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## Biological reference points for Atlantic surfclam (*Spisula solidissima*) in warming seas

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### ABSTRACT

Atlantic surfclam (*Spisula solidissima*) are a large, commercially important shellfish in the United States faced with several important management challenges. Compared to many harvested fish and shellfish, their life history is relatively unknown. They are undergoing contraction in the southern and inshore parts of their range, as well as expansion into deeper water. Atlantic surfclam are thermally sensitive, and the changes in their distribution track changes in maximum bottom temperature. Sessile species cannot emigrate and are limited to recruitment and mortality as mechanisms for redistribution in response to changing climate. Management of Atlantic surfclam should account for these challenges. We describe a simulation designed to calculate biological reference points that will work well for Atlantic surfclam relative to biological and fishery goals, over a range of life history parameters, assessment uncertainties, and increases in temperature. Simulations of the trade-off between somatic growth and mortality under increased temperature led to target fishing mortality rates higher than the status quo, but also to increased variability in yield. Results suggest that increasing temperature may adversely affect the Atlantic surfclam industry, which prefers stable catches to short term increases in yield, due to market limitations. The results of this analysis are specific to Atlantic surfclam, but the methods described here could be used to enhance management for other harvested species facing similar challenges.

### 1. Introduction

The Atlantic surfclam (*Spisula solidissima*) is a sessile invertebrate that has supported an important US fishery for decades (NEFSC, 2010). The species is noteworthy in its sensitivity to warming of the bottom waters of the Mid-Atlantic Bight, which has resulted in a substantial change in range, and dramatic dislocations in the fishery over the last few decades (Weinberg, 2005; McCay et al., 2011). Large bivalves are particularly sensitive to climate change (Kaustuv et al., 2001) and Atlantic surfclam are among the largest non-symbiont containing bivalves on earth, competing with the pinnids (Butler and Brewster, 1979), certain oysters (Titschack et al., 2010), and the geoducks (Hoffmann et al., 2000). Atlantic surfclam have a limited range of thermal tolerance and are particularly susceptible to increased mortality due to rising ocean bottom water temperatures (Hoffmann et al., 2018). The enhanced sensitivity of this clam stems from the physiological constraints typical of many bivalves amplified by this species' large size. Filtration rates in bivalves tend to follow a left-skewed parabolic relationship with temperature, and typically scale as the

square of the length (Buxton et al., 1981; Hofmann et al., 2006; Flye-Sainte-Marie et al., 2007; Munroe et al., 2013), whereas respiratory rates follow an allometric curve and typically scale as the cube of the length (Powell and Stanton, 1985). Consequently, at increasing size, the scope for growth declines (Buxton et al., 1981; Munroe et al., 2013). These physiological relationships establish an optimal temperature for growth, limit maximum length, and result in a temperature dependency on growth rate and maximum length, exhibited as a latitudinal cline along the east coast of the US. This pattern is often observed in bivalve species, including Atlantic surfclam (e.g. Nicol, 1964; Lomovskiy et al., 2011; Munroe et al., 2016).

The left skewed parabolic relationship between filtration rate and temperature results in a north-to-south gradient of increasing adult mortality rate, with the increase biased towards the larger animals. The salient physiological constraint is triggered when bottom water temperature rises sufficiently to create an energy imbalance as respiratory demand exceeds ingestion capacity. This portion of the animal's physiological ambit wherein scope for growth is negative, but where temperature remains below the thermal tolerance limit, was termed the

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transient event margin by Woodin et al. (2013) (see also Moore and Remais, 2014), and is characterized by compromised energetics, leading to increased morbidity. For Atlantic surfclam, the animal accumulates what Narvaez et al. (2015) termed deficit stress during this period, where condition decreases and, ultimately, starvation and death ensue. Kim and Powell (2004) ascribed the well-documented early 2000s mortality event off Delmarva due to this cause, and Narvaez et al. (2015) argued that periods of significant deficit stress have increased in frequency and extent over the last few decades, leading to a continuing physiological constraint along the inshore and southern range boundary in the southwestern Mid-Atlantic Bight, the end result being recession of the range boundary north and offshore.

Atlantic surfclam mature well below the size captured in the commercial fishery today. Maturation occurs within the first two years of life (Chintala and Grassle, 1995). Thus, individuals are able to experience several years of reproduction before becoming vulnerable to the fishery. Munroe et al. (2013) argued that planktonic primary production is insufficient to sustain Atlantic surfclam of market size (> 119 mm), which supports the notion that benthic primary production may be relatively important. Little is known about benthic primary production on the inner continental shelf of the Mid-Atlantic Bight, but anticipating relatively high rates would be consistent with observations elsewhere (Munroe et al., 2013). Presumably, food supply decreases with increasing depth offshore (Rowe et al., 1974; Hofmann et al., 2008). Atlantic surfclam condition declines offshore (Marzec et al., 2010), providing strong evidence that food supply does decline, as lower temperature and thus lower respiratory rates in deeper waters would not compromise condition (Narvaez et al., 2015). This offshore gradient suggests that range expansion offshore with increasing bottom water temperatures will be of limited success as both growth and maximum size may become limited by declining light penetration and consequently declining benthic primary production.

Management of the Atlantic surfclam fishery presents several challenges, exacerbated by the physiological constraints brought on by increasing bottom water temperatures. Atlantic surfclam are lightly fished over the stock area, but may experience higher fishing pressure over fine spatial scales. If population segments of relatively high fishing pressure also experience relatively rapid warming, local depletion is possible. Shifts in the fishing fleet and processing plants northward have occurred (McCay et al., 2011; Powell et al., 2015, 2016). Further dislocations can be expected in the future, although simulations of area management options suggest a possible mitigatory influence on regional population declines (Kuykendall et al., 2017). In addition, many important life history parameters, including the average rate of natural mortality and the shape of the relationship between spawning stock and recruitment are poorly understood, and much of what information is available (e.g., Weinberg, 1999) is based on a period of time prior to the most recent and most dramatic range shift, which limits applicability to present-day conditions. Finally, stock assessments of Atlantic surfclam tend to be uncertain in scale, which makes determination of absolute biomass and the level of fishing mortality difficult (NEFSC, 2017).

Fishery managers cannot affect ocean temperature, but they can influence the behavior of fisheries. A principal tool available to fishery managers in the US is catch limitation, which can be adjusted to maintain the desired rates of fishing and abundance of the spawning stock that theoretically maintains maximum sustainable yield. In the case of Atlantic surfclam, theoretical maximum sustainable yield cannot be estimated accurately due to a poor understanding of the stock and recruitment relationship. Current management relies on proxies for this, and other management quantities, including the threshold levels of biomass and fishing mortality that trigger reductions in catch limits (Atlantic surfclam harvest control rules are discussed below). Before this analysis, these proxy threshold values were not evaluated for performance relative to fishery or management goals.

The current stock assessment is implemented using two separate population segments (Mid-Atlantic Bight, MAB and Georges Bank, GB

population segments), which are combined for management purposes. The basis for separating the population segments were differences in exploitation patterns, growth, recruitment and the timing of surveys. Expected changes in ocean temperature are likely to impact the MAB portion of the stock to a greater degree than the GB portion because, although range expansion is ongoing in the north (Powell et al., 2017), in the south both range expansion offshore and range recession at the southern and inshore stock boundary are occurring (Weinberg, 2005; Weinberg et al., 2005). It is also possible that, due to expansion into deeper water over time, a substantial portion of the stock will reside there, and the stock might be reasonably divided into three population segments, each with different productivity parameters. The population segments used here are GB, MAB, and offshore, which was defined by water deeper than 45 m, the approximate 95th quantile of depth distribution for Atlantic surfclam in the southernmost regions (NEFSC, 2017).

Employing the biological reference points for Atlantic surfclam presents managers with challenges. The current maximum fishing mortality rate threshold depends on the estimate of absolute biomass of the stock, which tends to be uncertain. An early version of this analysis (NEFSC, 2017) found  $F = 0.12 \text{ yr}^{-1}$  to be a reasonable threshold (i.e., sufficient to maintain both relatively high yield and SSB near target levels). However, comparing current  $F$  in the assessment to an  $F_{Threshold}$  is only meaningful if the estimated scale of assessment is accurate. The Atlantic surfclam fishery has historically been lightly fished; therefore, the dynamics of the resource under fishing pressure near threshold intensity are unknown. Regional dynamics exist in the fishery and biology as well (i.e., recruitment, growth, and  $M$ ), and changes in fishing pressure across regions occur over time. The current control rule biomass target, also a proxy, is a fraction (0.5) of the unfished biomass, and the minimum stock size threshold is set at a fraction (0.1) of the current control rule target. Are these reference points likely to maintain the stock near target biomass and exploitation levels, given the likely partitioning of the stock into spatially distinct population segments of differing life history parameters?

Thorny management issues are increasingly investigated using simulation, but most address mobile species (e.g., Pan et al., 2001; Miller et al., 2010; Martell et al., 2014). Fewer have addressed management of sessile species, which have limited capacity to rapidly respond to climate change and routinely demonstrate sensitivity of management options to environmental variation (Spillman et al., 2009; Bald et al., 2009; Kuykendall et al., 2017). Here we address a particularly challenging sessile species by means of a simulation with the goal of evaluating reference point options during a period of climate change.

## 2. Methods

### 2.1. Simulation model

The population simulation model was age structured, such that for ages  $a$ :

$$N_{t,a} = \begin{cases} R_t & \text{if } a = 1 \\ N_{(t-1),(a-1)} [e^{-Z_{t-1,(a-1)}}] & \text{if } 1 < a < a_{max} \\ N_{(t-1),(a_{max}-1)} [e^{-Z_{t-1,(a_{max}-1)}}] + \\ N_{(t-1),a_{max}} [e^{-Z_{t-1,a_{max}}}] & \text{if } a = a_{max} \end{cases} \quad (1)$$

where  $a_{max} = 30$ ,  $N_{t,a}$  was the number of animals in year  $t$  at age  $a$ ,  $R_t$  was the number of recruits in year  $t$  (see below).  $Z_{t,a}$  was the instantaneous total mortality defined by:

$$Z_{t,a} = F_t S_{t,a} + M_{t,a} \quad (2)$$

where  $F_t$  was the fully selected fishing mortality, and  $M_{t,a}$  was the natural mortality rate at time and age, which was constant except when modified by temperature (Eq. (10)), where it was derived from  $M$  at length.  $S_{t,a}$  was the fishery selectivity at time  $t$  and forage  $a$ , and was

converted from selectivity at length. Selectivity at length was constant in time, but selectivity at age was not because length was modified by temperature (see later, and note that length at age,  $L_{t,a}$ , will vary by population segment, Eq. (14)).

$$S_{t,a} = \int 1 - \frac{1}{1 + e^{-7.63+0.105L_{t,a}}} dL_{t,a} \tag{3}$$

Fishery selectivity at age ( $S_{t,a}$ ) determined the relative impact of fishing on different age groups. It was defined as the relative proportion of age  $a$  animals in the population encountered and caught. The selectivity curve was logistic and taken directly from a previous Atlantic surfclam assessment for the GB population segment (NEFSC, 2013).

The spawning stock biomass for each age in each year  $SSB_{t,a}$  was determined by:

$$SSB_{t,a} = N_{t,a}(\Gamma_a)W_{t,a} \tag{4}$$

where maturity ( $\Gamma_a$ ) was 0.5 at age 1 and 1 at all other ages (Chintala and Grassle, 1995).

Weight at age was modelled as a function of mean length, time and age and differed by population segment.

$$W_{t,a} = \begin{cases} \int e^{-9.27L_{t,a}^{2.73}} dL_{t,a}; \text{ MAB population segment} \\ \int e^{-9.16L_{t,a}^{2.73}} dL_{t,a}; \text{ GB population segment} \\ \int e^{-8.55L_{t,a}^{2.70}} dL_{t,a}; \text{ off shore population segment} \end{cases} \tag{5}$$

where  $W_{t,a}$  is the weight (g), and  $L_{t,a}$  is the predicted length, at time  $t$  and age  $a$  (mm). Growth is described below (Eq. (14)). The parameters used in Eqs. (5) and (14) were averaged values for each population segment derived as in NEFSC (2013).  $W_{t,a}$  was constant in time unless modified by temperature as in (Eq. (14)).

The yield from the fishery was calculated as:

$$Y_t = \sum_a \frac{F_{t,a}}{F_{t,a} + M_{t,a}} N_{t,a} W_{t,a} (1 - e^{-(F_{t,a} + M_{t,a})}) \tag{6}$$

where  $F_{t,a} = F_t S_a$  (Baranov, 1918) and  $F_{t,a}$  is natural mortality at time  $t$  and age  $a$ , which was constant over time within a simulation run, except where modified by temperature as in (Eq. (10)).

Recruitment ( $R_t$ ) followed Beverton Holt (Beverton and Holt, 1957):

$$R_t = \frac{SSB_{t-1}}{\frac{SSB_{f=0}(1-h)}{4h} + \frac{5h-1}{4hR_0}SSB_{t-1}} \epsilon_t \tag{7}$$

or Ricker (Ricker, 1954) dynamic:

$$R_t = \frac{SSB_{t-1}}{SSBR_{f=0}} e^{-\frac{\log(5h)}{0.8R_0SSBR_{f=0}}SSB_{t-1}-R_0SSBR_{f=0}} \epsilon_t \tag{8}$$

where  $SSBR_{f=0}$  is the equilibrium unfished spawning stock biomass per recruit,  $R_0$  is equilibrium unfished recruitment, and steepness ( $h$ ) is simulation specific (Table 1). The bounds on  $h$  were based on He et al. (2006) and further modified based on the results of sensitivity testing in the assessment model. The selection of Ricker or Beverton Holt recruitment dynamics was simulation-specific, and each occurred with equal probability. In either case  $R_t$  was multiplied by an error term  $\epsilon_t$ , where  $\epsilon_t = e^{\psi - \frac{\sigma_\psi^2}{2}}$  and  $\psi$  was a random normal deviate, with mean 0 and standard deviation  $\sigma_\psi$ , based on values estimated in the recent stock assessment (NEFSC, 2017; and see Table 1).

### 2.2. Temperature

Bottom temperature was modeled as a random walk with a positive offset in the MAB population segment; temperature is ignored in the GB and offshore population segments where, to provide contrast, we presume any changes in temperature will be less pronounced.

**Table 1**

Sampling distributions of random variables used in simulation. The variable  $h$  is steepness,  $M$  is natural mortality,  $F_t$  is fully selected fishing mortality target,  $\sigma_R$  was the standard deviation of  $\psi$  the recruitment error term,  $\varphi$  is the autocorrelation coefficient for assessment error,  $\sigma_{A_t}^2$ ,  $\sigma_{F_t}^2$  are the standard deviation of annual assessment and implementation error, respectively,  $\sigma_{L_\infty}^S$ ,  $\sigma_{L_\infty}^N$ ,  $\sigma_{L_\infty}^D$ ,  $\sigma_K^S$ ,  $\sigma_K^N$ ,  $\sigma_K^D$ ,  $\sigma_{l_0}^S$ ,  $\sigma_{l_0}^N$ ,  $\sigma_{l_0}^D$ , are standard deviations of the growth parameters for each population segment,  $\zeta_t$  and  $\epsilon$  are parameters describing the random walk in temperature, and  $\frac{SSB_{Cease}}{SSB_0}$  is the control rule (stock replenishment) threshold, and  $\frac{SSB_{Target}}{SSB_0}$  is the control rule target for fishery management. A random value for each variable was drawn from the sampling distributions shown for each simulation run. The source for the range of each parameter is shown in the third column where available. When no source was available, indicated by a blank row, the authors selected a range they believed would encompass truth.

Variable	Sampling distribution	Source
Continuous		
$h$	Unif(0.3,0.99)	He et al., 2006
$M(\text{yr}^{-1})$	Unif(0.1,0.25)	
$F_{Target}(\text{yr}^{-1})$	Unif(0.0001,0.5)	
$\sigma_R$	Unif(0.25,0.8)	NEFSC, 2017
$\varphi$	Unif(0.25,0.95)	
$\sigma_{A_t}$	Unif(0.25,0.75)	
$\sigma_{F_t}$	Unif(0.0,0.5)	
$\sigma_{L_\infty}^S$	Unif(1.95,3.9)	NEFSC, 2013
$\sigma_{L_\infty}^N$	Unif(3.9,7.8)	NEFSC, 2017
$\sigma_{L_\infty}^D$	Unif(0.9,1.8)	NEFSC, 2017
$\sigma_K^S$	Unif(0.0,0.025)	NEFSC, 2017
$\sigma_K^N$	Unif(0.0,0.061)	NEFSC, 2017
$\sigma_K^D$	Unif(0.0,0.03)	NEFSC, 2017
$\sigma_{l_0}^S$	Unif(0.0,0.249)	NEFSC, 2017
$\sigma_{l_0}^N$	Unif(0.0,0.59)	NEFSC, 2017
$\sigma_{l_0}^D$	Unif(0.0,0.2)	NEFSC, 2017
$\zeta_t$	Unif(-0.1,0.2)	
$\epsilon$	Unif(0.003,0.005)	
Discrete		
$\frac{SSB_{Cease}}{SSB_0}$	[0.05,0.1,0.15,0.2,...,0.5]	
$\frac{SSB_{Target}}{SSB_0}$	[0.1,0.15,0.2,0.25,...,1.0]	
SR	Ricker or BevertonHolt	
$T^l$	[0, 1, 2, 3, 4]	
$T^u$	[1, 2, 3, 4, ∞]	
$\Delta^{L_\infty}$	[0, 10, 15, 20, 25]	
$\Delta^K$	[0, 0.03, 0.06, 0.12, 0.18]	

$$T_t = \epsilon + \sum_{i=1}^{t-1} \zeta_i \tag{9}$$

where  $T_t$  was temperature at time  $t$ ,  $\zeta_i$  were uniform random numbers, and  $\epsilon$  was the positive offset (Table 1). The temperature model is intended to cover a broad range of reasonable outcomes and should not be taken as indicative of the most probable bottom temperatures in each region. Temperature was 0 until fishing began and then allowed to follow a random walk as described above.

The effect of temperature on Atlantic surfclam was to modify growth and natural mortality. Growth was adjusted so that at higher temperatures Atlantic surfclam grew faster but to a smaller maximum size (Munroe et al., 2013). Adjustments to parameters (see Eq. (14)) allowed the Von Bertalanffy  $L_\infty$  parameter to range between 116 and 181 mm, while the Von Bertalanffy  $K$  parameter ranged between 0.07 and  $0.41\text{yr}^{-1}$  (values taken from survey observations by population segment; NEFSC, 2017). By design, temperature changes did not affect the GB or offshore population segments. Natural mortality increased at high temperatures for all animals longer than 100 mm.

$$M_{t,a}^{>100\text{mm}} = \int M_{t,a}(\omega_T) \frac{L_{t,a}}{100} dL_{t,a} \tag{10}$$

The baseline natural mortality ( $M_{t,a}$ ) was multiplied by an

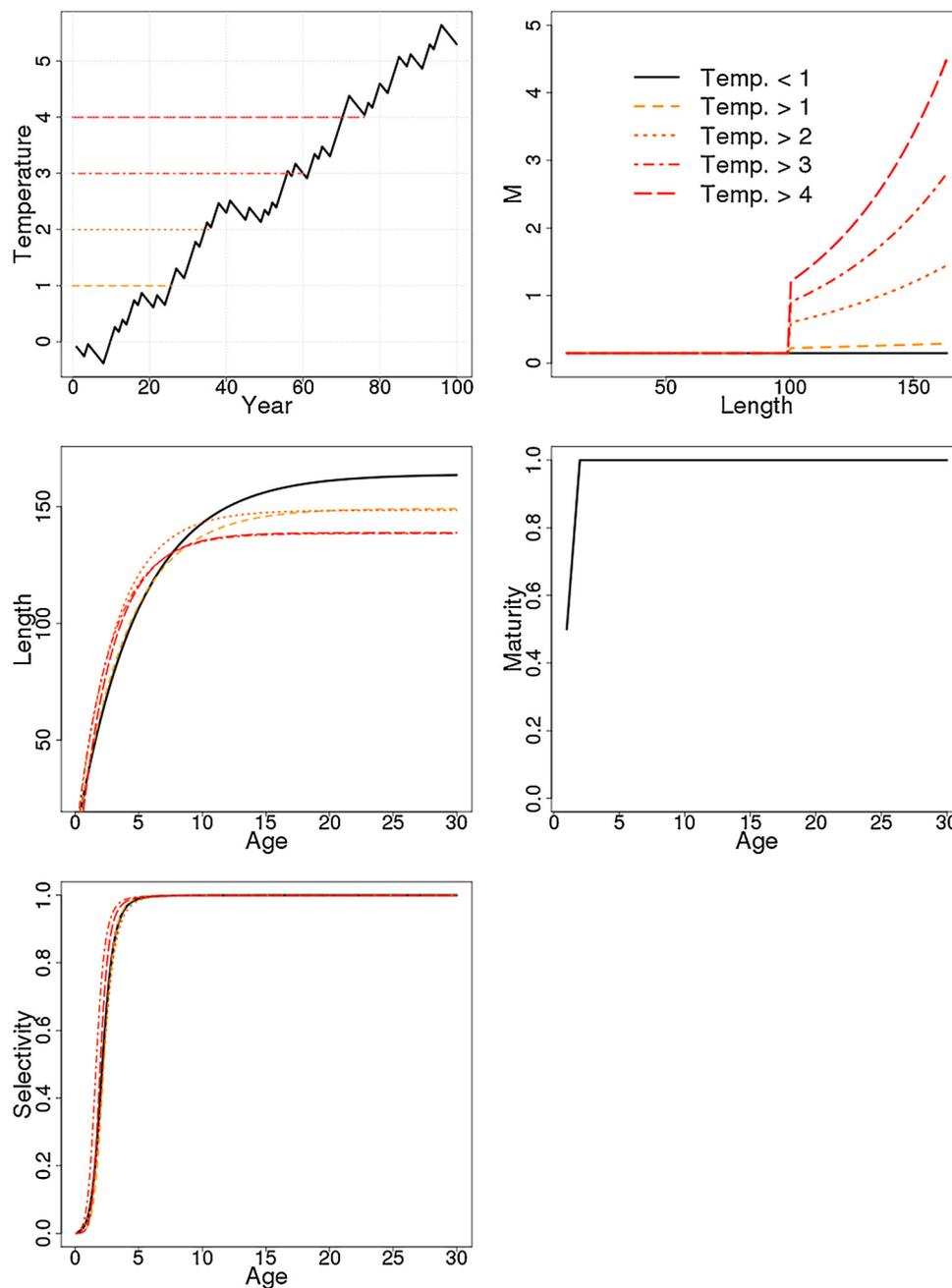


Fig. 1. Temperature in the MAB population segment was modeled as a random walk (top left). Natural mortality increased rapidly for all animals larger than 100 mm when temperature was high (top right). Growth was faster, but to a smaller maximum size when temperature was high (middle left). Maturity was constant over temperature (middle right) and selectivity depended on length and thus temperature (bottom).

exponential function of length and  $\omega_T$ , where  $\omega_T$  ranged from 1 to 8 depending on temperature (Fig.1).  $M$  at length was translated to  $Mat$  age, using length at age. Selectivity and weight at age, were modified to account for changes in growth when they occurred.

### 2.3. Control rule

The current process for setting catch and associated landings limits (i.e., quotas) for the Atlantic surfclam fishery is complicated. Acceptable biological catch limits (ABC) are set at a level less than the catch associated with the maximum fishing mortality threshold rate ( $F = 0.15\text{yr}^{-1}$ ) using a control rule that is a combination of the pre-determined manager's risk policy (i.e., maximum tolerance for over-fishing under specific conditions) and the scientific advisory panel's

decisions on the degree of uncertainty associated with the stock assessment. Because setting these catch limits involves a committee decision on the degree of uncertainty in the assessment, and is not a purely formulaic control rule, direct application is difficult and requires some simplification for simulation in this analysis.

Simulations of a managed population such as Atlantic surfclam must account for management actions, because the actions of managers will affect population dynamics. Management actions were simulated using a control rule based on a simplified version of the current Atlantic surfclam control rule, with target (the control rule inflection point) and stock replenishment threshold levels of  $SSB$  in the base simulation routine. The target was the desired level of  $SSB$ . The threshold was the minimum acceptable  $SSB$ . If  $SSB_t$  fell below  $SSB_{Target}$ ,  $F_t$  was reduced linearly, finally reaching 0 where  $SSB_t = SSB_{Cease}$  (Restrepo and Powers,

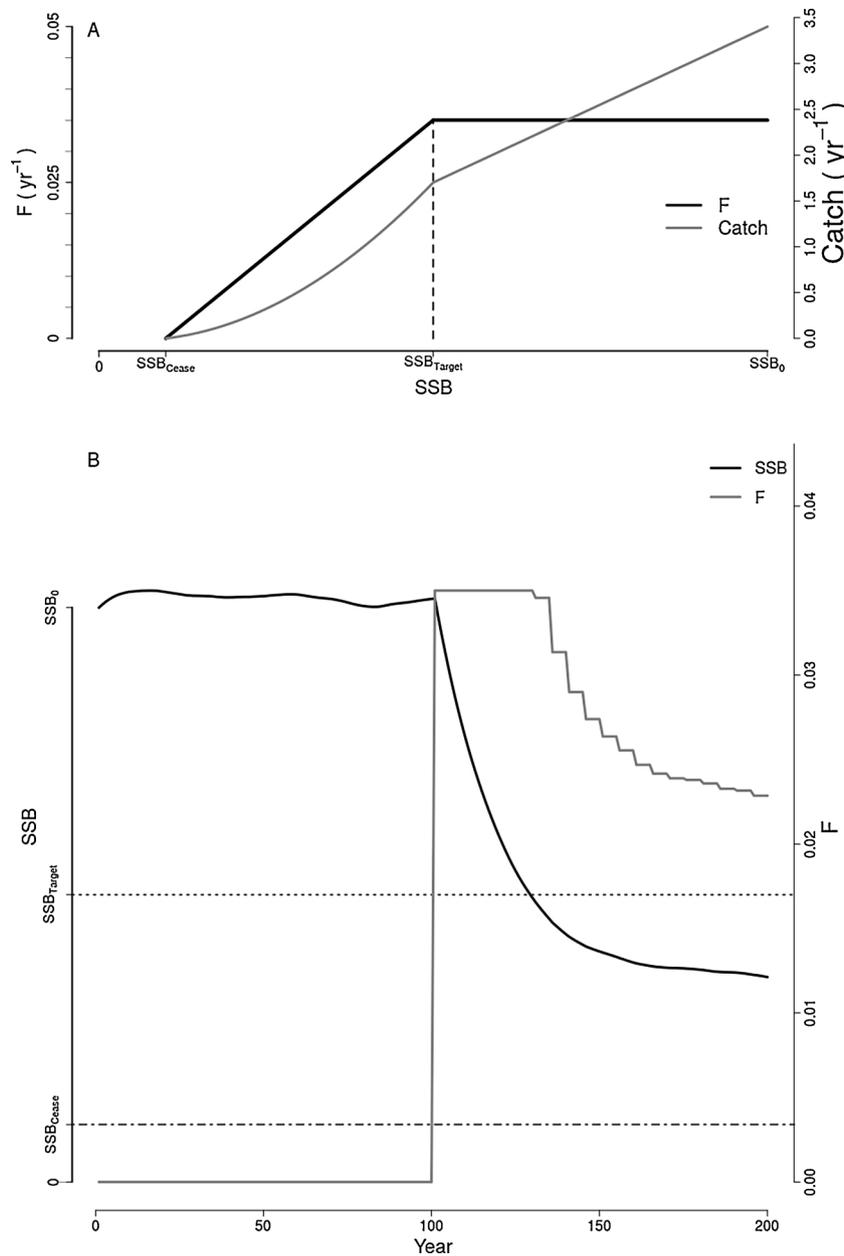


Fig. 2. Panel (A) Control rule for Atlantic surfclam in terms of  $F$  and  $SSB$ . Fishing mortality is constant unless  $SSB$  drops below  $SSB_{Target}$ , it then declines linearly until it reaches 0 at  $SSB_{Cease}$ . The catch implied by the  $F$  is shown in gray. Panel (B) The control rule applied in a simulation run. Fishing mortality was constant when  $SSB_t > SSB_{Target}$ , and was reduced when  $SSB_t < SSB_{Target}$ . Each simulation was initiated with 100 years of no fishing.

1999; Fig.2). This framework allowed a comparison of various candidate control rule reference points ( $SSB_{Cease}$  and  $SSB_{Target}$ ), as well as an examination of the response of the population to management. Control rule reference points were  $\frac{SSB_{Target}}{SSB_0}$  and  $\frac{SSB_{Cease}}{SSB_0}$ , the fraction of unfished biomass ( $SSB_0$ ) that corresponded to target and threshold biomass levels respectively. For the purposes of simulation,  $SSB_0$  was the estimated  $SSB$  in the first year of fishing, which included the assessment error described in Eq. (11).  $\frac{SSB_{Cease}}{SSB_0}$  levels between 0.05 and 0.5 and  $\frac{SSB_{Target}}{SSB_0}$  levels between 0.1 and 1.0 (in increments of 0.05) were explored by drawing randomly with replacement from the candidate values (Table 1). Values for  $\frac{SSB_{Target}}{SSB_0}$  were always set relative to  $\frac{SSB_{Cease}}{SSB_0}$ , such that  $\frac{SSB_{Target}}{SSB_0} > \frac{SSB_{Cease}}{SSB_0}$ .

Under the current Fisheries Management Plan for Atlantic surfclam, the control rule has never been applied, because  $SSB$  has always been above target levels. In theory, the application of the control rule would involve setting  $F_t$  based on the assessed level of  $SSB$ . The mechanism for

achieving  $F_t$  is to set an Overfishing Limit (OFL) based on  $F_t$  applied to the estimated  $SSB$  from the assessment. However, in practice, there would also be the additional step of incorporating the scientific advisory panel's decisions on the degree of uncertainty associated with the stock assessment as a buffer around the final Acceptable Biological Catch (ABC) value chosen. This buffer could in theory shift  $F_t$  down depending on the deliberations of the scientific advisory panel, but could also leave ABC equal to OFL. The scientific advisory panel's decisions on the degree of uncertainty associated with the stock assessment might be simulated as a positive random number, or correlated to assessment uncertainty, but has been ignored here.

#### 2.4. Simulation set up

All simulations included lognormal autocorrelated assessment error. Assessment error was included to mimic the uncertainty around

biomass estimates from an assessment, and that error was auto-correlated to reflect a situation where an error in the assessment in one year was more likely to produce an error in the following assessment(s) (Deroba and Bence, 2008). Assessment error was described by:

$$\hat{SSB}_t = SSB_t \left( e^{\varepsilon_t - \frac{\sigma_{A_t}^2}{2}} \right) \tag{11}$$

$$\varepsilon_t = \varphi(\varepsilon_{t-1}) + \sqrt{1-\varphi^2}\eta_t \tag{12}$$

where  $\eta_t \sim N(0, \sigma_{A_t}^2)$  was the assessment error,  $\varphi$  was the autocorrelation coefficient, and  $\varepsilon_t$  was the year-specific autocorrelated random deviation. The parameterization of Eq. (11) makes  $\hat{SSB}_t$  an unbiased estimate of  $SSB_t$  (Deroba and Bence, 2012).

A manager may decide on a particular  $F_t$  for a fishery, but that  $F_t$  may not be achieved exactly. This discrepancy is often referred to as implementation error. Implementation error was included by modifying  $F_t$  (the intended fishing mortality based on interpretation of the control rule) such that

$$\hat{F}_t = F_t \left( e^{\varepsilon_{F_t} - \frac{\sigma_{F_t}^2}{2}} \right) \tag{13}$$

where  $\hat{F}_t$  was an unbiased estimate of  $F_t$ , including lognormal implementation error  $\varepsilon_{F_t}$  with error variance  $\sigma_{F_t}^2$ .

Simulated management included an “assessment” at the end of every five years. That is, a decision to adjust  $F_{t+1}$  from its initial value ( $F_t$ ) was made at the end of each five-year period depending on the value of  $\hat{SSB}_t$  relative to  $\frac{SSB_{target}}{SSB_0}$  and  $\frac{SSB_{cease}}{SSB_0}$ . The actual fishing mortality experienced by the simulated population ( $\hat{F}_t$ ) was then based on the (potentially) adjusted  $F_t$  using Eq. (13).

### 2.5. Simulated spatial differences

Recruitment, growth, and natural mortality in the US Atlantic surfclam population are not uniform across space. The Atlantic surfclam stock is assessed using two distinct areas, and biological considerations of the potential effects of a warming ocean indicate the high probability of at least three distinct population segments. Simulated total abundance results from independently recruiting population segments experiencing different life history parameters. Simulations were set up to mimic the biological parameters expected in each population segment. Recruitment events occurred separately in each population segment according to (Eqs. (7)–(8)). Growth in each population segment was determined by

$$L_a = \begin{cases} (162.6 - \Delta_{L_{\infty}}^l + V(0, \sigma_{L_{\infty}, S})) * (1 - e^{[-0.23 + \Delta_{K,S}^k + V(0.0, \sigma_{K,S})][a + 0.14 + V(0.0, \sigma_{t_0, S})])} \text{ MAB (S)} \\ (145.0 + V(0, \sigma_{L_{\infty}, N})) * (1 - e^{[-0.29 + V(0.0, \sigma_{K,N})][a - 0.64 + V(0.0, \sigma_{t_0, N})])} \text{ GB (N)} \\ (133.3 + V(0, \sigma_{L_{\infty}, D})) * (1 - e^{[-0.19 + V(0.0, \sigma_{K,D})][a + 0.14 + V(0.0, \sigma_{t_0, D})])} \text{ Off shore (D)} \end{cases} \tag{14}$$

where the  $V$  were normally distributed with parameters  $(0, \sigma_{x,p})$ . The  $x$  represented either  $k$ ,  $t_0$ , or  $L_{\infty}$ , the growth parameters describing the curvature, location and asymptote (respectively) of the growth curve (vonBertalanffy, 1938), and the subscript  $p$  represented the MAB or southern population segment (S), GB or northern population segment (N), and the deep off shore population segment (D). The ranges of the  $\sigma_{x,p}$  were twice the observed standard deviations of growth parameters from (NEFSC, 2017). The  $\Delta_i^x$  were scalar values proportional to temperature  $T_t$ . The value of the vectors  $\Delta_i^x$  were determined by  $T_t$ , where  $T_i^l \leq T_t < T_i^u$  and  $T^l, T^u$  are vectors of temperature units above starting temperature, and  $i$  are the vector elements (Table 1). If for example,  $T_t = 2.5$ , then  $T_3^l \leq T_t < T_3^u$ , then  $\Delta_3^x$  would be used in Eq. (14).

Simulation-specific regional growth and natural mortality parameters were selected from the distributions described in Table 1 and then held constant for each population segment over that simulation. All other parameters ( $F_t, \varphi, \sigma_{A_t}^2, \sigma_{F_t}^2, \frac{SSB_{target}}{SSB_0}$  and  $\frac{SSB_{cease}}{SSB_0}$ ; Table 1) were

simulation-specific, but shared between the population segments.

The sum of the estimated biomasses from all population segments ( $\hat{SSB}_t = \sum_p \hat{SSB}_{t,p}$ ) was compared to the control rule reference points ( $\frac{SSB_{cease}}{SSB_0}$ , where  $\hat{SSB}_0 = \sum_p \hat{SSB}_{0,p}$ ), and  $F_t$  for all population segments was adjusted if necessary. Population segments ( $p$ ) were all fished according to the resulting  $\hat{F}_t$ , and yield was extracted from each according to Eq. (6), but using the population segment-specific  $M_{t,p}, N_{t,p}, M_{a,p}$  and  $W_{a,p}$  values. Total yield and total biomass were the sum of the yield and biomass in all population segments (e.g.  $Y_t = \sum_p Y_{t,p}$ ), and the cv of yield was the expectation of the cv of yield in all population segments ( $cv = E_p[ cv_p ]$ ). Yield and biomass metrics were divided by  $\hat{SSB}_0$  in all results. In all scenarios, the period between assessments, and subsequent adjustments to fishing mortality rates, was five years to mimic an assessment interval similar to the current interval for Atlantic surfclam.

### 2.6. Simulation

Some parameters in the model had unknown true values, such as steepness ( $h$ ) and natural mortality ( $M$ ). Other parameters, such as potential values for management quantities like  $F_t$  or  $\frac{SSB_{cease}}{SSB_0}$ , had unknown effects on biomass and yield. To understand how these parameters affected the outcome of simulations, a range of values for each was examined.

In each simulation, a random variable was drawn for population parameters:  $h, M, F_t$ , assessment uncertainty parameters,  $\varphi, \sigma_{A_t}^2, \sigma_{F_t}^2$ , and management inputs  $\frac{SSB_{cease}}{SSB_0}$  and  $\frac{SSB_{target}}{SSB_0}$  (Table 1). These were constant for the duration of the run (except where  $M$  was modified by temperature, or  $F_t$  by the control rule). The simulation was initialized at equilibrium numbers at age. All simulations included an initial period of 100 years without fishing, which was intended to allow the population to stabilize. The simulation continued through 100 years with fishing, and then new values were drawn for 99,999 subsequent runs.

Results from simulations were compared for values of  $F_t, \frac{SSB_{cease}}{SSB_0}$  and  $\frac{SSB_{target}}{SSB_0}$ , while considering the effects of  $\varphi, \sigma_{A_t}^2, \sigma_{F_t}^2, M$  and  $h$ , to determine how reference points affected biomass and yield.

### 2.7. Analysis

The effects of temperature were examined only for the MAB population segment, where the temperature effects were operational. Other analyses apply to the entire stock (all population segments;  $p$ ). To understand how the stochastic parameters affected simulation results,

mean scaled true biomass  $\frac{\overline{SSB}}{SSB_0} = \frac{E_t \left[ \sum_p SSB_{p,t} \right]}{SSB_0}$ , mean scaled yield

$\frac{\overline{Y}}{SSB_0} = \frac{E_t \left[ \sum_p Y_{p,t} \right]}{SSB_0}$ , coefficient of variation in yield  $cv(Y)$  and time without fishing due to implementation of the control rule ( $t_{F=0}$ ), were compared

to natural mortality ( $M$ ), steepness ( $h$ ), target fishing mortality  $F_t, \frac{SSB_{cease}}{SSB_0}, \frac{SSB_{target}}{SSB_0}, \varphi, \sigma_{A_t}^2, \sigma_{F_t}^2$ , temperature ( $T$ ), and stock recruit relationship (Ricker vs. Beverton-Holt SR), over the 100-year period in which fishing occurred. For these comparisons, the true simulation-specific  $SSB_0 = \sum_p SSB_{0,p}$  were used for scaling purposes. Interactions and main effects were examined with generalized linear models (R Core Team, 2013; McCullagh and Nelder, 1989). In an example predicting mean biomass, the saturated model contained all the main effects and selected interactions between the predictor variables as

$$\frac{\overline{SSB}}{SSB_0} = f \left( \vec{b} \left[ 1 + \left( h * F_t * \frac{SSB_{cease}}{SSB_0} * M \right) + \varphi + \sigma_{A_t}^2 + \sigma_{F_t}^2 + SR + T \right] \right) \tag{15}$$

where  $f$  represents the link function and  $\vec{b}$  is the vector of coefficients estimated in the model. Models predicting biomass and yield were overdispersed relative to the Poisson distribution so the error structure

for the models described generally by Eq. (15) was quasipoisson with a log link function (R core development team; McCullagh and Nelder, 1989). This distribution includes a dispersion parameter for variance and reduces the degrees of freedom for estimation accordingly. Simulation results were also plotted and inspected visually for indications of nonlinearity.

The relative importance of predictors (e.g.  $h$ ,  $F_t$ , and  $M$ ) was determined using deviance tables. The number of simulations was large, and simulation results are not data in the statistical sense. Therefore model selection approaches based on AIC could result in very complicated models in which nearly all covariates and interactions tested would be significant. The deviance table approach may also be better than conventional  $\chi^2$  tests, which are more sensitive to the order in which explanatory variables are tested (Ortiz and Arocha, 2004).

Variables tested included each categorical and continuous predictor variable, and several interactions between them. Linear models for deviance table analyses were fitted by sequentially adding main effects and interactions. Explanatory variables were judged quantitatively relevant as they entered the model if they reduced model deviance by at least 5% of the deviance associated with the null (intercept only) model. This allowed the exclusion of the explanatory variables that least affected the response variables of interest from further consideration.

Additional simulations were conducted with the biological reference points fixed at current values ( $SSB_{Target} = \frac{1}{2}SSB_0$  and  $SSB_{Cease} = \frac{1}{10}SSB_{Target}$ ) using only the MAB population segment. The objective of these runs was to isolate the affect of temperature on potential  $F$  reference points, which initial simulations indicated were more important than biomass reference points for maintaining stock biomass, and average yield, and for reducing variation in yield and time without fishing due to management intervention.

Reference points are applied to the entire stock, not just the MAB population segment. Using the spatial structure described above, different levels of  $F_t$  and  $SSB_{Cease}$  applied to the three population segments were contrasted using contour plots. The motivation for this step was identification of levels of  $F_t$  and  $SSB_{Cease}$  that would maintain biomass and provide relatively high yield, in conjunction with the current control rule, as reference points over a broad range of potential and unknown life history traits for Atlantic surfclam as well as a range of possible increasing bottom water temperatures over the next 100 years.

### 3. Results

Using  $\frac{SSB_{Cease}}{SSB_0}$  and  $\frac{SSB_{Target}}{SSB_0}$  as predictors of mean biomass, yield, variation in yield and time without fishing produced results that were quite similar. For simplicity only results using  $\frac{SSB_{Cease}}{SSB_0}$  as a predictor are discussed here.

Deviance tables show that the effects of  $F_t$ , steepness ( $h$ ),  $M$  and temperature ( $T$ ) were better predictors of mean biomass, whereas yield, variation in yield and time without fishing were also predicted by  $\frac{SSB_{Cease}}{SSB_0}$  (Table 2). Biomass tended to decrease with increasing  $F_t$ , whereas variation in yield and time without fishing were proportional to  $F_t$  (Figs. 3–6). Yield increased initially with increasing  $F_t$  before decreasing at higher values of  $F_t$  (Fig. 5), although this effect was masked by the relative importance of temperature, natural mortality, steepness, and  $SSB_{Cease}$ . Increasing natural mortality resulted in higher yields, less variation in yield and less time without fishing. Higher steepness resulted in higher biomass and yield and less variation in yield and time without fishing. Higher temperatures produced lower biomass, more time without fishing, and more variation around less yield.

Deviance tables also demonstrated the relative unimportance of several factors, including the type of stock-recruit relationship, implementation error, assessment error and autocorrelation in assessment error. Interactions between the various predictors did not strongly influence the results, with the exception of the  $h:SSB_{Cease}$  interaction,

**Table 2**

Deviance table results for models predicting mean Atlantic surfclam biomass ( $\frac{SSB}{SSB_0}$ ), mean ( $\frac{Y}{SSB_0}$ ), and cv of yield ( $cv(Y)$ ) and years without fishing due to management ( $t_{F=0}$ ), over ( $n = 100,000$ ) 100-year simulations. The candidate predictors were fishing mortality target ( $F_t$ ), steepness ( $h$ ), natural mortality ( $M$ ), the fraction of  $SSB_0$  that corresponds to the control rule threshold ( $\frac{SSB_{Cease}}{SSB_0}$ ), assessment error ( $\sigma_{A_t}^2$ ), amount of auto correlation in assessment error ( $\phi$ ), implementation error ( $\sigma_{F_t}^2$ ), the type of stock recruit relationship (Ricker vs. Beverton-Holt SR), and temperature ( $T$ ) as well as interactions of potential interest. Results are for the portion of the stock most affected by temperature (the MAB population segment). Only predictors that explained  $\geq 5\%$  of the deviance relative to the null model are shown.

Response	Relevant predictors (% dev. explained)
Biomass $\frac{SSB}{SSB_0}$	$F_t$ (21.6), $h$ (45.7), $M$ (17.0), $T$ (8.7)
Yield $\frac{Y}{SSB_0}$	$h$ (40.3), $M$ (21.6), $SSB_{Cease}$ (16.4), $T$ (9.7)
$cv(Y)$	$F_t$ (13.9), $h$ (36.1), $M$ (10.8), $SSB_{Cease}$ (23.3), $T$ (9.7)
Years without fishing $t_{F=0}$	$F_t$ (6.6), $h$ (27.0), $M$ (7.7), $SSB_{Cease}$ (37.3), $h:SSB_{Cease}$ (11.5)

which contributed to the prediction of time without fishing. In general, a higher steepness stock showed more resilience when  $SSB$  was allowed to go to low levels (low  $SSB_{Cease}$ ), and thus the fishery spent less time closed due to management intervention.

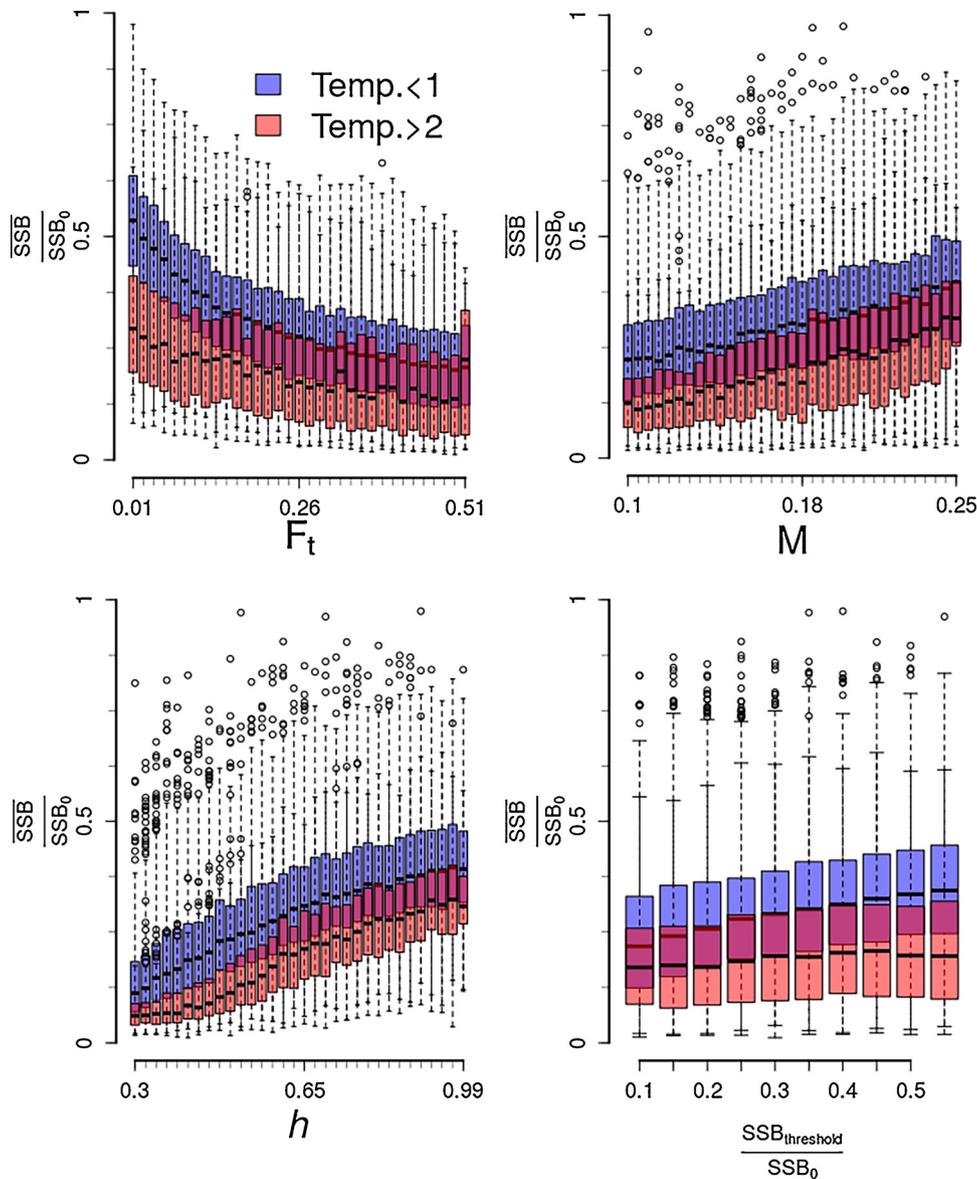
Fixing the biomass reference points at current levels while varying  $F_t$  showed that temperature could have a marked effect on potential  $F$  reference points if they were applied in the MAB population segment alone. The yield curve had a clearly defined peak at low temperature, but was relatively flat at high temperature (Fig. 5). The probability of time without fishing and variation in yield were higher at high temperature, while the average biomass was lower.

Contour plots based on the three spatial population segments showed that relatively high yield and biomass, with little variation in yield and few years without fishing could be achieved at a variety of  $F$  and  $SSB$  reference points (Fig. 7). Contour plots also demonstrated how targeted management could exploit potential tradeoffs between these metrics.

### 4. Discussion

Simulation can be a useful tool for determining reference points that provide for stable, sufficient yields and sustainable biomass, given a variety of life history traits and possible states of nature (Punt et al., 2016). Currently, many aspects of Atlantic surfclam biology are poorly understood. The future response of the Atlantic surfclam stock to ocean warming is uncertain, and the needs of the fishery may change over time as well. This simulation study used a broad distribution of possible values intended to capture both the unknown biological parameters and a reasonable suite of potential assessment and implementation uncertainty. The  $F_t$  and control rule reference points were simulated over 100 years using random combinations of important biological and fishery parameters. The results of these simulations should describe management quantities that maintain the stock and the fishery under many possible combinations of life history traits and fishery conditions.

An objective of this study was to evaluate potential reference points for a sessile species under conditions of increasing bottom temperature. Increasing bottom temperature has clear implications for the MAB population segment. When the MAB population segment was considered alone, higher temperatures caused a shift in yield as a function of  $F$  (Fig. 5). At lower temperatures, yield was maximized at about  $F = 0.12 \text{ yr}^{-1}$ . At higher temperatures, yield was about equal at any  $F \geq 0.1 \text{ yr}^{-1}$ . The implication is that fishing harder at high temperature induces less of a penalty on the spawning stock than equivalent fishing pressure at lower temperature, because higher temperature is already causing



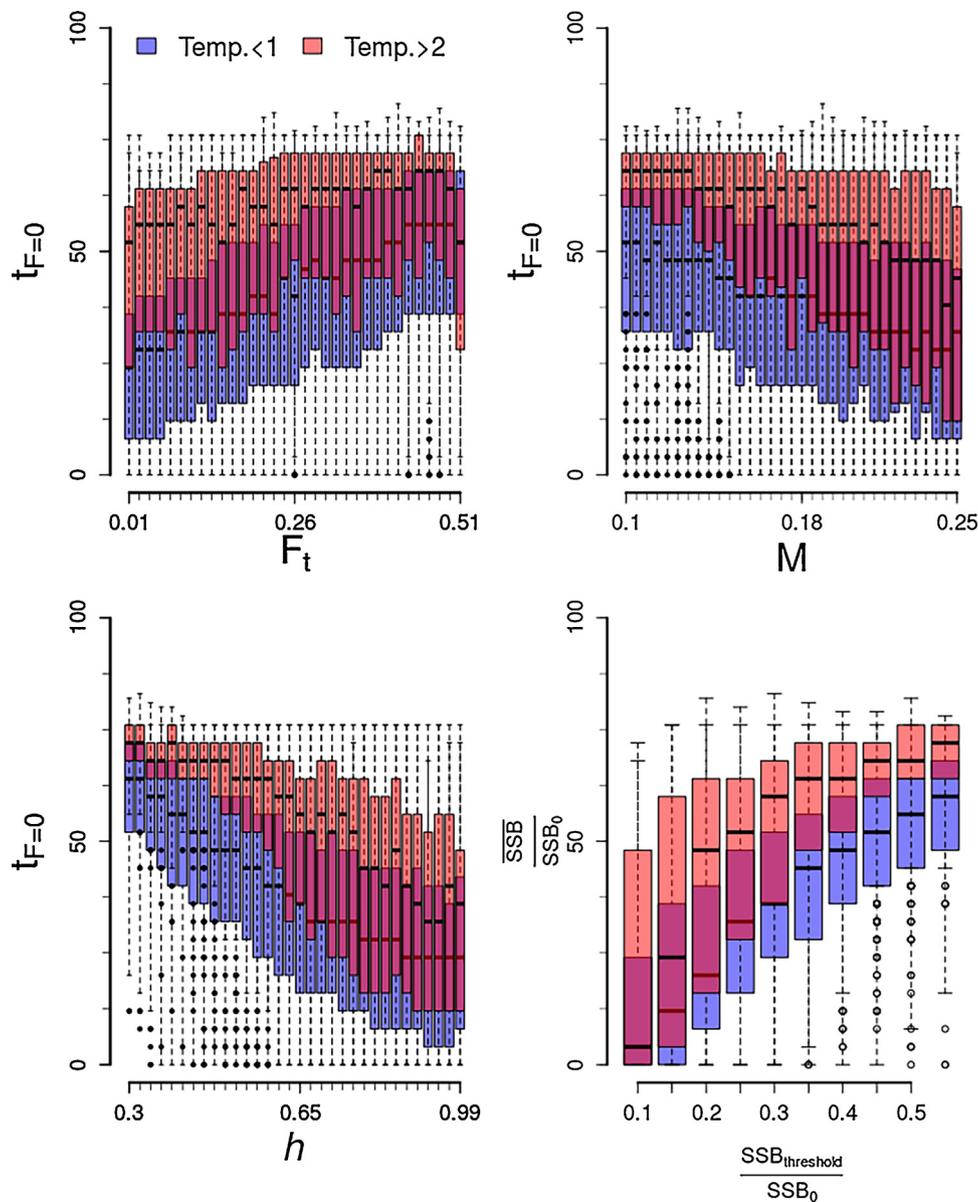
**Fig. 3.** Mean biomass ( $\frac{SSB}{SSB_0}$ ) in 100-year simulations, by values of target fishing mortality ( $F_t$ ), steepness ( $h$ ), assessment error ( $\sigma_{A_t}^2$ ), natural mortality ( $M$ ) and the fraction of  $SSB_0$  that corresponds to the control rule (stock replenishment) threshold ( $SSB_{cease}$ ). Results are for the portion of the stock affected by temperature (the MAB population segment) and the results for higher and lower temperatures are shown in red and blue boxes. The boxes represent interquartile range, solid horizontal lines in each box are the medians, and the whiskers indicate the range between the 0.025 and 0.975 quantiles ( $n = 100,000$ ).

increased natural mortality at the sizes targeted by the fishery. The relative importance of compensatory mortality in permitting increased harvest at no cost to the stock has been considered in oyster populations where mortality from disease and fishing may co-occur (Klinck et al., 2001). The relative roles of disease as a compensatory or additive source of mortality is commonly considered (Hassell et al., 1982; Holmes, 1982) because the disease process often occurs simultaneously and in addition to other sources of mortality. Compensation however, is rarely considered in fisheries contexts, other than as density dependence, such as when Ricker stock recruitment relationships are explained by cannibalism or inter-species competition (Hilborn and Walters, 2013). The appropriateness of its consideration for Atlantic surfclam derives from the relatively continuous harvest of these clams over the course of the year (NEFSC, 2017) and the assumption that natural mortality is also a continuous process. Removing animals through fishing mortality that were likely to die due to increased temperature has less impact on the spawning stock. This assumption depends on the relative timing of temperature related mortality and

spawning. However, because both processes are likely to depend on multiple unknown factors, with unknown inter-annual variation, further consideration of the interaction between spawning and temperature related mortality was not pursued here.

There are, however, tradeoffs for increasing  $F$  at high temperature. Variation in yield was greater at higher  $F$  at all temperatures, but the magnitude of the effect was greatest at high temperature. Time without fishing due to management intervention was relatively short at  $F \leq 0.12 \text{ yr}^{-1}$  at low temperature, but longer at all  $F$  at high temperature (Fig. 4).  $SSB$  was highest at low  $F$  and declined rapidly as  $F$  increased (Fig. 3) at both high and low temperatures.

The effects of natural mortality on population level response variables can appear counter intuitive. Higher  $M$  were associated with higher yield and biomass, and less variation in fishing and time without fishing. Although a higher  $M$  implies a more productive population, there was no direct correlation between  $M$  and  $h$  built into the simulation. There were, however, some indirect correlations between  $M$  and productivity, including compensation in those runs that used a Ricker



**Fig. 4.** Time not fished due to management intervention ( $t_{F=0}$ ) in 100-year simulations, by values of target fishing mortality ( $F_t$ ), steepness ( $h$ ), assessment error ( $\sigma_{A_t}^2$ ), natural mortality ( $M$ ) and the fraction of  $SSB_0$  that corresponds to the control rule (stock replenishment) threshold ( $SSB_{cease}$ ). Results are for the portion of the stock affected by temperature (the MAB population segment) and the results for higher and lower temperatures are shown in red and blue boxes ( $n = 100,000$ ).

stock-recruitment relationship, and to a lesser degree, the discarding of unrealistic combinations of  $M$  and  $h$  that produced biomasses far above or below  $SSB_0$  after the burn in phase. The relationship between  $M$  and time without fishing due to depletions and closures is perhaps also unexpected. The mechanism behind this result is the interaction of growth and relative longevity. When  $M$  was low, the population age structure tended to accumulate in the old age classes, where growth was very slow. At low  $M$ , Atlantic surfclam lived a long time beyond the age when they reach maximum length (Fig. 1, bottom panel). The result, when fishing was applied, was a depletion in biomass that took longer to rebuild. When  $M$  was high, the population age structure was more concentrated in the young ages, where growth is relatively rapid and the population can replace lost biomass with growth in fewer years.

If we consider only  $F_{Threshold} \leq 0.12 \text{ yr}^{-1}$  ( $F_{Threshold}$  is the threshold for defining overfishing) little need exists to concern ourselves with variation in yield or the probability of fishery closures. The contour plots (Fig. 7) demonstrated the utility of potential reference points relative to metrics of fishery performance. For example,  $SSB$  was

maximized at low  $F$  regardless of  $\frac{SSB_{cease}}{SSB_0}$ , but  $\frac{SSB_{cease}}{SSB_0}$  becomes more important at higher levels of  $F$ . Yield was maximized at intermediate levels of  $F$  and lower values of  $\frac{SSB_{cease}}{SSB_0}$ . Examination of the relative  $SSB$  and yield at various  $F$  and  $\frac{SSB_{cease}}{SSB_0}$  allow for comparison of the likely performance of competing reference points. Variation in yield and time without fishing due to closures were near minimum at most values of  $\frac{SSB_{cease}}{SSB_0}$  or  $\frac{SSB_{Target}}{SSB_0}$  tested when  $F \leq 0.12 \text{ yr}^{-1}$ .

The current  $SSB_{cease}$  is  $0.05 * SSB_0$  and the current  $SSB_{Target}$  is  $0.5 * SSB_0$ . Using these values, yield was maximized at  $F \leq 0.12 \text{ yr}^{-1}$ , while  $0.5 * SSB_0$  occurred at  $F \leq 0.11 \text{ yr}^{-1}$ . The current stock assessment had difficulty in precisely estimating absolute  $SSB$ . The trend in biomass, however, was precisely determined, and the results indicate Atlantic surfclam is lightly fished and near its unfished abundance (NEFSC, 2017). The Atlantic surfclam stock is likely underfished relative to the  $F_t$  identified here as a good range for an  $F$  reference point.

The Atlantic surfclam fishery is market limited, and currently fished under quota (NEFSC, 2017). This may limit interest from either industry or management in increasing yield. Under these conditions,

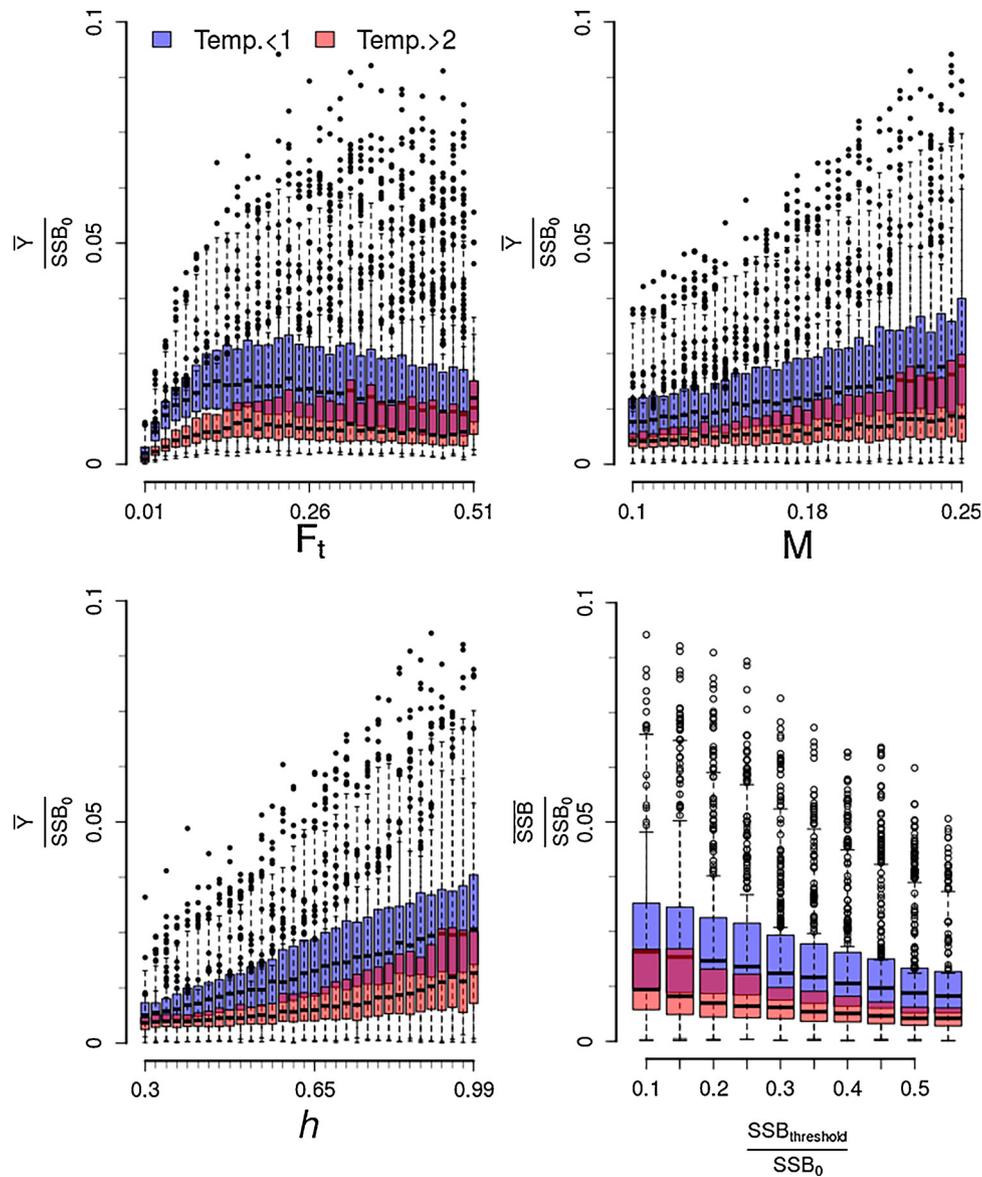


Fig. 5. Mean yield ( $\frac{\bar{Y}}{SSB_0}$ ) by values of target fishing mortality ( $F_t$ ), steepness ( $h$ ), assessment error ( $\sigma_{A_t}^2$ ), natural mortality ( $M$ ) and the fraction of  $SSB_0$  that corresponds to the control rule (stock replenishment) threshold ( $SSB_{C_{case}}$ ). Results are for the portion of the stock affected by temperature (the MAB population segment) and the results for higher and lower temperatures are shown in red and blue boxes ( $n = 100,000$ ).

weighting  $SSB$  somewhat more than yield might be advantageous when choosing between reference points. Under the current management plan, which does not account for spatial differences, tactical management designed to maintain a higher  $SSB$  could provide a buffer against increasing bottom temperature. Maintaining higher biomass in cooler regions might offset some loss of biomass due to increasing temperatures in the warmer population segments.

It is possible the simulation presented here is optimistic regarding the resiliency of the stock. Because Atlantic surfclam have been lightly fished, spawning stock has remained high, and recruitment at low stock size is unknown. This makes any estimate of steepness purely speculative. It is possible that the range of steepness values presented here is too broad. The inclusion of the Ricker stock recruitment relationship implies a compensatory response to moderate fishing pressure. The applicability of this type of response function is also unknown because the stock has always been near its theoretical carrying capacity. Compensatory response has been observed in other bivalves (Hancock, 1973; Powell et al., 1995, 2009) so it may be less reasonable to exclude it. Sensitivity runs using only the Beverton-Holt stock recruit function

did not fundamentally alter the results, though  $\frac{SSB}{SSB_0}$  and  $\frac{\bar{Y}}{SSB_0}$  tended to be slightly lower at most values of  $F_t$ . The density of Atlantic surfclam aggregations required for successful spawning is unknown. Although sessility is generally considered to sensitize species to decreased fertilization efficiency at low abundance, recent behavioral observations for hard clams, *Mercenaria mercenaria* (Tettelbach et al., 2017) suggest that mobile clams such as Atlantic surfclam may be able to limit the effect of low density by repositioning to enhance successful procreation. Refinements in the state of knowledge regarding optimal density might inform both the estimates of the resiliency of the stock and the candidacy of spatial areas for protection as potential sources for downstream settlement.

It is possible that the effect of temperature has been overstated or understated. For example, the increase in  $M$  at high temperature may, in reality, only affect animals that are larger than the temperature threshold (100 mm) set in this simulation. Pushing the effect of temperature up the growth curve to larger animals tends to reduce the effect of temperature. The magnitude of the effects of temperature on growth and  $M$  are, of course, rough estimates (though see Narvaez et al.,

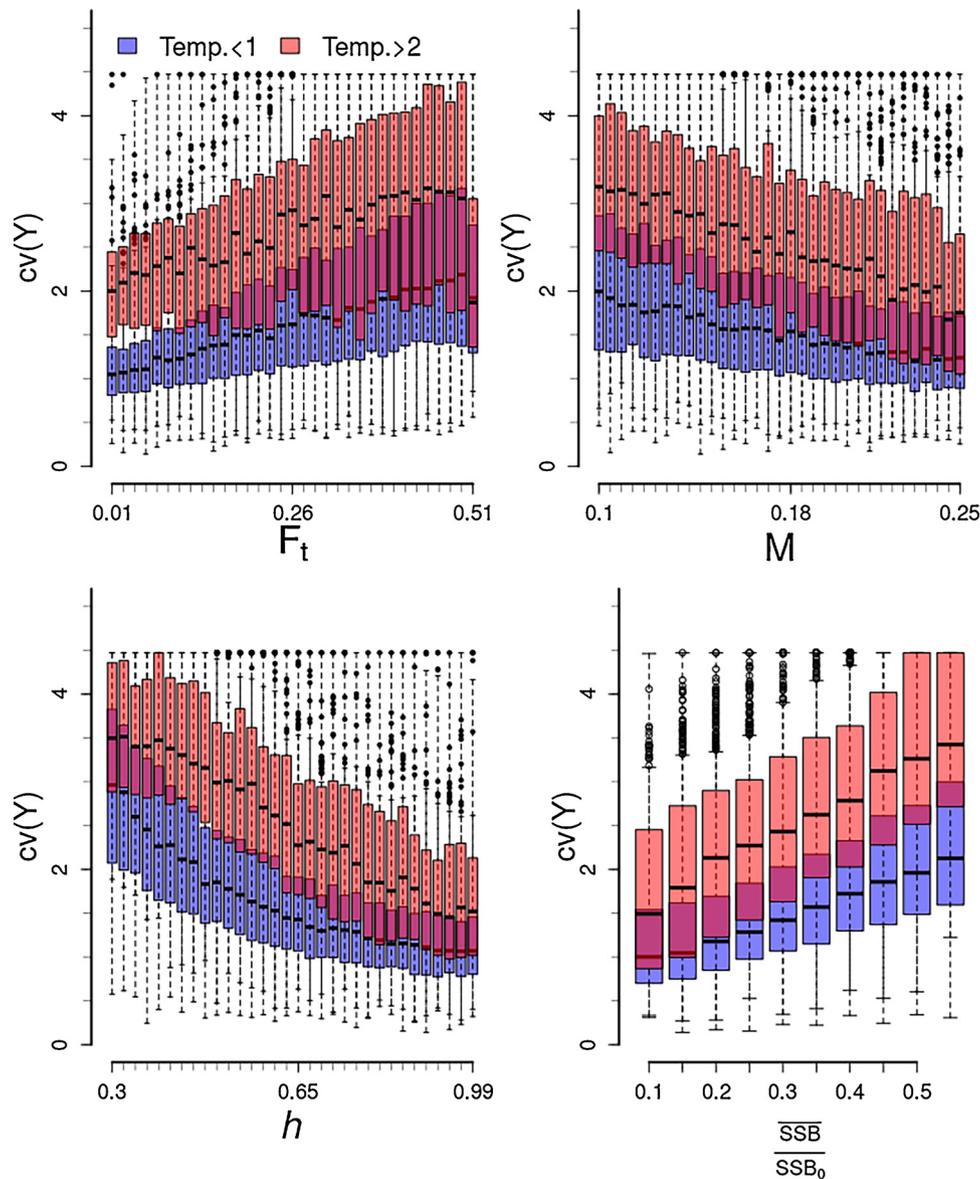


Fig. 6. Coefficient of variation (CV) in yield in 100-year simulations, by values of target fishing mortality ( $F_t$ ), steepness ( $h$ ), assessment error ( $\sigma_{A_t}^2$ ), natural mortality ( $M$ ) and the fraction of  $SSB_0$  that corresponds to the control rule (stock replenishment) threshold ( $SSB_{cease}$ ). Results are for the portion of the stock affected by temperature (the MAB population segment) and the results for higher and lower temperatures are shown in red and blue boxes ( $n = 100,000$ ).

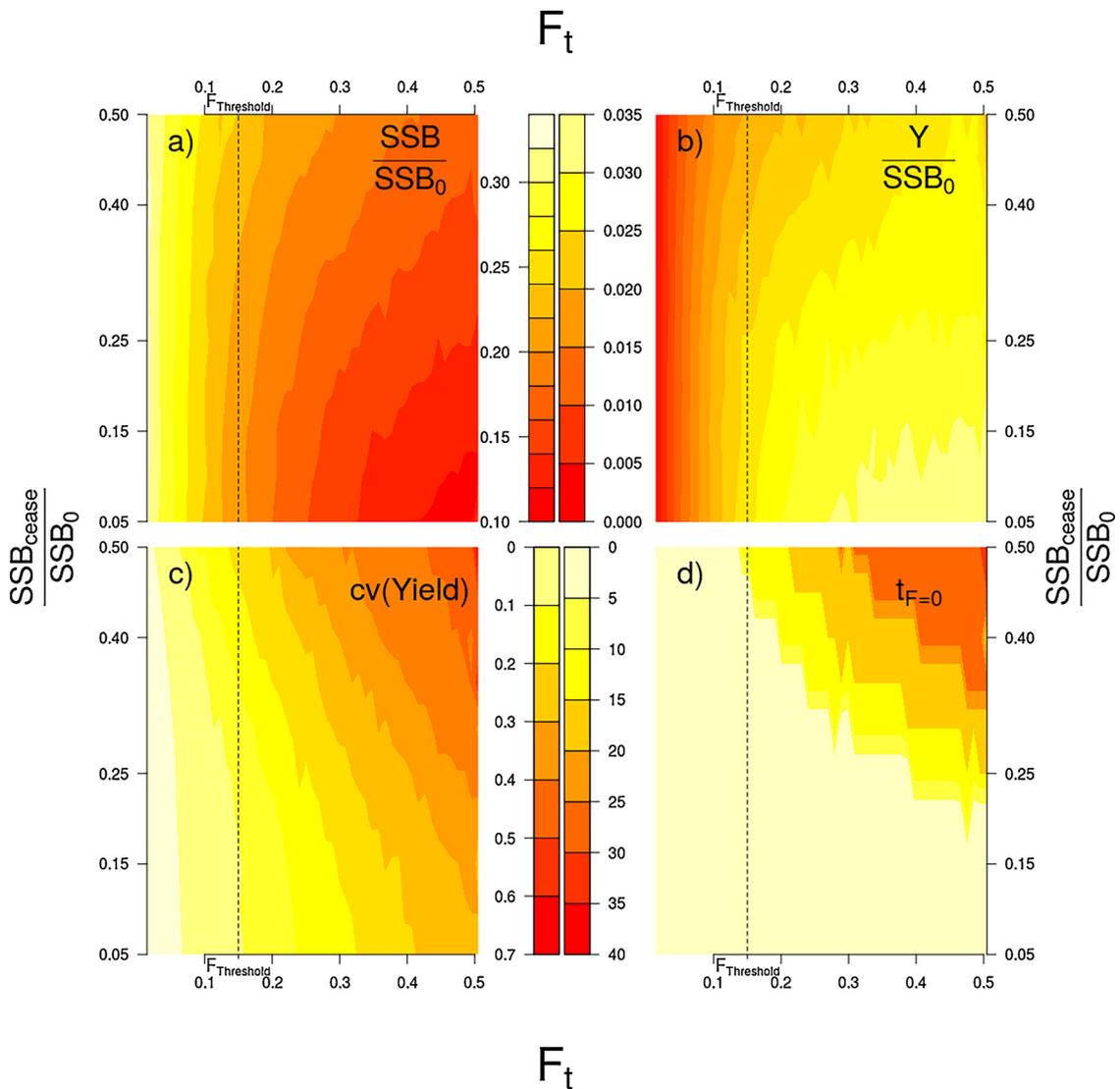
2015) and suffer from the inherent imprecision of expert opinion. The feedback between temperature and food supply adds additional complexity (see Yoder et al., 2002). Food supply under warming conditions and in deeper water is unknown and could either improve or exacerbate the effects of increased temperature. Finally, attempting to predict the magnitude of temperature change adds uncertainty. It is possible that temperature change on GB could reflect that of MAB, in which case the results for the entire stock would more closely follow the results observed for MAB, rather than being dampened as seen in Fig. 7.

The broad range of the various life history parameters considered here may swamp the more subtle effects of other parameters, such as assessment uncertainty, that are often considered important (Walters and Pearse, 1996; Engen et al., 1997; Hilborn et al., 2002; Punt, 2003; Deroba and Bence, 2008). The results, however, provide the means to unmask subtle effects through a careful examination of subsets that limit the range of strong predictors like  $M$  and  $h$ . As the state of knowledge regarding life history parameters of Atlantic surfclam grows, these results might be refined over narrowing ranges of some of these predictors. Making decisions to limit their ranges given the current state

of knowledge, however, would limit the generalizability of this study and the reference point recommendations that result.

Others have shown, using another clam (ocean quahog; *Arctica islandica*), that spatially precise tactical management can increase average yield and biomass (e.g., Hennen, 2015). They showed that when growth and recruitment vary between population segments within a stock, an advantage accrues from managing those population segments separately. Under conditions of increasing water temperature, spatially precise management might be even more important. In the current study, plots of average yield over  $F_t$  (Fig. 3) show that maximum yield is achieved at higher  $F_t$  when the temperature is higher. This implies that managing based on historical low temperatures might lead to underfishing. A sustained increase in bottom temperature probably warrants reevaluation of  $F$  reference points in the Atlantic surfclam fishery. The results here support the notion that harvest control rules for other sessile species may need to be re-evaluated if temperature changes enough to trigger shifts in life history parameters.

Our results emphasize an important difference between sessile and mobile biota with respect to the influence of temperature change on the



**Fig. 7.** Contour plots showing the combined effects of  $F_t$  and the fraction of  $SSB_0$  that corresponds to the control rule (stock replenishment) threshold ( $SSB_{cease}$ ) on: (a)  $\frac{SSB}{SSB_0}$ , (b)  $\frac{Y}{SSB_0}$ , (c)  $cv(Y)$  and (d)  $t_{F=0}$ . In each plot the darker colors are associated with less preferred values (e.g. in plot (a) the lowest  $\frac{SSB}{SSB_0}$  occurs on the right side, where  $F_t$  is high, and in plot (c) the highest variation in yield occurs on the right side, where  $F_t$  is high). A recent  $F_{Threshold}$  (0.15; NEFSC, 2013) is marked with a dashed line for reference. These simulations were based on a single stock where recruitment followed either Beverton-Holt or Ricker stock recruitment dynamics.

stock and the influence on management decisions. First, species with mobile adults readily reposition their populations with respect to changes in the temperature regime at the geographic scale through migration of individuals. Examples from the area of interest here, the northwest Atlantic, abound (e.g., Rose, 2005; Lucey and Nye, 2010). Sessile individuals reposition largely through the processes of mortality and recruitment. The former is typically more rapid than the latter, so shifts in range are often accompanied by transient, but potentially of long duration, contractions in the geographic footprint of the stock. Atlantic surfclam are an exemplar. Recession of the southern boundary through mortality of the adults has been observed to occur on catastrophically short time scales. Advance of the range northward or into deeper water has been well documented, but has taken a much longer time, the hydrodynamics of the northwestern Atlantic impeding northward larval movement being one of many potential restraints (Zhang et al., 2015, 2016). At any time, the status of the stock is in some measure a function of the amount of the range impacted by range expansion versus range recession, and a transient, though potentially long duration, forced range contraction is a possibility. Interestingly, transient retraction can be found in range transitions of terrestrial as

well as marine immobile species (e.g., Butler et al., 2012). It is unlikely that bivalves have the option of modifying recruitment capacity as a function of stock size under transient range contraction because the limitations on fecundity are local, not stock wide. The penalty of sessility is exacerbated further by the potential change in available food in the newly occupied range. For Atlantic surfclam, movement offshore almost assuredly implies movement into waters of lower food quantity (Hofmann et al., 2017). As a consequence, the management challenges imposed by increasing temperature on a sessile stock are substantively more complex than for a mobile species.

The results presented here demonstrate a potential direct link between an environmental indicator, bottom water temperature, and a management quantity of interest, the overfishing reference point. In a changing climate, monitoring the environmental conditions experienced by a valuable resource such as the Atlantic surfclam is likely important for effective management. As ocean temperatures increase, managers of sessile species will need to consider potential range expansion, and contraction. Simulation can be a useful tool for evaluating the interaction of increasing ocean temperature and management choices.

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