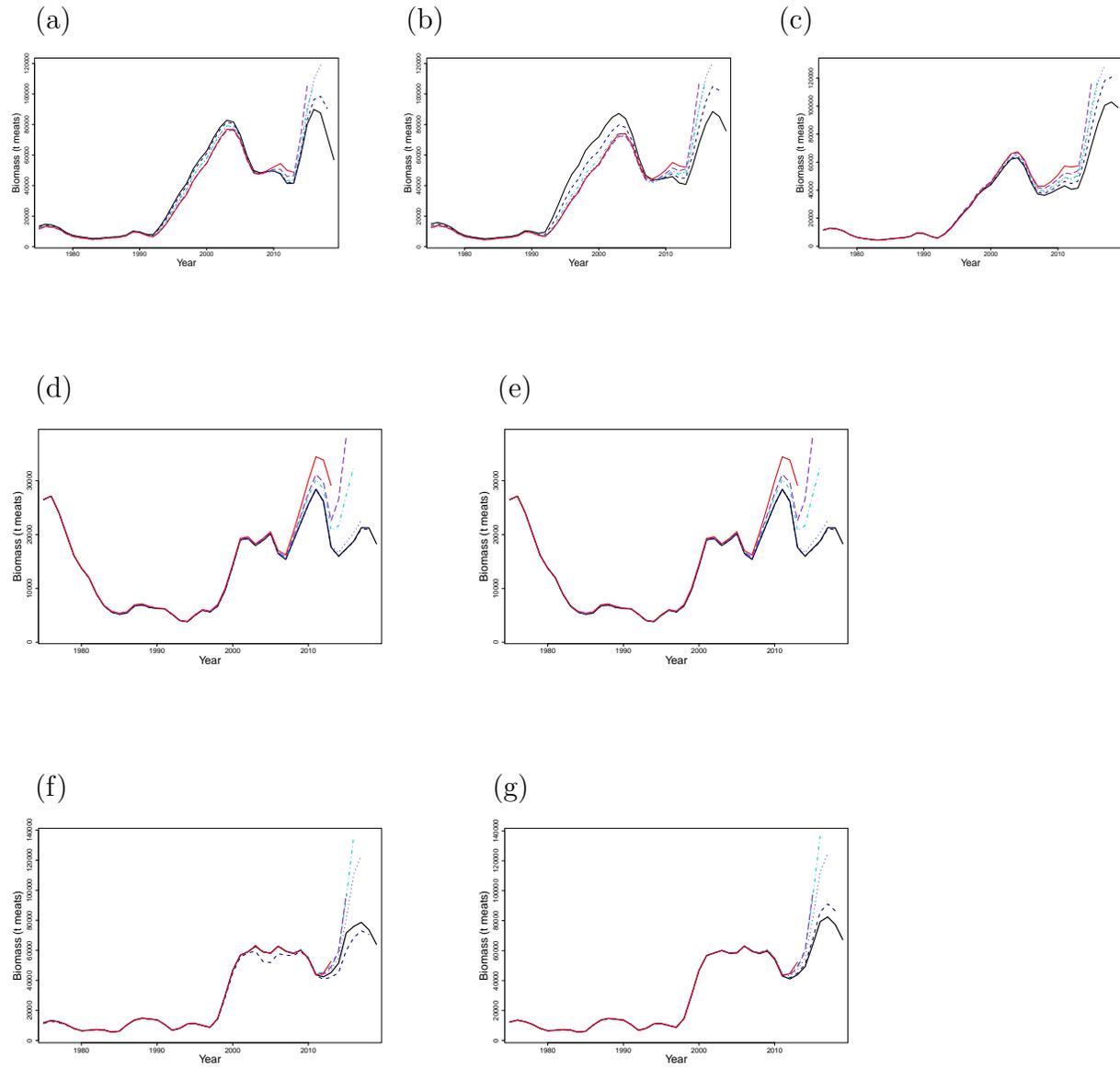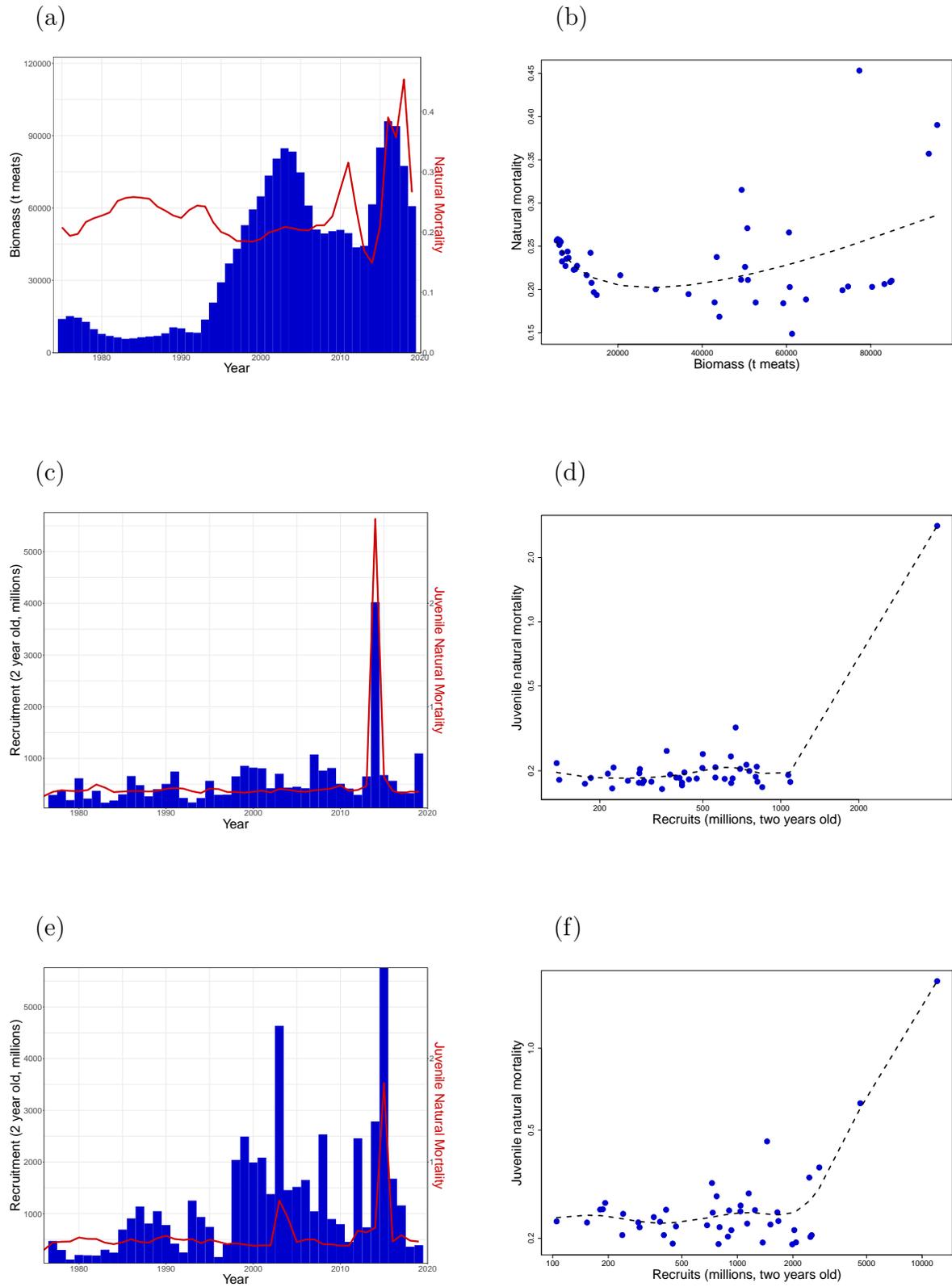
Figure 5

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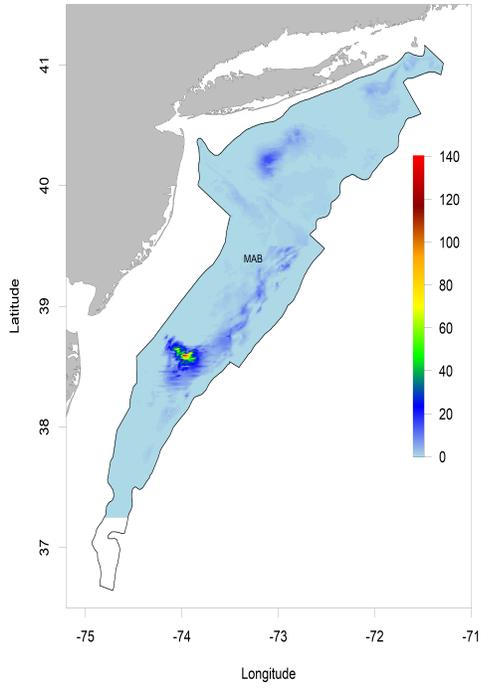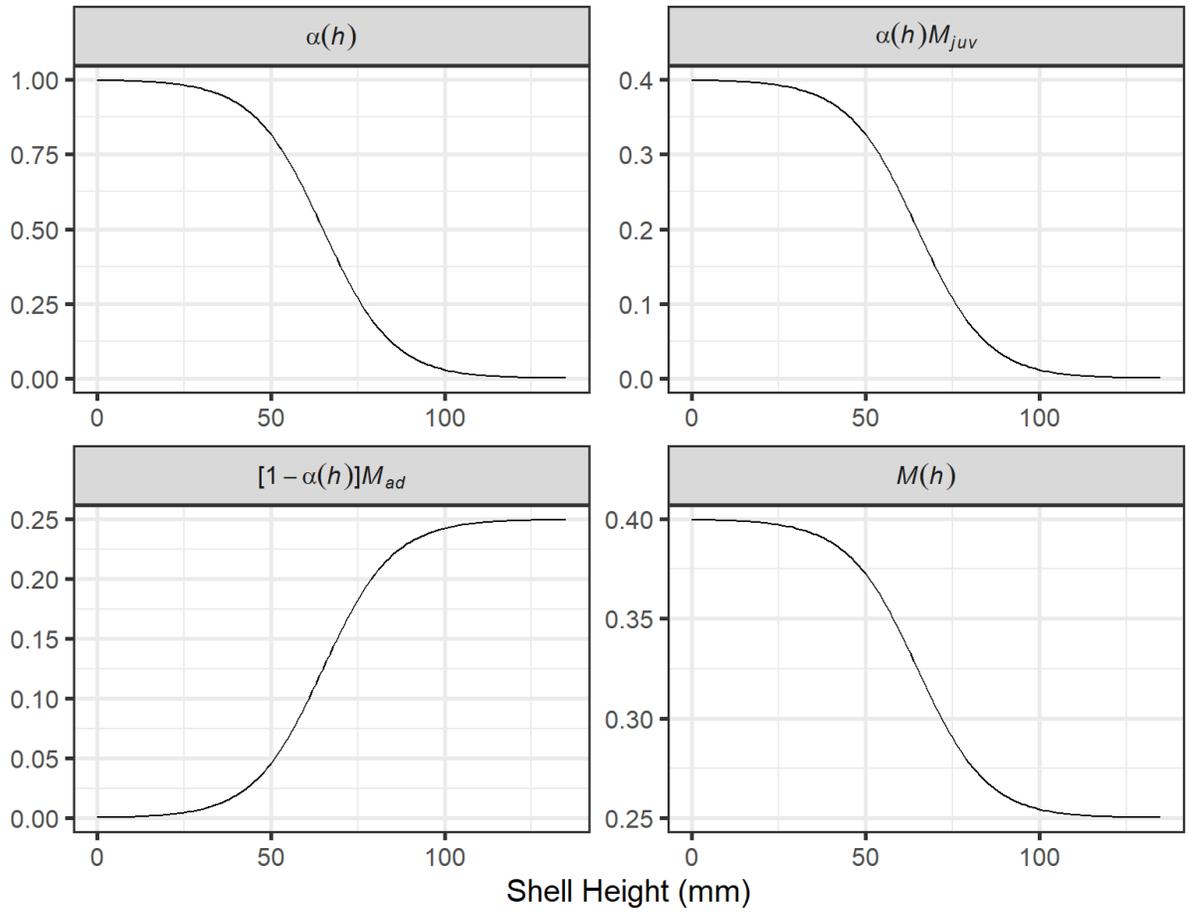
Figure Legends

Fig. 1. Charts of U.S. sea scallop grounds, showing the Mid-Atlantic Bight (MAB, left) and Georges Bank (GB, right), split into open and closed portions, with densities as estimated by the 2018 Habcam survey. The eastern portions of Georges Bank is in Canadian waters and was not modeled.

Fig. 2. Example plots showing the calculation of natural mortality by size in the Mid-Atlantic, assuming $M_{\mathrm{juv}} = 0.4$ and $M_{\mathrm{ad}} = 0.25$. Clockwise, from the upper left, the figures show the logistic curve $\alpha(h)$, the contribution at shell height to natural mortality by the juvenile component of natural mortality $(\alpha(h)M_{\mathrm{juv}})$, the contribution at shell height to natural mortality by the adult component of natural mortality $([1 - \alpha(h)]M_{\mathrm{ad}})$, and natural mortality $M(h)$ at shell height.

Fig. 3. Comparison of model estimates and the dredge survey for (a) Georges Bank Closed, (b) Georges Bank Open, and (c) the Mid-Atlantic Bight. The solid black line shows estimates for models that estimate M by year, whereas the red dashed line are from models where M is fixed. The black dots show estimates directly from the dredge survey, and the blue dashed-dotted line (Georges Bank Closed model only) shows output from the model that estimates mean M only.

Fig. 4. Six peel retrospectives for the Georges Bank Closed model with (a) M estimated by year, (b) only the mean M estimated and (c) M fixed; for the Georges Bank Open model with (d) juvenile M estimated by year and (e) M fixed; for the Mid-Atlantic model with (f) juvenile M estimated by year and (g) M fixed.

Fig. 5. Natural mortality (red line) and recruitment estimates in the variable M runs for (a) Georges Bank Closed, (c) Georges Bank Open and (e) Mid-Atlantic. (b) Plot of estimated M vs. biomass for Georges Bank Closed. Plots of estimated M vs. (2 year old) recruitment in (d) Georges Bank Open and (f) Mid-Atlantic. The dashed lines in (b), (d) and (f) show GAM fits.