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Non-stationary Natural Mortality Influencing the Stock Assessment of Atlantic Cod (*Gadus morhua*) in a Changing Gulf of Maine

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Climate changes have increasingly driven diverse biological processes of fish and lead to non-stationary dynamics of populations. The Gulf of Maine (GOM) is vulnerable to climate change, which should be considered in fishery stock assessment and management. This study focuses on the effects of possible non-stationary natural mortality (*M*) on the stock assessment of Atlantic cod (*Gadus morhua*) in GOM. We evaluated different assumptions about stationary and non-stationary *M* driven by sea surface temperature (SST) using a simulation approach. We found that adopting non-stationary *M* could effectively improve the quality of stock assessment compared to the commonly used stationary assumption for the GOM cod. Non-stationary scenario assuming a non-linear relationship between SST and *M* had the lowest estimation errors of spawning stock biomass (SSB) and fishing mortality, and the younger and the older age groups tended to be less accurately estimated. Different assumptions in *M* led to diverged estimates of biological reference points and yielded large differences in the determination of stock status and development of management advices. This study highlights the importance of including non-stationary vital rates in fisheries assessment and management in response to changing ecosystems.

Keywords: non-stationary dynamics, climate change, natural mortality, Gulf of Maine, *Gadus morhua*

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INTRODUCTION

Climate change and environmental variability have occurred throughout history (Brander, 2010), in which context concerns have been mounting regarding the state of fisheries' population and yield (Cheung et al., 2012; Free et al., 2019). Climate change has both direct and indirect impacts on fish stocks, driving a multitude of environmental factors vital to the survival and growth of fish species, such as temperature, salinity, and current (Koenigstein et al., 2016; Guan et al., 2017a). Fish may react directly by altering their spatial distribution to avoid unfavorable conditions and move into environmentally suitable areas (Biro et al., 2007; Guan et al., 2017b). Meanwhile, climate change impacts key processes in fish life history, which includes recruitment success, juvenile survival, feeding, and individual growth (Shelton and Mangel, 2011; Lynch et al., 2016; Zimmermann et al., 2019). The specie-level responses further result in ecosystem-level changes in productivity and trophic interactions (Fernandes et al., 2013), which are then compounded by commercial fisheries' exploitation (Britten et al., 2017).

Climate change has affected many aspects of fish populations, and the impact of climate change on natural mortality is one of the worthiest of discussions but poorly understood

(Punt et al., 2021). Natural mortality rate (*M*) is a critical parameter in stock assessment, as its magnitude relates directly to stock productivity, sustainable yields, optimal exploitation rates, and biological reference points (Brodziak et al., 2011). *M* is affected by many factors such as changing population dynamics, biotic interactions, exploitation of fish stocks, and abiotic conditions (Jørgensen and Fiksen, 2010; Swain, 2011; Deroba and Schueller, 2013; Neira and Arancibia, 2013; Powers, 2014), which are driven by climate change either directly or indirectly (Rijnsdorp et al., 2009), particularly by thermal tolerance for many species (Pauly, 1980). The changes in *M* would be sufficient to affect fishery reference points and sustainable levels of fishing mortality for commercially fishery species; however, *M* is commonly assumed constant in stock assessment due to a lack of understanding of *variation in M* and the difficulty in the estimation (Lee et al., 2011).

Therefore, despite the acknowledged climate-driven changes in fish populations (Bakun et al., 2010; Punt et al., 2013), non-stationary processes (i.e., there is a trending change in population dynamics) have rarely been incorporated into fishery population dynamic models and stock assessments (Finley, 2011; Litzow et al., 2018), and stationary assumptions still prevail in traditional stock assessment models (Plagányi, 2019). Evaluating the effects of climate change-induced non-stationary population dynamics is crucial to stock assessment and fishery management (Lee and Punt, 2018), because non-stationary dynamics will affect the setting of target and limit reference points and further the reliability of forward projections from management strategy evaluation (Merino et al., 2019). Incorporating non-stationary processes can also help to improve the accuracy of stock assessments and hence stock status determinations (Jiao et al., 2012; Li et al., 2019). The general disregard of non-stationary dynamics may be a culprit for unaccounted bias in stock assessment of fishing mortality and biomass (Szuwalski and Hollowed, 2016; Guan et al., 2017b), which is critical for understanding current and future climate change impacts (Barange et al., 2018). There have been previous works that examine the non-stationary *M* (Jacobson et al., 2016; Punt et al., 2021). For example, varying M was used in the assessment of North Sea herring by the ICES herring assessment working group (ICES, 2017), and it was also considered in the assessment of the Barents Sea capelin (Jacobsen and Essington, 2018). Additionally, Aanes et al. (2007) used a Bayesian state-space model to describe the dynamics of arctic cod, the simulation estimated the dynamical pattern of natural mortality but did not quantify the true value of Rose and Walters (2019) conducted stock assessment for cod based on a VPA model within changing M. The results demonstrated that M has been variable but the VPA model using a non-stationary M did not fit well. In general, the non-stationary dynamics in M have not yet been incorporated in most stock assessments (Li et al., 2019), and the difficulty of quantifying natural mortality calls for increased caution in the assumptions of M.

This study focuses on Atlantic cod (*Gadus morhua*) in the Gulf of Maine (GOM) with regard to non-stationary assumptions in natural mortality. Climate change has had a considerable impact on GOM (Pershing et al., 2018), where a steady increase in temperature has been observed since 1982 (**Supplementary Figure 1A**) and the cod stock is particularly sensitive to the warming temperature (Kjesbu et al., 2010). Ocean warming has been evidenced to result in the rapid decline of biomass and loss of yield of GOM cod (Fogarty et al., 2008; Pershing et al., 2015). Therefore, the impact of climate change should be explicitly considered in the stock assessment and management of this stock.

Here, the GOM Atlantic cod fishery was examined with regard to non-stationary assumptions in natural mortality using an age-structured assessment program model (ASAP; Legault and Restrepo, 1998). We used increasing sea surface temperatures (SSTs) to represent climate change and factored climate variability into GOM cod dynamics. The purpose of the study is (1) to address the plausibility of non-stationary dynamics in natural mortality of the cod stock and (2) to demonstrate how the non-stationary dynamics of *M* may affect stock assessment and the interpretation of stock status. We aim to highlight the risk of ignoring non-stationary dynamics in *M* in the assessment and management of fishery resources under the pressure of climate changes.

MATERIALS AND METHODS

Data Collection

In this study, we used historical survey abundance index and catch data of GOM cod for the stock assessment. Both fishery-dependent and fishery-independent survey data were documented for GOM cod by the Northeast Fisheries Science Center (NEFSC), which covers the time period from 1982 to 2018. The most recent stock assessment was updated in 2019 based on the 2013 benchmark assessment (NEFSC, 2013, 2019).

We obtained global SST from the extended reconstructed SST (ERSST, version 5) dataset[1] and averaged the SST over the GOM region (the region between latitudes 40.375 and 45.125 N and longitudes 70.875 and 65.375 W) to produce a yearly time series SST (for the detailed information of the SST analysis, refer to **Supplementary Material**). The observed yearly SST in the GOM ranged from 10.51 to 13.37°C with an increasing trend from 1982 to 2018 (**Supplementary Figure 1A**). SST is often used to indicate climate changes as it connects the thermodynamic interaction between the atmosphere and the ocean (Nnamchi et al., 2015), and the changes in SST can be transmitted to deeper waters as the water is mixed seasonally (Alexander et al., 2018). SST correlates with deeper water temperature in the GOM, both spatial and temporal variability are similar in the SST and the bottom temperature (Thomas et al., 2017). In addition, SST data are well collected with high temporal and spatial resolution compared to other environment data (Barron and Kara, 2006).

Assumptions of Natural Mortality

A series of *M* assumptions were considered in our study with respect to the stock assessment by NEFSC (2013, 2019), in which GOM cod was assessed with the age-structured assessment model with the formal stationary *M* (equals to 0.2 from 1982 to 2018).

[1]https://www1.ncdc.noaa.gov/pub/data/cmb/ersst/v5/ascii/

Besides, a non-formal, non-stationary scenario, M-ramp, was suggested (NEFSC, 2013, 2019), in which M was equaled to 0.2 in 1982–1988, then increased linearly to 0.4 between 1989 and 2003, and remained at 0.4 for 2004–2018.

Accordingly, seven scenarios of M dynamics were designed for our simulation. First, to be consistent with the current assessment of this stock, the current assumptions for GOM cod were included:

(1) Ms1 represented $M = 0.2$, constant among years;
(2) Ms2 represented M-ramp, varying among years;
(3) Ms3 adopted Pauly's empirical formula and used the average SST of GOM from 1982 to 2018 to estimate M, constant among years. This scenario represented a commonly used approach for estimating M when other methods are unavailable (Kenchington, 2014).

Ms1 and Ms3 fell into the category of stationary assumptions, whereas Ms2 represented the non-stationary assumptions. For the three scenarios, we used retrospective analysis to evaluate the performance of stock assessment model as the magnitude of retrospective errors (REs) is a critically important measure for quantifying stock assessment quality (Mohn, 1999). Retrospective patterns are consistent directional changes in assessment estimates of biomass or fishing mortality in a given year when additional years of data are added to an assessment (Deroba, 2014). The appearance of a retrospective pattern suggests that an assessment is subjected to bias for the terminal year of the assessment (Kilduff et al., 2009), with positive RE indicating overestimated results and negative RE pointing to underestimated results. A 7-year retrospective analysis was carried out for each model (Mohn, 1999):

$$RE_{SSB.t} = \frac{SSB_{t|data\ to\ year\ t} - SSB_{t|data\ to\ year\ t+1}}{SSB_{t|data\ to\ year\ t+1}}, \quad (1)$$

$$RE_{F.t} = \frac{F_{t|data\ to\ year\ t} - F_{t|data\ to\ year\ t+1}}{F_{t|data\ to\ year\ t+1}}, \quad (2)$$

$$RE_{SSB} = \left(\sum_{t=2018-7}^{2018} \frac{SSB_{t|data\ to\ year\ t} - SSB_{t|data\ to\ 2018}}{SSB_{t|data\ to\ year\ t}}\right)/7, \quad (3)$$

$$RE_{F} = \left(\sum_{t=2018-7}^{2018} \frac{F_{t|data\ to\ year\ t} - F_{t|data\ to\ 2018}}{F_{t|data\ to\ year\ t}}\right)/7, \quad (4)$$

where $SSB_{t|data\ to\ year\ t}$ and $F_{t|data\ to\ year\ t}$ are the estimated spawning stock biomass (SSB) and fishing mortality in year t using data up to year t, respectively.

To further understand the impact of non-stationary M on stock assessment, four temperature-dependent scenarios were designed to address the possible linear and non-linear relationships between SST and M, given that the true relationships remain unknown yet. As the summer temperatures are closely related to the survival of larval and juvenile cod and cod recruitment (Friedland et al., 2013), we used summer SST (average SST in June, July, and August) to develop M assumptions (**Supplementary Figure 1B**). Particularly, it was evident that high-temperature conditions in summer are correlated with a decrease in the survival rate of late-stage larvae for GOM cod (Pershing et al., 2015). To make the simulation scenarios comparable to the current assessment, these mean and variance of M in the four assumptions were set up according to M-ramp, in which M increased from 0.2 to 0.4 between the years 1988 and 2003 (NEFSC, 2013):

(4) Ms4 represented the linear relationship between SST and M. The linear relationship was fitted according to the M-ramp. Consideration of this situation is expected to further account for the effect of climate variability on stock assessment.
(5) Ms5 was similar to Ms4 in terms of the linear relationship, but accounted for the impact of highest temperature in summer. The parameters of the linear were also calculated according to M-ramp.
(6) Ms6 represented the non-linear relationship between SST and M, described by the West, Brown, and Enquist model (WBE, West et al., 1997, 1999) model. The WBE was used to describe the organismal metabolic rate that has a temperature dependence (Price et al., 2012). As M is related to metabolic rate (Peterson and Wroblewski, 1984), due to swimming abilities and encounter rates with predators (Jørgensen and Holt, 2013), we assumed that the natural mortality of GOM cod was also driven by temperature.
(7) Ms7 was similar to Ms6 but use the highest temperature in summer as SST, in order to account for the extreme impact from warming. The parameters of non-linear WBE model were also calculated according to M-ramp.

The related biological parameters used in M scenarios were obtained from the 2013 benchmark report including growth coefficient K, asymptotic length L_{∞} (NEFSC, 2013). The detailed description of different M scenarios is shown in **Table 1** and **Figure 1**.

Simulation Framework

The simulation framework used to evaluate the effects of different M scenarios on stock assessment and management was briefly described below (for further details, see Sun et al., 2019). The framework consisted of (i) an operating model to emulate the population dynamics of cod, (ii) a sub-model describing fleet dynamics under the operating model to allocate the total allowable catch (TAC), for which the catch of the GOM cod from 1982 to 2018 was used as TAC for the simulation year, (iii) an observation model to emulate the data collection process (i.e., catch data and survey abundance indices), and (iv) an age-structured assessment program model (ASAP; Legault and Restrepo, 1998) to conduct the stock assessment.

Operating Model

Operating model (OM) was the core part of the framework. In order to evaluate the rationality and practicality of non-stationary dynamics in natural mortality, the age-based

TABLE 1 | The description of three common assumptions of *M* and four non-stationary assumptions of M driven by SST.

M scenarios	Description	References
Commonly *M* assumptions		
Ms1 (Stationary *M*)	$M = 0.2$	NEFSC, 2019
Ms2 (Non-stationary *M*)	*M*-ramp, the early years of the assessment (1982–1988) assumed *M* equaled 0.2, then increased linearly to 0.4 between 1989 and 2003, and remained at 0.4 for the remaining years 2004—2018.	NEFSC, 2019
Ms3 (Stationary *M*)	*M* calculated by Pauly's empirical formula, $\ln M = -0.0152 - 0.279 \ln L_\infty + 0.6543 \ln K + 0.4634 \lg T$ in which L_∞ is asymptotic body length, K is growth parameter, and T is average SST of GOM from 1982 to 2018. L_∞ = 150.93 cm, K = 0.11 year^{-1} according to NEFSC (2013)	Pauly, 1980
Non-stationary assumptions driven by SST		
Ms4	$M = 0.110 \times SST - 0.960$. *M* calculated by the formula with yearly SST for each year.	Calculated from M-ramp
Ms5	$M = 0.087 \times SST - 1.173$. *M* calculated by the formula using the summer SST (average SST in June, July and August).	Calculated from M-ramp
Ms6	$M = M_0 W^{3/4} e^{-E/kT}$ where T is the absolute temperature (in degrees K), E is average activation energy (~0.6 eV), $W^{3/4}$ is the mass to the 3/4 power, and k is Boltzmann's constant (8.617×10^{-5}). We calculated $M_0 W^{3/4}$ through the least square method, $M_0 = 0.312$, $M_0 W^{3/4}$ = 13325644189 in this hypothesis. M calculated by the formula with yearly SST for each year.	Price et al., 2012; Calculated from M-ramp
Ms7	$M = M_0 W^{3/4} e^{-E/kT}$ $M_0 = 0.299$ and $M_0 W^{3/4}$ = 8521315335 in this hypothesis. M calculated by the formula using the summer SST for each year.	Price et al., 2012; Calculated from M-ramp

population dynamic models (Sun et al., 2019) were constructed in this study, with different assumptions to account for both stationary and non-stationary dynamics in *M*. The age-structured population dynamic models described (i) the abundance variation in age-structure, (ii) the total mortality which was acquired by summing up natural mortality and fishing mortality, (iii) the catch for each year which was obtained by accumulating catch from all age groups, and (iv) the Ricker stock–recruitment relationship (SRR) (Ricker, 1954) to describe the recruitment dynamics for cod stock which had been proven reliable for stock in the region (Fogarty et al., 2001). The detailed description of age-structured population dynamics was presented in **Supplementary Material** (age-based population dynamic model). The model generated age-specific parameters that include abundance, size, maturity, and mortality.

Stock Assessment

We conducted stock assessment of the stock using ASAP method according to the current stock assessment of GOM cod. ASAP assumes separable annual fishing mortality to estimate population sizes using forward projection, given catch-at-age and an index of abundance. To determine how population dynamics and stock status differed among different scenarios, the estimated SSB, age-1 recruitment, and fishing mortality (F) were used as indicators for comparative purposes. The age-1 recruitment was generated by the SRRs based on the assumption that the recruitment of the following year was dependent on the precedent year SSB.

The impacts of *M* assumption on the assessment scenarios were evaluated with respect to their effects on the estimates of stock status and fishing removals. Estimation error, calculated as follows, was used to measure error associated with abundance, SSB and F:

$$EE_y = \frac{\hat{A}_y - A_y^{true}}{A_y^{true}}, \quad (5)$$

where $\hat{A}_y$ is the estimated quantity, and A_y^{true} is the simulated "true" quantity in year y generate from OM. Age-specific estimation error was calculated for fishing mortality (EE_F) and abundance (EE_N), and yearly estimation error was calculated for SSB (EE_{SSB}) for all scenarios.

Moreover, the stock status, overfished and overfishing, was evaluated (Cordue, 2012; Guillotreau et al., 2017), and the corresponding probability was compared for different scenarios. To be consistent with the current assessment of this stock, we used $F_{40\%}$ (fishing mortality that would reduce the spawning biomass-per-recruit to 40% in a theoretically unfished population) for overfishing threshold, and the $SSB_{40\%}$ (the long-term equilibrium, corresponding to $F_{40\%}$) for overfished threshold, according to NEFSC (2019). Thus, target biological reference points (BRPs) were calculated including $F_{40\%}$ and $SSB_{40\%}$ in this study.

RESULTS

Retrospective Analysis

The commonly used *M* assumptions, Ms1–Ms3, were evaluated in the retrospective analysis of cod stock assessments. Non-stationary dynamics in natural mortality (Ms2) could effectively reduce REs of both SSB and F, demonstrated by minor RE_{SSB} and RE_F (RE_{SSB} = 0.293, RE_F = −0.161). Major RE_{SSB} and RE_F were found in Ms1 (RE_{SSB} = 0.518, RE_F = −0.288) and Ms3 (RE_{SSB} = 0.523, RE_F = −0.291)

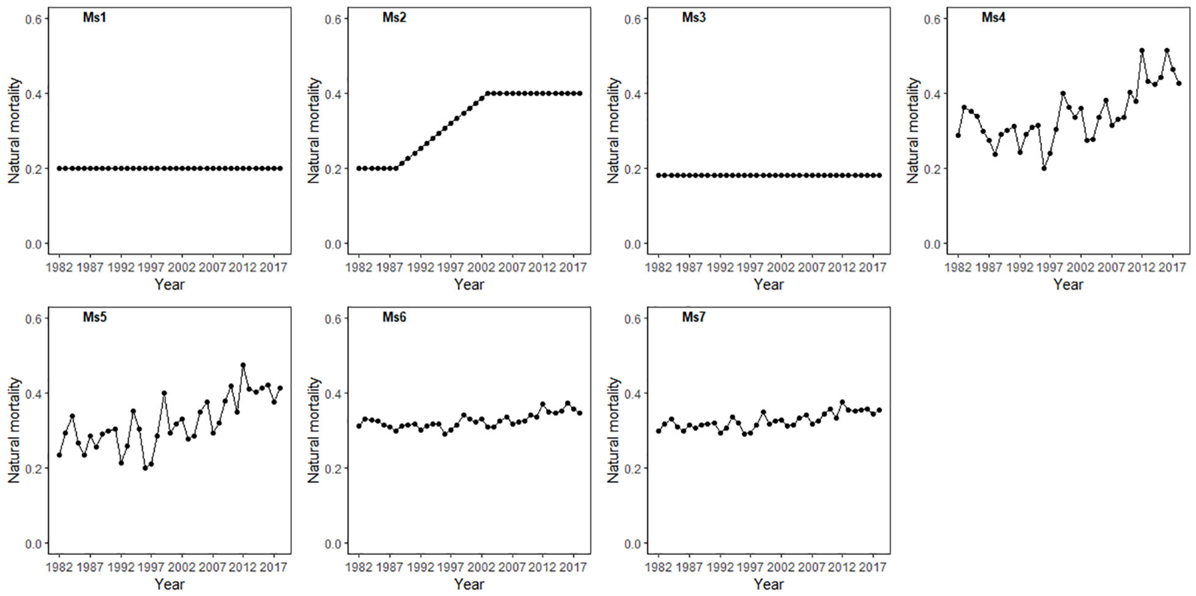

FIGURE 1 | Different scenarios of natural mortality (*M*) in simulation and stock assessment process. Ms1 and Ms3 fell into the category of stationary scenarios, and Ms2 and Ms4—Ms7 represented the non-stationary scenarios.

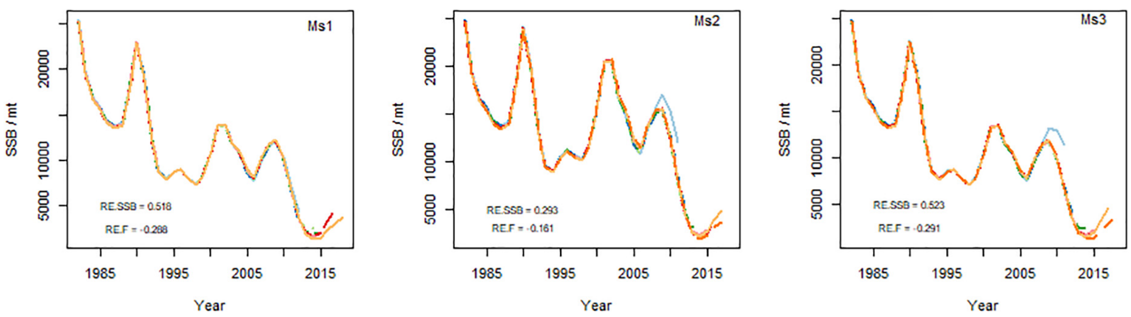

FIGURE 2 | Retrospective analyses of Atlantic cod stock assessment of SSB for Ms1, Ms2, and Ms3. The results were averaged for the last 7-years and compared among different M scenarios. Ms1 represented $M = 0.2$, Ms2 represented M-ramp, Ms3 adopted Pauly's empirical formula and used the average SST of GOM from 1982 to 2018 to estimate M. Different color represents different terminal year of input data.

(**Figure 2** and **Supplementary Table 2**). The result demonstrated the plausibility of the assumption that natural mortality has non-stationary dynamics under climate changes.

Estimation Errors in Population Dynamics

The simulated population trends were similar in all *M* assumptions (**Figure 3**). A dramatic overall decline in the GOM cod SSB was observed in the simulation time period (**Figure 3A**). The stock experienced high F from the mid-1980s onward, especially during early 1990s and 2010s. Since 2015, the fishing pressure on cod fishery has decreased drastically (**Figure 3B**). For production potential, the recruitment of cod has been at a low level since the 1990s (< 20,000 individuals) (**Figure 3C**). The declining SSB and the irrecoverable recruitment reflected the impact of climate change.

For the estimation errors, similar trends were observed for SSB in both stationary and non-stationary scenarios. EE_{SSB} was less than 10% before 2010, which suggests that the overall SSB was well estimated even though *M* assumption was different before 2010. However, it showed a clear overestimation after 2015 when the impact of climate change gradually intensifies, especially in stationary scenarios (Ms1 and Ms3) (**Figure 4**).

All assessment scenarios yielded certain estimation errors in fishing mortality, which was overestimated by approximately 10% on average. The younger (age 1 and age 2) and the older age groups (age 7, age 8, and age 9) tended to be less accurately estimated, compared to the age group from age 3 to 6 (**Figure 5A** and **Supplementary Table 3**). A similar pattern was identified in the estimation errors in age-specific abundance (**Figure 5B**). Non-stationary *M* produced better estimation results for SSB and F compared to the stationary scenario, whereas all scenarios led to similar estimation errors for age-specific abundance. In general,

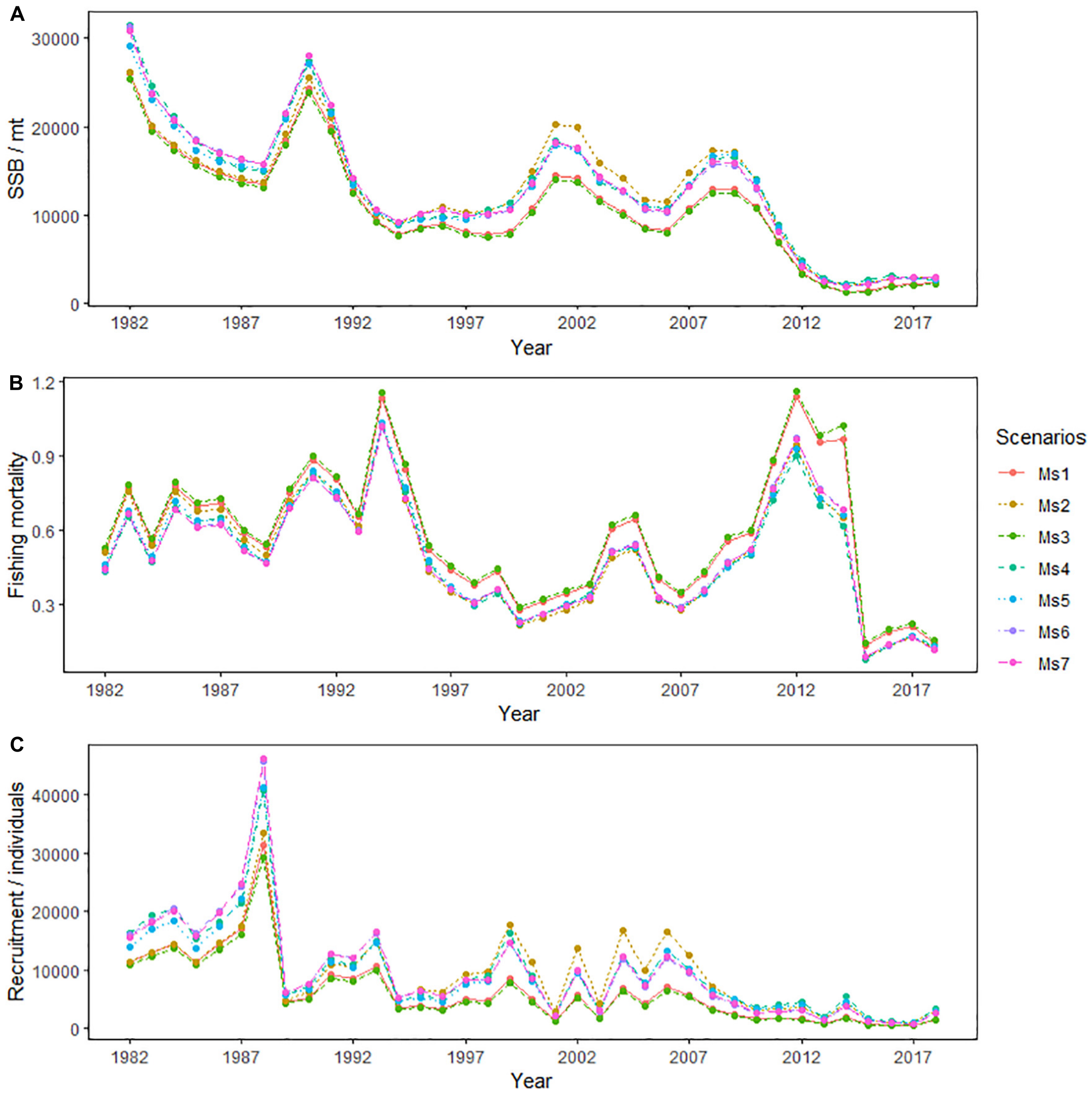

FIGURE 3 | The simulated SSB, fishing mortality (F), and age-1 recruitment (Recruitment) from 1982 to 2018 of different M scenarios. **(A)** SSB, **(B)** year-specific fishing mortality at full selectivity, **(C)** estimated trends in age-1 recruitment. Different colors and line types represent different M scenarios.

non-stationary scenario assuming a non-linear relationship between SST and *M* (Ms6 and Ms7) had the lowest estimation errors (**Supplementary Tables 3**, **4**).

Biological Reference Point and Stock Status

Large variations were found in the resulting values of estimated BRPs. Stationary scenarios (Ms1 and Ms3) tended to result in $F_{40\%}$ estimates lower than non-stationary scenarios (Ms2, Ms4–Ms7). Ms4 predicted the maximum value ($F_{40\%}$ = 0.44), whereas Ms3 tended to give the minimum values for $F_{40\%}$ (0.15). For SSB_{MSY}, the estimated results from the stationary scenarios were higher than those for the non-stationary scenarios. Ms3 predicted the maximum values for $SSB_{40\%}$ ($SSB_{40\%}$ = 37,329 mt), whereas Ms4 returned $SSB_{40\%}$ which is only a quarter of Ms3 estimate (8,679 mt). The average $F_{40\%}$ and $SSB_{40\%}$ among all scenarios were 0.31 and 17,995 mt, respectively (**Table 2**).

For stationary scenarios (Ms1 and Ms3), the risk that both overfishing and overfished occurred simultaneously ($P_{F>F40\% and SSB<SSB40\%}$) was 100% in the time period. For the non-stationary scenarios, the risk of overfishing from the early 1980s to the early 1990s was estimated as high in all five non-stationary scenarios, but the risk decreased somewhat around the mid-1990s, before increasing again in the early 2010s. After 2015, overfishing was not occurred but the population was estimated as overfished. The risk of simultaneously overfishing and overfished ($P_{F>F40\% and SSB<SSB40\%}$) mostly occurred in the early 2010s, and the probability was 24.32, 10.81, 16.22, 56.76, and 48.65% in the five non-stationary scenarios, respectively (**Figure 6** and **Supplementary Table 5**).

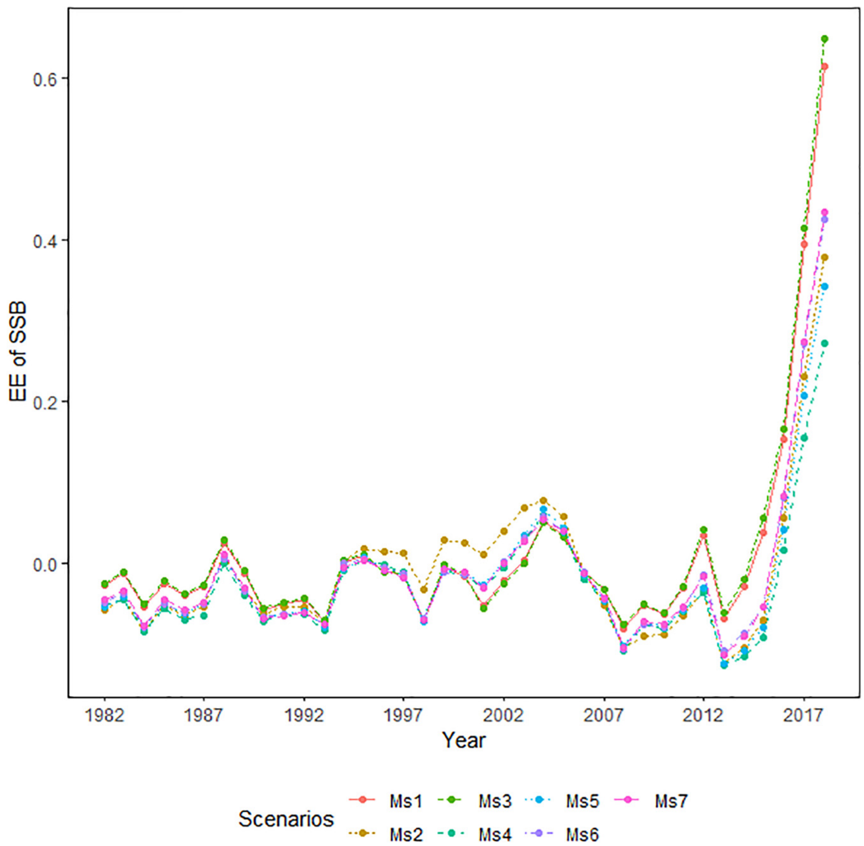

FIGURE 4 | Yearly relative estimation error (*EE*) of SSB from 1982 to 2018. The colors and line types represent different M scenarios.

DISCUSSION

It is generally believed that ignoring the effect of climate change when conducting stock assessment can lead to a biased view of stock status and hence to misleading management advice (Holling, 2001). This study used a simulation approach to identify the reliability of non-stationary dynamics in natural mortality under climate change and examined the potential impacts of climate variability on stock assessment through the non-stationary dynamics in *M* for GOM cod. We found that allowing non-stationary dynamics in *M* when conducting stock assessments could effectively reduce REs, and ignoring non-stationary dynamics in *M* lead to considerable biases in the estimation of SSB, F, and stock status. Different *M* assumptions greatly influence the outputs of stock assessment, which indicates the necessity to develop and adopt more accurate non-stationary dynamics in *M*.

The simulated population dynamics from the operating model showed that the GOM cod SSB and recruitment has continued to decline. In fact, strict management plans have been implemented for the cod fishery. For example, quota-based management was implemented in 2010 (Pershing et al., 2013) and the quotas were cut in 2013 (Harris, 2013). In addition, a revised 10-year rebuilding plan was implemented in 2014 (Patrick and Cope, 2014). However, cod stocks still failed to recover when placed under low fishing pressure. Overfishing is still the principal driver of the collapse of the Gulf of Maine cod, and reducing fishing pressure should be the priority for fishery management (Brander, 2018), but climate change also plays an important role in the decline of this stock (Drinkwater, 2002; Chaput, 2011), which prompts managers to strengthen management strategies progressively in response to the failure of fishery recovery under climate change.

In retrospective analysis, Ms3 gave a minor RE than Ms1, and similar results were obtained from the stock assessment report of GOM cod (NEFSC, 2019), in which *M* = 0.2 had a major RE whereas M-ramp had a minor RE. These results further illustrated the reliability of non-stationary *M* assumption in age-structure models. The results also implicated an advantage to incorporating non-stationary dynamics in *M* for the reduction of REs. Ms4 showed the best performance for retrospective analysis among all scenarios (**Supplementary Table 2**), which indicates that assuming a linear relationship between annual SST and natural mortality could improve the stock assessment for GOM cod.

Retrospective patterns in stock assessment results are a notable problem for fisheries management (Hurtado-Ferro et al., 2015). One way to reduce REs arising from changes in population processes over time is to allow a process to vary within the assessment method (Stewart and Martell, 2014). According to the results of retrospective analysis, incorporating the dynamics in *M*

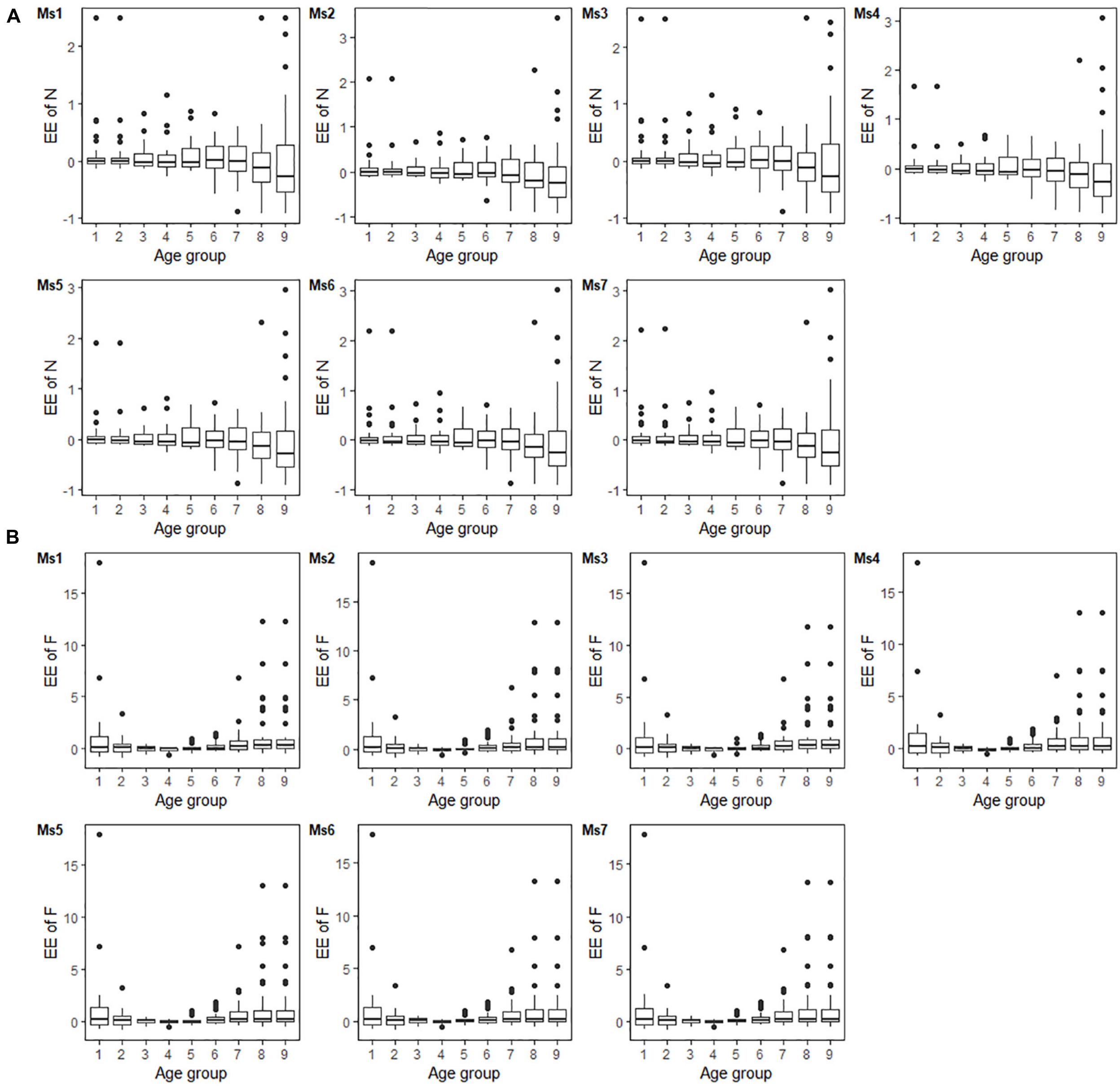

FIGURE 5 | Age-specific relative estimation error (*EE*) of **(A)** population abundance (EE_N) and **(B)** fishing mortality (EE_F) of GOM cod in seven M Scenarios.

to account for climate variability can effectively reduce biases in stock assessment. Although temporal trends in natural mortality have been observed for the eastern Georges Bank Atlantic cod assessment (Wang and O'Brien, 2012) and the GOM Atlantic cod assessment (e.g., Ms2) (NEFSC, 2013), the current stock assessment only uses M-ramp scenario to address retrospective patterns without realistic basis (Legault and Palmer, 2016). In addition, the assessment results of Northern cod used VPA model also proved that *M* has been variable, but the same result was not observed when using a state-space model (Rose and Walters, 2019). Our study provides some alternatives in this regard.

The results showed that the population dynamics was overestimation in stationary scenarios when the impact of climate change gradually intensifies, which indicates the unreliability of stationary *M* assumption under the situation of climate change. The results of estimating stock status showed that considering non-stationary *M* in stock assessment can make the results of the evaluation more in line with the actual population dynamics. This may happen because stationary *M* assumptions ignore the changes such as shifting distribution, vulnerable interspecific relationships, and predation under climate change (Dutil and Lambert, 2000; Suda et al., 2005; Cheung et al., 2010; Guan et al., 2017b). All of the above illustrate the plausibility of the non-stationary *M* assumption caused by climate variability, which indicates that allowing these assumptions of *M* to weaken the retrospective bias is acceptable (Szuwalski and Hollowed, 2016).

TABLE 2 | The estimated biological reference points for each scenario.

Scenario	$F_{40\%}$	$SSB_{40\%}$/mt
Ms1	0.17	32,481
Ms2	0.39	10,524
Ms3	0.15	37,329
Ms4	0.44	8,679
Ms5	0.40	9,328
Ms6	0.31	14,286
Ms7	0.33	13,341
Average	0.31	17,995

Large variations were shown in estimated biological reference points and stock status, which indicates that neglecting non-stationary dynamics in *M* can lead to either under- or overestimating the population status, which results in missing fishing opportunity or putting future fishery production at a greater risk of overfishing and being overfished. The natural mortality assumption has a large role here, and the error in management reference points is related directly to the error associated with *M* (Punt et al., 2021). In light of the downward trends in production and rebuilding potential of GOM cod, incorporating the non-stationary dynamics of *M* could be an alternative way to improve the current GOM cod stock assessment. Owing to the difficulty in predicting non-stationary dynamics in *M*, model ensemble provides a solution that balances the trade-off between best model fitting and model-selection uncertainty (Katsanevakis, 2006; Jiao et al., 2009). Based upon model averaging, we suggest using the average $SSB_{40\%}$, $F_{40\%}$ of all *M* assumptions as BRPs to ensure a precautionary approach in setting cod TAC or quotas.

In addition to the annual average temperature, linking high-temperature condition of SST to natural mortality (Ms5 and Ms7) was also found to be reliable in simulation analysis. The rationality of those assumptions was further reinforced, considering that extreme temperature events will undoubtedly become more frequent with the progression of climate change (Rijnsdorp et al., 2009). The consequences of high-temperature condition include profoundly negative impacts on fisheries as well as the productivity of fish populations (Oliver et al., 2018). Further, the oceans are warming even faster than originally predicted (Cheng et al., 2019). Effective scientific and precautionary management strategies are more important now than ever in adapting to climate change. More accurate stock projections are required as well as more robust harvest strategies are expected (Ianelli et al., 2011).

As this study only aims to improve the stock management practice by considering non-stationary dynamics associated with *M*, we did not consider the effect of climate change on other population dynamic processes in the operating models and stock assessment. For example, the non-stationary dynamics of species distribution, growth, maturation, and recruitment were not taken into consideration in this study. These processes can also vary in response to climate-driven changes in the environment (Biro et al., 2007; Tallack, 2009; Guan et al., 2017a). For

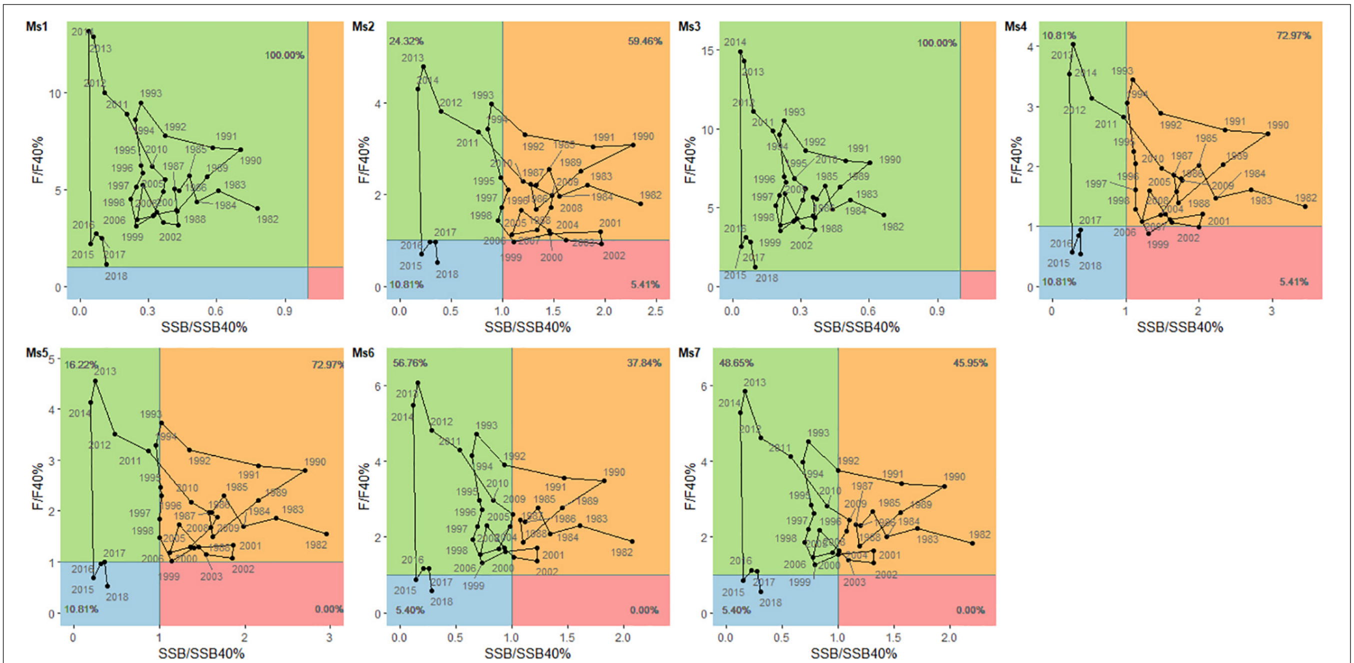

FIGURE 6 | The estimated stock status for GOM cod from 1982 to 2018 for different M scenarios. Ms1 and Ms3 fell into the category of stationary scenarios, and Ms2 and Ms4–Ms7 represented the non-stationary scenarios. Different color blocks represent different stock status. Green area means overfishing and overfished simultaneously ($F > F_{40\%}$, $SSB < SSB_{40\%}$), red area means neither overfishing nor overfished ($F < F_{40\%}$, $SSB > SSB_{40\%}$); orange area means stock was overfishing but not overfished ($F > F_{40\%}$, $SSB > SSB_{40\%}$); blue area means stock was not overfishing but stock was overfished ($F < F_{40\%}$, $SSB > SSB_{40\%}$).

GOM cod, conclusions have been drawn that the warming temperature results in a marked decrease of catch probabilities in a specified area (Fogarty et al., 2008) and change in stock structure and distribution (Guan et al., 2017b). The increase of *M* lines up with declines in cod stock's main food supply, especially the pelagic capelin (Regular et al., 2022). Ignoring such effects would lead to a significant bias in recruitment estimates (Pershing et al., 2015). These processes should be considered in further studies.

Our study provided several alternative methods for incorporating non-stationary dynamics of *M* induced by climate variability into stock assessment. The conclusions drawn from this study are not intended to replace the stock assessment for GOM cod. Instead, the stock is used as a case study to highlight the plausibility and applicability of non-stationary dynamics in the stock assessment and management, thus contributing a potential tool for climate change vulnerability assessments of marine fishes.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: https://apps-nefsc.fisheries.noaa.gov/saw/sasi/sasi_report.php.

AUTHOR CONTRIBUTIONS

NC: conceptualization, methodology, data analysis, and writing–original manuscript. MS: conceptualization, methodology, and writing–review. CZ: methodology, editing, writing–review, and funding acquisition. YR: writing-review and funding acquisition. YC: conceptualization and writing–review. All authors contributed to the manuscript preparation.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.845787/full#supplementary-material

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