Modeling Atlantic sea scallop (Placopecten magellanicus) scope for growth on the Northeast U.S. Shelf

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Abstract

Atlantic sea scallops support one of the most valuable fisheries in the eastern United States. The scallop population is susceptible to climate-related environmental stress. Assessing and projecting climate impacts rely on the fundamental understanding of scallop ecophysiology, including the influences of temperature and food supply on its energy balance and growth potential. In this study, we developed a scope for growth (SFG) model driven by high-resolution hydrodynamic and biological models to assess the spatial and seasonal variability of scallop energy dynamics. The overall SFG on the Northeast U.S. Shelf is higher in May-June and lower in January-February, with substantial spatial heterogeneity. In the Mid-Atlantic Bight (MAB), negative SFG occurs from July to October due to strong thermal stress. Particulate organic matter in detrital form is an important food source for scallops, with higher/lower contribution in the cold/warm seasons, respectively. Warming and food deficiency induce a noticeable contraction of suitable scallop habitats in the MAB, while their impacts on Georges Bank are insignificant. Known seasonal spawning patterns and observed growth rates in these regions match the patterns of SFG generated by the model. The sensitivity of SFG to the variations in food and temperature increases with scallop size. Large scallops are more likely to experience low or negative SFGs than smaller ones, implying that the habitats shrink as scallops grow older/bigger. This study provides key information about scallop growth potential and biogeography from the perspective of energy balance, thus helping the development of adaptive fisheries management strategies.

Keywords: Atlantic sea scallop, Northeast U.S. Shelf, scope for growth, seasonality, food availability, thermal stress, habitats

1. Introduction

The Atlantic sea scallop (Placopecten magellanicus) supports one of the most economically important fisheries on the Northeast U.S. Shelf (NES) (Cooley et al., 2015; Lee et al., 2017). The U.S. sea scallop fishery generated average annual ex-vessel revenues of over $500 million in the 2010s, about quadruple those during the 1990s (NMFS, 2014). The severe overfishing from the 1970s to the mid-1990s led to the depletion of sea scallops and other groundfish species, resulting in losses of billions of dollars to the New England economy (Edwards and Murawski, 1993). Since 1994, a series of fishery management regulations, including fishing effort reductions, gear and crew restrictions, and closed areas were implemented to rebuild the depleted sea scallop stocks (Hart and Rago, 2006). The biological features of sea scallops (e.g., rapid growth, low natural mortality and limited mobility) allow them to benefit greatly from spatial management schemes in the fishing grounds (Hart, 2003). Because of these measures, the abundance of sea scallops recovered rapidly and was fully rebuilt by 2001 (Hart and Rago, 2006).

The habitats of the Atlantic sea scallop range from the north shore of the Gulf of St. Lawrence to Cape Hatteras, North Carolina (Stewart and Arnold, 1994). The primary harvest areas in the northeast U.S. are Georges Bank (GB), the Great South Channel (GSC) and the Mid-Atlantic Bight (MAB) with bottom depth between 35 and 120 m (Fig. 1; Hart and Rago, 2006). Sea scallops also occur in estuaries and embayments along the Gulf of Maine and Canada, where water depths can be as shallow as 2 m (Naidu and Anderson, 1984; Hart and Chute, 2004; Torre et al., 2019). The highest scallop population densities can be found in areas with suitable temperature, salinity, substrate, high larvae retention, along with low predation pressure and high food availability (Tremblay and Sinclair, 1992; Hart and Chute, 2004; Hart 2006; Harris et al., 2018).

Sea scallop growth shows strong spatial heterogeneity on the NES, with some of the highest growth rates on GB (Stewart and Arnold, 1994). The linear mixed-effect model developed by Hart and Chute (2009) indicated that scallop populations in the MAB have smaller asymptotic shell heights than those in GB, although the speed to reach asymptotic size (so called Brody growth coefficient) in the MAB is relatively higher. Sea scallops in both GB and the MAB have smaller asymptotic shell heights in deeper water due to limited food supply (Hart and Chute, 2009). The impacts of many biotic and abiotic conditions (e.g., water temperature, food availability, latitude, bottom depth, flow velocity, fishing pressure, and age) on the growth of scallops have been extensively investigated in previous studies (e.g., MacDonald and Thompson, 1985; Shumway et al., 1987; Wildish et al., 1987; Thouzeau et al., 1991; Harris and Stokesbury, 2006; Hart and Chute, 2009). Among all the environmental factors, temperature and food are likely to be the most important ones for scallop growth (Cranford et al., 1998). The optimal temperature for the growth of adult scallops occurs at 10–15 ºC, and mortality increases greatly as the bottom temperature approaches 21 ºC (Stewart and Arnold, 1994). Compared with water temperature, food availability may be even more crucial because growth can be virtually independent of temperature once food supply is sufficient (MacDonald and Thompson, 1986). The principal food source for scallops is thought to be phytoplankton, supplemented by detritus and attached microbes (e.g., bacteria) when phytoplankton becomes limiting (Shumway et al., 1987; Grant and Cranford, 1991). The analysis of gut contents indicated that the diet of scallops contains more than 20 species of algae ranging from 10-350 μm, as well as miscellaneous items including detritus and other particulate organic matter (e.g., pollen grains; Shumway et al., 1987). The abundance of different diet components varies in the cross-shelf direction: sea scallops in coastal areas and bays can feed on seagrass detritus, and benthic and pelagic food items are equally important; for offshore sea scallops, the importance of benthic food items outweighs that of pelagic ones, and resuspended organic material can be a crucial food supplement (Shumway et al., 1987; Grant and Cranford, 1991). The seasonality of algal species composition ingested by sea scallops coincides with their bloom periods, indicating sea scallops are opportunistic feeders that take advantage of available organic matter in their surrounding habitats (Shumway et al., 1987). The feeding behavior of sea scallops can be greatly influenced by food quality (particulate organic matter content per unit dry weight of diet particles). A high concentration of inorganic particles in food (i.e., low food quality) can inhibit scallop nutrition by reducing absorption efficiency, whereas the scallop diet utilization can be enhanced by exceptionally low concentration of inorganic particles (< 0.5 mg/l; Cranford and Gordon, 1992).

Scope for growth (SFG) represents the residual energy available for growth and reproduction after all metabolic demands have been met (Bayne and Newell, 1983). As a proxy for the growth potential, SFG has been widely applied to assess the responses of scallop growth to environmental stress and physiological traits (e.g., MacDonald and Thompson, 1986; Grant and Cranford, 1991; Bacon, 1994; MacDonald et al., 1998). Short-term laboratory feeding experiments revealed that the SFG approaches an asymptote with increasing food quantity and quality

(MacDonald et al., 1998). Although the annual cycle of SFG generally has low or negative values in the cold season and higher values in the warm season (MacDonald and Thompson, 1986), high SFGs can be detected at both high and low bottom temperatures, implying that the SFG can be influenced by other factors (e.g., food availability) rather than temperature alone (Bayne and Newell, 1983; MacDonald and Thompson, 1986).

Although many previous studies based on the laboratory experiments shed light on the response of SFG to the ambient environments, its spatiotemporal variations over the primary sea scallop habitats on the NES and the effects of multiple stressors are not well quantified. In this study, we constructed a scallop SFG model driven by high-resolution hydrodynamic and biological models, which are capable of reproducing the concentrations of major food items (phytoplankton and detritus) for sea scallops, as well as the water temperature near the bottom (Chen et al., 2011; Zang et al., 2021). The objectives of this study are to (1) reveal the seasonality and spatial heterogeneity of SFG for sea scallops on the NES, (2) quantify the respective contributions of different food sources to scallop energy balance, and (3) explore the impacts of warming and changing food availability on the SFG of scallops. Two contrasting years in the 2000s (normal year 2010 vs. warm year 2012) were selected for comparative numerical simulations in order to assess the sensitivity of SFG for sea scallops of different sizes to changes in food availability and temperature.

2. Data and Methods

2.1 Bottom temperature and food concentration

The bottom temperature used in this study was extracted from the outputs of Finite Volume Community Ocean Model–Gulf of Maine Version 3 (FVCOM–GOM3). FVCOM–GOM3 is a hydrodynamic model nested within the FVCOM–Global model (Chen et al., 2003, 2011, 2021a). The model domain covers the NES from the Scotian Shelf to the MAB and adjacent slope and basin regions. The horizontal grid resolution varies from 0.5 to 10 km depending on the complexity of topography (Chen et al., 2011). The model grid is discretized vertically into 45 layers using a hybrid terrain-following coordinate. Mooring and ship measurements of temperature, salinity, and current profiles are assimilated into FVCOM–GOM3 to improve the quality of its outputs (Chen et al., 2009). Many physical variables of FVCOM–GOM3, including water level, temperature, salinity, and current fields, have been calibrated carefully in previous studies (Chen et al., 2011; Sun et al., 2013, 2016; Li et al., 2015). The daily bottom temperature was estimated by averaging the hourly mean outputs of FVCOM–GOM3. The FVCOM–GOM3 model outputs were downloaded from the data server of the University of Massachusetts Dartmouth (http://fvcom.smast.umassd.edu) (Fig. S1).

The daily concentrations of bottom phytoplankton and detritus were extracted from the outputs of the 3-D lower trophic marine food web model (Zang et al., 2021). This nitrogen-based biological model is driven by FVCOM–GOM3 in an offline coupling mode. The model has ten functional groups, including two types of phytoplankton (small phytoplankton (SP) and large phytoplankton (LP)) and one type of large detritus (LD). Multiple physical and biogeochemical processes regulating the dynamics of phytoplankton and detritus (e.g., horizontal advection, vertical mixing and sinking, resuspension, phytoplankton growth, decomposition) are explicitly resolved in the model to reproduce their concentrations on the NES. Readers are referred to Stock and Dunne (2010), Song et al. (2010, 2011) and Zang et al. (2021) for more details regarding the model's structure and governing equations. The comparisons between the model results and observations in Zang et al. (2021) indicated that the marine food web model can reasonably capture the seasonal and spatial patterns of phytoplankton on the NES, although it is difficult to evaluate the distribution of detrital organic matter near the bottom due to the lack of observational data.

2.2 Sea scallop SFG model

We applied a sea scallop SFG model to simulate the spatiotemporal variability of energy balance by following the carbon (C) budget over the primary scallop fishing grounds from GB to the MAB. The SFG (unit: mg C/ind/day) of an individual scallop can be estimated by the difference between the energy gain through absorption and the loss due to respiration:

$$SFG = 24 \cdot (AR_{Phy} + AR_{Det} - \frac{RR}{32} \cdot RQ \cdot 12)$$

Where AR_{Phy} and AR_{Det} are the absorption rates for phytoplankton and detritus, respectively (unit: mg C/ind/hr). RR represents the respiration rate of sea scallops (mg O_2/ind/hr). RQ is the molar ratio of CO_2/O_2. Absorption rates are calculated as the product of clearance rate ($CR_{Phy(Det)}$), absorption efficiency ($AE_{Phy(Det)}$), and the concentrations of phytoplankton and detritus in the bottom layer ($C_{Phy(Det)}$):

$$AR_{Phy(Det)} = CR_{Phy(Det)} \cdot AE_{Phy(Det)} \cdot C_{Phy(Det)}$$

The absorption efficiency varies greatly with dietary quality, and previous studies suggested that the food quality of phytoplankton is better than that of detritus (Grant and Cranford, 1991), so we adopted higher absorption efficiency for phytoplankton (AE_{Phy}) and lower absorption efficiency for detritus (AE_{Det}; see Table. 1 for more details). Phytoplankton and detritus concentrations in the biological model are the values at the center of bottom grid cells, which are several to more than 100 cm above bed (cmab). Since scallops live at the water-sediment interface and a strong vertical gradient of particulate matter concentration exists near the bottom boundary layer, directly applying the biological model results to the SFG model might underestimate the absorption rate and the SFG. Here, phytoplankton and detritus concentrations 1 cmab are estimated using the Rouse profile to represent food condition for scallops (Rouse, 1937; Swart, 1976):

$$C_{Phy(Det)} = C_{Phy(Det),model} \left(\frac{z}{z_{model}}\right)^{\frac{-W_{s,Phy(Det)}}{\kappa u_*}}$$

Where $C_{Phy,model}$ and $C_{Det,model}$ are the simulated bottom phytoplankton and detritus concentrations. z_{model} is the height of the bottom grid center above the sea floor. z is the half of scallop shell width (i.e., distance from the sea bed to the scallop valve opening; 1 cmab). $W_{s,Phy}$ and $W_{s,Det}$ represent the settling velocities of phytoplankton and detritus, respectively. κ is the von Karman constant. The shear velocity u_* is estimated following the law of the wall:

$$u_* = \frac{\kappa \cdot U(z_{model})}{\ln\left(\frac{z_{model}}{z_0}\right)}$$

Where U is the current speed at elevation z_{model}. z_0 is the apparent bottom roughness as inferred from the height of the zero intercept of $U(z_{model})$.

The clearance rates for phytoplankton and detritus ($CR_{Phy(Det)}$) are regulated by ambient water temperature and individual dry tissue weight (DTW):

$$CR_{Phy(Det)} = CR_{std,Phy(Det)} \cdot f_{CR}(T) \cdot (\frac{DTW}{DTW_{std}})^{b_{CR}}$$

Where $CR_{std,phy(Det)}$ is the clearance rate of scallops with standard dry tissue weight (DTW_{std}) at the reference temperature (T_{ref}). b_{CR} is a consistent weight exponent for clearance. $f_{CR}(T)$ represents the temperature limiting factor based on the Arrhenius relationship with a temperature tolerance term (Kooijman, 2010; Fig. 2a):

$$f_{CR}(T) = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \cdot \frac{[1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_{L\_CR}}\right) + \exp\left(\frac{T_{AH}}{T_{H\_CR}} - \frac{T_{AH}}{T}\right)]^{-1}}{[1 + \exp\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_{L\_CR}}\right) + \exp\left(\frac{T_{AH}}{T_{H\_CR}} - \frac{T_{AH}}{T_{ref}}\right)]^{-1}}$$

Where T_A and T_{ref} are the Arrhenius temperature and reference temperature, respectively. T_{L_CR} and T_{H_CR} relate to the lower and upper boundaries of the tolerance range for clearance, and T_{AL} and T_{AH} are the Arrhenius temperatures for the rate of decrease at both boundaries. Compared with other monotonous temperature relationships (e.g., Q_{10} relationship), the Arrhenius relationship can well represent the negative effects of thermal stress on scallop physiological features at a temperature above the optimal range.

The respiration rate of sea scallops (RR) varies with temperature ($f_{RR}(T)$) and scallop dry tissue weight:

$$RR = RR_{std} \cdot f_{RR}(T) \cdot (\frac{DTW}{DTW_{std}})^{b_{RR}}$$

Where RR_{std} is the respiration rate of scallops with standard dry tissue weight (DTW_{std}) at the reference temperature (T_{ref}). b_{RR} is a consistent weight exponent for respiration. Arrhenius relationship with the temperature tolerance term is applied to estimate the impact of thermal stress on respiration rate ($f_{RR}(T)$; Fig. 2b):

$$f_{RR}(T) = \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \cdot \frac{[1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_{L\_RR}}\right) + \exp\left(\frac{T_{AH}}{T_{H\_RR}} - \frac{T_{AH}}{T}\right)]^{-1}}{[1 + \exp\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_{L\_RR}}\right) + \exp\left(\frac{T_{AH}}{T_{H\_RR}} - \frac{T_{AH}}{T_{ref}}\right)]^{-1}}$$

Where T_{L_RR} and T_{H_RR} are the lower and upper boundaries of the tolerance range for respiration. Values for the model parameters mentioned above and related references are listed in Table 1. The MATLAB-based SFG model source code and parameters are available at http://ulysse2.whoi.edu:8080/thredds/catalog/data/zzang/Project_Scallop/catalog.html.

2.3 Experimental design

We designed both the realistic 2-dimensional (2-D; longitude-latitude) experiments covering the entire NES and the idealized 0-dimensional (0-D) experiments to explore the responses of SFG to the variations of ambient environments and scallop size. Daily sea scallop absorption rate, clearance rate, and SFG on the NES were simulated using daily averaged water temperature and food concentration extracted from the hydrodynamic and biological model results in 2010 (Figs. S1-S4), with the same horizontal spatial resolution as the FVCOM–GOM3 (0.5 to 10 km). The bimonthly mean absorption rate, clearance rate, and SFG were estimated based on daily results. We chose the year 2010 as the benchmark run because its water temperature in 2010 can overall represent the thermal climatology before the significant warming since 2012 (Kleisner et al., 2017; Chen et al., 2021b), and the main purpose of the benchmark run is to establish a baseline for the sea scallop energy budget. We estimated bimonthly mean sea scallop absorption rate, clearance rate, SFG, and their standard deviations using daily model outputs to reveal their seasonality and spatial heterogeneity.

To estimate the impact of warming on scallop energy balance, a sensitivity test was conducted based on the bottom temperature in 2012, which has been widely recognized as a "warm year" on the NES (Pershing et al., 2015; Chen et al., 2021b). Phytoplankton and detritus concentrations in both the benchmark run and the sensitivity test were based on the biological model results in 2010, so the SFG difference between 2010 and 2012 was induced only by temperature variation. The DTW of scallop in the 2-D experiments was assigned as 5 g (4-year-old adult; MacDonald, 1986).

Food availability is another important factor regulating scallop energy balance and growth potential. The comparisons of bottom phytoplankton and detritus between 2010 and 2012 demonstrate strong spatiotemporal variations of scallop food concentration on the NES (Figs. S5, S6 and S7). To quantitatively examine the response of SFG to the variation of food availability, we conducted four 2-D sensitivity tests in 2010 with 20% and 40% increase/decrease in phytoplankton and detritus concentrations.

Idealized 0-D experiments were also used for sensitivity testing. We estimated the SFG of sea scallops under different food concentration and bottom temperature scenarios. To simplify the simulations, only one type of food representing the mixture of phytoplankton and detritus was used in these 0-D simulations. The clearance rate and absorption efficiency for the mixed food were specified as the mean values for phytoplankton and detritus. Food concentration increased from 0 to 6 mmol N m^{-3} with 0.2 mmol N m^{-3} interval, and temperature ranged from 0 to 21 ºC with 1 ºC interval. Different DTW values were applied in the cases (DTW = 1 g, 5 g, 10 g, and 15 g) to examine the influence of scallop size on SFG.

3. Results

3.1 Spatiotemporal patterns of absorption rate, respiration rate, and SFG

The seasonal variations of the scallop absorption rate for phytoplankton and its standard deviation over the NES (Figs. 3 and S8) were correlated with phytoplankton concentration (Figs. S2 and S3), with elevated magnitude from March to August (peak value > 40 mg C/ind/day and standard deviations > 20 mg C/ind/day) and lower magnitude in the rest of the year (peak value < 20 mg C/ind/day and standard deviations < 10 mg C/ind/day). The correlation coefficient between the spatially averaged bimonthly absorption rate for phytoplankton and phytoplankton concentration was 0.93 (p=0.008). Regions with higher absorption rates were primarily located nearshore in most seasons. An exception was found from July to October, during which the enhanced absorption mainly occurred in the deeper MAB (> 35 m; Fig. 3d and 3e). High bottom temperatures exceeding the optimal range for clearance rate resulted in a lower absorption rate on the inner shelf (Figs. 3 and S1), indicating the importance of thermal stress in modulating scallop growth and spatial distribution.

Due to the differences in productivity and resuspension intensity, spatial heterogeneity of LD on the NES was substantial, with higher concentration in GB and the northern MAB and lower concentration in the southern MAB (Zang et al., 2021; Fig. S4). The absorption rates for LD in the southern MAB were lower than that in the northern MAB and GB throughout the year (Fig. 4). Within the southern MAB, higher absorption rates for LD (> 20 mg C/ind/day) occurred from November to June due to the joint effects of favorable bottom temperature and LD supply (Fig. 4a, 4b, 4c and 4f). Over GB and the northern MAB, the absorption rates for LD exceeded 25 mg C/ind/day for the entire year with the exception at the edge of GB (Fig. 4). Relatively high standard deviations of the absorption rate for LD (> 10 mg C/ind/day) mainly distributed in the northern MAB and along the southern flank of GB (Fig. S9), implying the great variabilities of LD availability and physical environments in these regions.

To quantitatively estimate the relative importance of different food sources for sea scallops, we compared the bimonthly absorption rates for phytoplankton (SP + LP) and LD (Fig. 5). The comparison of absorption rates revealed that detritus was the primary food source for scallops over the entire NES from November to February due to low phytoplankton concentrations (Fig. 5a and 5f). With the increase of primary production from March to October, the relative importance of phytoplankton in food composition was elevated, suggesting the improved food quality for scallops (Fig. 5b, 5c, 5d, and 5e). Over GB and the northern MAB, the absorption rate for LD outweighed that for phytoplankton year round. In the southern MAB, however, phytoplankton was the predominant food item from March to October (Fig. 5).

The respiration rate of scallops at a given size was only regulated by temperature in our model, so its seasonality matched that of bottom temperature (Fig. S1). The peak respiration rate occurred in September and October (> 18 mg C/ind/day), and the low rate occurred in March and April (< 12 mg C/ind/day) (Figs. 6 and S1). An exception was found in July and August, when very high bottom temperatures in the southern MAB nearshore regions resulted in the dramatic decline of respiration rate to almost zero (Fig. 6d). This relationship between bottom temperature and respiration rate suggested that the exceptional high temperature imposed strong negative effects on the metabolism of scallops, making the coastal southern MAB inhospitable for scallop growth and survival. Compared with the standard deviations of absorption rates for phytoplankton and LD, the standard deviations of the respiration rate were lower with limited spatial heterogeneity throughout the year (0-8 mg C/ind/day; Fig. S10).

The bimonthly spatiotemporal patterns of scallop SFG depending: 1) solely on phytoplankton and 2) on both phytoplankton and detritus are shown in Figs. 7 and 8, respectively. When phytoplankton was treated as the only food source for scallops, the long duration of negative SFG covering the primary scallop fishing grounds suggested that phytoplankton alone was insufficient to meet the energy demands of sea scallops (Fig. 7). The spatiotemporal variability of SFG standard deviation was similar to that of absorption rate for phytoplankton (Figs. S8 and S11), suggesting that the food uptake was responsible for the variations of sea scallop energy balance.

With both phytoplankton and detritus included, the SFG increased dramatically and remained positive in most regions throughout the year (Fig. 8). In January and February, the SFG was low and homogeneous over the entire shelf, ranging from 20 to 30 mg C/ind/day with relatively low standard deviations (2-15 mg C/ind/day) (Figs. 8a and S12a). Subsequently, an increase in SFG primarily occurred over GB, the northern MAB, and the coastal southern MAB from March to June (Fig. 8b and 8c). The SFG over NES reached a maximum in May and June, at more than 60 mg C/ind/day on the inner shelf (Fig. 8c). In July and August, the SFG became negative in coastal areas due to high temperatures and at the shelf break due to low food availability (Fig. 8d). In September and October, negative SFG in the MAB covered larger areas, limiting the regions with positive SFG to a belt between the 35 and 100 m isobaths (Fig. 8e). The standard deviations of SFG on the NES were high in nearshore regions and the southern flank of GB from March to October (> 20 mg C/ind/day; Fig. S12). The SFG became positive again with lower standard deviations over the entire NES in November and December (Figs. 8f and S12f) due to the decreased energy loss associated with lower respiration and increased absorption rate for LD.

3.2 Impacts of warming and food availability on scallop SFG over the NES

To explore the impacts of warming on the energy balance of scallops, we compared the bottom temperature and the 2-D simulated SFG in 2010 (normal year) and 2012 (warm year). Here, we only analyzed the temperature and SFG differences between these two years from July to October, during which thermal stress was strongest (Fig. 9). Bimonthly mean bottom temperature from July to October was ~2 ºC higher in 2012 than in 2010, except for the shelf break and central GB in July-August and Hudson shelf valley in September-October (Fig. 9a and 9b). In July and August, the coastal region with negative SFG expanded seaward in 2012, implying the potential shrinking of scallop habitats due to strong thermal limitation (yellow color in Fig. 9c). The regions with high uncertainties (i.e., SFG > 0 or SFG < 0 is not statistically significant in 2010 or 2012 based on one-tailed z-test) only covered small areas in the MAB (grey color in Fig. 9c). The spatial coverages of negative SFG at the MAB shelf break in 2010 and 2012 were almost identical due to minor differences in bottom temperature between these two years (Fig. 9a and 9c). In September and October, the seaward expansion of negative SFG in 2012 could be found in the MAB between 38.5 ºN and 40 ºN (Fig. 9d). The regions with high uncertainties are mainly distributed on the MAB inner shelf with very low sea scallop densities (grey color in Fig. 9d). Although warming in 2012 was dominant over GB, its influence on the SFG spatial distribution was minor (Fig. 9c and 9d), implying that temperature might not be the primary limiting factor over GB.

Decreasing the food concentration at the bottom by 20% caused only a slight change in the region with positive SFGs in July-August in the MAB (Fig. 10a). In September-October, a 20% decrease in food concentration caused a noticeable reduction of the positive SFG region in the MAB towards the mid-shelf (Fig. 10b). A 40% decrease in food concentration led to the dramatic contraction of the positive SFG region, and the entire southern MAB had negative SFG in September-October (Fig. 10c and 10d). The results of sensitivity tests with increasing food concentrations showed that the positive SFG region only changed marginally with additional food supply in July-August (Fig. 10e and 10g), while enhanced food supply in September-October contributed to an expansion of positive SFG in both onshore and offshore directions in the MAB (green area in Fig. 10f and 10h). The spatial distribution of SFG over GB was less sensitive to the variation of food concentration than that in the MAB.

3.3 Sensitivity of SFG to food, temperature, and scallop size

The results of the idealized 0-D simulations were analyzed to examine the influences of food abundance, temperature, and scallop size on the SFG (Fig. 11). The responses of SFG to food and temperature variations were very similar for scallops in different weight classes: the SFG increased with food concentration and peaked between 12 and 15 °C (Fig. 11). The sensitivity of SFG to food concentration variation increased with bottom temperature from 0 °C to the upper limit of the optimal range (around 15 °C). Once temperature exceeded the optimal range, the SFG dropped sharply and became negative. The SFG was always negative when food concentration was lower than 1 mmol N m^{-3} or the bottom temperature exceeded 18 °C (Fig. 11). The range of SFG increased with scallop size (1 DTW: -6.5–29.0 mg C/ind/day; 5 DTW: -23.7–86.6 mg C/ind/day; 10 DTW: -41.2–138.5 mg C/ind/day; 15 DTW: -57.0–182.2 mg C/ind/day), suggesting the energy balances of large scallops were more sensitive to the variations of ambient environments than small scallops. The boundaries between positive and negative SFGs for different weight classes (black solid lines in Fig. 11) illustrated that the SFG for larger sea scallops became negative in more temperature and food conditions. The model results suggested that young age classes have larger habitats, thus explaining the absence of adults in the southern MAB scallop habitats (Fig. S13; Hart et al., 2020).

4. Discussion

4.1 Impacts of warming on scallop population dynamics and biogeography

The scallop habitats from GB to the MAB have been experiencing rapid warming over the last several decades due to the synergistic effects of multiple physical processes (e.g., along-shelf transport, air-sea heat exchange, and shelf-basin scale interactions; Shearman and Lentz, 2010; Chen et al., 2014; Saba et al., 2016). Given the apparent vulnerability of scallops to high temperature, climate-driven rapid warming is expected to profoundly influence their population dynamics and biogeography (Hare et al., 2016; Lowen et al., 2019). A comprehensive understanding of warming impact has long been recognized as critical in terms of scallop fisheries management and conservation planning in a changing climate (Cooley et al., 2015; Hare et al., 2016; Chen et al., 2021b).

One of the most dramatic effects of warming is the changes in scallop distribution. The comparison of SFG model results between a normal year (2010) and a warm year (2012) shows the offshore expansion of the negative SFG region, suggesting habitat shrinkage and potential reduction of total abundance of scallops in the southern MAB under rapid warming (Fig. 9). The period from summer to early fall should gain more attention in the future due to the strong thermal limitation in the MAB (Fig. 8d and 8e). Unlike our simulated offshore shift of scallop habitats in the MAB and the marginal change over GB due to warming (Fig. 9), an ensemble species distribution model (SDM) based on the projected warming scenario (NOAA GFDL CM2.6; Saba et al., 2016) over the next eight decades indicate the northward shift of scallop habitat, with a marked decline of the habitat suitability over GB and the MAB (Tanaka et al., 2020). The discrepancy between our study and the SDM results can be attributed to different time scales the two studies focus on: the SFG model only tests the ramification of one-year warming with ~ 2 ºC bottom temperature increase (Fig. 9a and 9b), while the SDM projection represents the impacts of ~ 4-5 ºC warming over the next eighty years (Saba et al., 2016; Kleisner et al., 2017). If we apply the long-term temperature projection to the SFG model, the extra 2-3 ºC temperature increase would result in further contraction of scallop habitats, and the entire MAB and GB could become unsuitable for scallops as well. Also, the SDM projection represents scallop habitat shift due to the changes in abiotic factors alone (i.e., bottom temperature and salinity), while holding all other top-down and bottom-up variables constant (Tanaka et al., 2020). Our SFG model, however, incorporates the impacts of both temperature and food availability. According to the results of the idealized 0-D tests, SFG becomes more sensitive to food concentration with increasing temperature from 0 to 15 ºC, and sufficient food supply may help scallops to compensate for the energy loss due to respiration and provide extra energy for growth and reproduction within the optimal temperature range. Given the importance of food supply in scallop energy balance (MacDonald and Thompson, 1986), the inclusion of the food effect in our study could explain the different responses of scallop habitat changes to warming in the two models.

Warming influences the spatial distribution and abundance of scallops via not only modulating the physiological processes of scallops, but also regulating the phenology and magnitude of spawning. Scallop spawning over the NES has a strong semi-annual cycle with spatial heterogeneity: spawning on GB is more dominant and consistent in fall (September-October), and relatively protracted and erratic spawning occurs in spring (May-June; Barber et al., 1988; Dibacco et al., 1995; Thompson et al., 2014). In the MAB, spring spawning is often stronger with a longer duration than the fall spawning (Kirkley and DuPaul, 1991; Schmitzer et al., 1991). Spawning timing and magnitude can be related to temperature fluctuation, because rapid temperature change acts as a cue for spawning induction (Culliney, 1974; Parsons et al., 1992). Under the influence of longer summer duration associated with climate-related warming, the rapid change of bottom temperature will occur earlier during the spring warm-up and later during the fall cool-off (Thomas et al., 2017). If this trend continues in the future, the spawning season will be shifted to wintertime when stronger onshore and southward transport is more frequent on the NES, which might expose scallop larvae to more coastal and southern regions that are often associated with higher thermal-induced mortality (Munroe et al., 2018; Fuchs et al., 2020).

Warming can also affect scallop spawning magnitude by changing food availability and uptake (Barber et al., 1988). Food plays a vital role in scallop spawning because gamete production requires a great deal of energy (MacDonald and Thompson, 1986). The energy uptake by scallops and related growth rate shows strong seasonality with dramatic spatial heterogeneity. Oxygen isotope results indicate the growth of adult scallops in GB and GSC is faster in late summer and fall than that in winter due to a better food supply associated with high primary production (Chute et al., 2012). Similarly, tagged scallops that mainly experienced warmer conditions grew faster than ones that experienced primarily cooler waters (Harris and Stokesbury, 2006). The energy reserved in the warm season supports the subsequent strong fall spawning in GB and GSC. Unlike GB and GSC, primary production in the MAB is high during late fall and winter, and that can provide enough energy for scallop rapid growth in the cold season and strong spring spawning in the next year (Brust et al., 2001; Chute et al., 2012). The simulated energy balance represented by SFG likely explains the difference of spawning magnitude between GB/GSC and the MAB, with higher SFG and stronger spawning in summer and fall in the GB/GSC area and higher SFG and stronger spawning in winter and spring in the MAB (Fig. 8). Since temperature can also influence food availability via many direct and indirect physical and biogeochemical processes (e.g., phytoplankton growth, stratification/mixing, detritus decomposition), it is reasonable to speculate that the warming-induced food supply variability will substantially impact scallop spawning magnitude and thus population size in the future.

Climate-related warming can influence scallop energy balance and abundance by changing the dispersal of scallop larvae during the pelagic stage. The results of an individual-based larval modeling study presented in Chen et al. (2021) showed that the enhancement of warming-induced clockwise gyre circulation limits scallop larval transport from GB to the MAB, resulting in higher retention rate and scallop recruitment over GB. Moreover, warming can shorten the duration of larvae stage and consequently, transport distance and mortality by accelerating the development of larvae (Tremblay et al., 1994; Gilbert et al., 2010). Given the joint effects of these processes, warming can potentially weaken the connectivity between different scallop habitats and enhance local retention and larval survival. For those self-sustaining scallop populations (e.g., GB and GSC; Tremblay et al., 1994; Chen et al., 2021), low connectivity between different habitats under rapid warming is favorable for biomass accumulation in upstream regions due to higher proportion of local settlement and development. Conversely, populations highly dependent on larval inputs from upstream regions (e.g., the Virginia Beach region; Munroe et al., 2018) might experience reduced recruitment owing to the decrease of external larvae supply. If so, the spatial heterogeneity of total energy demands for scallops on the NES might become stronger: for the habitats with elevated retention rate, the increasing population size and scallop density can raise the total energy demands and increase food limitation; the total energy demands in the habitats relying on external larval supply, however, can be reduced due to lower scallop abundance.

Warming can also affect sea scallop biogeography and population dynamics by altering top-down forcing. The major predators of sea scallops include sea stars, crabs, lobsters, and demersal fish species. The negative correlation between the density of the sea star Astropecten americanus, a predator of small invertebrates including juvenile scallops, and scallop recruitment in the MAB suggests that the top-down forcing can strongly influence scallop density (Hart, 2006; Shank et al., 2012), and is an important factor determining the offshore boundary location of scallop habitats (Hart, 2006; Lowen et al., 2019). Given the increase of sea star density and the decrease of scallop recruitment with water depth > 75 m in the MAB (Hart, 2006), the potential seaward shift of habitats under warming can expose scallop populations to higher predation pressure, thereby causing the reduction in abundance. Furthermore, laboratory experiments show that the predation rate of scallops by sea stars Asterias vulgaris and crabs Cancer irroratus increases significantly with temperature due to the intensified predator activities and decreased effectiveness of scallop escape response (Barbeau and Scheibling, 1994). In our model, the use of SFG to represent the suitability of scallop habitat only takes thermal stress and food condition into account. A future comprehensive study including the thermal responses of scallop physiology and phenology in different life stages and top-down forcing can provide a better understanding of warming's impact on scallop population dynamics and spatial distribution.

4.2 Food condition as a critical component in the climate impact assessment

Like other aquatic ectotherms, scallops need to increase their energy investment in response to climate-related environmental stress, such as warming and acidification. As stress level increases, the elevated energy demand for basal maintenance will affect life-history performance and energy fluxes within individuals (Sokolova, 2021). Food condition (e.g., food quantity and quality) is a critical component in the energy balance for scallops. Since stressor exposure often decreases the amount and rate of energy assimilation, a constraint in food availability could exacerbate the negative impact. On the other hand, favorable feeding conditions could enhance energy uptake by scallops and thus increase stress tolerance. In the case of ocean acidification (OA), bivalves like scallops consume more energy to cope with OA due to the changes in metabolism, acid-base regulation, and calcification (Saba et al., 2019). A reduction of energy available for growth and reproduction due to OA-induced extra-energy costs can be detrimental to scallop population growth (Cooley et al., 2015; Rheuban et al., 2018). However, laboratory and field measurements indicate that negative effects of OA on some bivalve species (e.g., Chilean scallop, king scallop, and mussel) can be offset by sufficient food supply, suggesting the vital role of food condition in scallop growth and survival under OA (Melzner et al., 2011; Sanders et al., 2013; Thomsen et al., 2013; Ramajo et al., 2016). Negative impacts of other stressors like warming can also be reduced by additional food supply. The coupling between food concentration and scallop asymptotic size in offshore direction suggests the overwhelming effects of food availability on scallop growth (Hart and Chute, 2009). To the best of our knowledge, only a few studies have examined the simultaneous limitations of food availability and other stressors (e.g., warming) on sea scallop, although their effects have been tested separately in short-term laboratory experiments (e.g., MacDonald and Thompson, 1985; Cranford and Grant, 1990; Grant and Cranford, 1991; Desrosiers et al., 1996). Future studies are needed to fill these knowledge gaps with a focus on the climate-induced multi-stressor impact on sea scallop population dynamics and biogeography.

4.3 Implications for scallop fishery management under climate change

The primary goal of fisheries management is to provide the greatest overall benefits by maximizing yield and preventing overfishing (Lee et al., 2019; Hart et al., 2020). The implementation of effective scallop fishery management on the Northeast U.S. Shelf since 1994 has dramatically increased scallop total biomass, landings, and prices (Hart and Rago, 2006; Lee et al., 2019). Given the climate-induced rapid warming in the NES sea scallop habitats over the last several decades, an adaptive fishery management plan can potentially offset to some degree the negative consequences of climate change (Gaines et al., 2018; Rheuban et al., 2018).

Sea scallop populations have greatly benefited from rotational and long term closures due to the sedentary nature of adult sea scallops (Hart, 2003; Hart and Rago, 2006; Cooley et al., 2015; Lee et al., 2019). However, as scallop distributions shift due to the changing climate, these areas may need to be moved. As suggested by our study and Tanaka et al. (2020), the scallop habitat suitability in terms of SFG and physical conditions can vary greatly from seasonal to decadal scales. Thus, establishing adaptive management strategies with long-term effectiveness becomes critical in protecting scallop stocks in the future, and it is essential to take multiple physical and biological stressors into account when designing management plans. As an effective tool to estimate the spatiotemporal variation of growth potential, our model explicitly resolves scallop SFG with high spatial and temporal resolutions, which can provide valuable information for improving the current fisheries management and spatial planning from the perspective of energy balance and growth potential.

The increased frequency of episodic events induced by climate change can change physical and biogeochemical conditions over scallop habitats rapidly, making the scallop fishery management even more challenging. There has been a general westward shift for the Gulf Stream destabilization point with increased basin-shelf interactions (Andres, 2016). Consequently, the MAB has been more frequently influenced by the direct intrusion of Gulf Stream and the shedding of anticyclonic warm-core rings (Gawarkiewicz et al., 2012; Gangopadhyay et al., 2019).The intrusion of oligotrophic Gulf Stream water at the surface can markedly reduce primary production on the shelf and food availability for scallops (Shumway et al., 1987; Zhang and Gawarkiewicz, 2015). On the other hand, recent field measurements and model results present the existence of subsurface diatom hotspots associated with the upwelling of nutrient-rich deep Gulf Stream water (Oliver et al., 2021). Such productivity enhancement over the shelf break might facilitate the offshore expansion of scallop habitats, especially considering the strong food limitation along the offshore boundary of the suitable scallop habitat. The rapid shift of the thermal regime induced by slope water intrusion can potentially impact the scallop population dynamics at short time scales. The hydrographic surveys and moored observations on the southern New England Shelf show that the onshore intrusion of near bottom slope water can stretch onto the inner shelf, with rapid temperature increase from 12 to 16 ºC lasting more than 3 weeks (Ullman et al., 2014). Since the optimal temperature for scallop growth is between 10 and 15 ºC, the intrusion of bottom slope water can impose stronger thermal stress on local scallop populations. Seasonally, more warm-core rings are produced in summer and fall, which overlap with the scallop spawning season on GB and the MAB (Silver et al., 2021). Given that spawning is triggered by abrupt temperature change (Culliney, 1974; Parsons et al., 1992), the intrusion of warm slope water could affect the scallop reproduction schedule and thus the connectivity between different habitats. How to incorporate the information of short-term oceanographic dynamics into management considerations remains a challenge, and warrants future investigation.

Our scope for growth model results indicate that larger scallops are more vulnerable to the unfavorable food and thermal conditions than smaller individuals, as has also been found in other bivalve species (e.g., Shumway, 1983; Yuan et al., 2010; Munroe et al., 2013a, 2013b; Rybovich et al., 2016). The enhanced sensitivity to stressors of larger bivalves is due to the imbalance between oxygen uptake and supply: the gill surface area per body weight decreases with size, and decreased tissue oxygen, and transition to anaerobic metabolism occurs earlier and more substantially in larger individuals under harsh conditions (Shumway, 1983; Pörtner, 2002, 2010). Since the fishery mainly takes large scallops, the effects of climate change may be more detrimental to the harvestable portion of the biomass. Additionally, large scallops disproportionally contribute to the reproduction due to the increase of sea scallop fecundity with age and shell height (Schmitzer et al., 1991; Hart and Chute, 2004; Hennen and Hart, 2012). Thus, the loss of large scallops due to environmental stressors could not only reduce the harvestable biomass directly but also the reproductive potential and subsequent recruitment.

4.4 Model limitations and future work

Although the model results in the present study yielded valuable insights into the factors modulating the spatiotemporal patterns of scallop SFG over the NES and the effects of food availability and rapid warming on biogeographic distributions, this work had some limitations which suggest future directions of inquiry. First, scallops were assumed to only consume phytoplankton and detritus, while other food items such as microzooplankton and bacteria were not taken into account (Shumway et al., 1987; Grant and Cranford, 1991). Estimation of food availability for scallops in the bottom boundary layer was based on simple parameterization schemes and warrant further improvements in future studies. The concentrations of phytoplankton and detritus at 1cmab are estimated using the Rouse profile with constant settling velocities. The settling velocities of phytoplankton and detritus in the ocean, however, are influenced by many biotic and abiotic factors (e.g., flocculation/deflocculation, swimming behavior, morphological features of cells; Bienfang et al., 1982; Kamykowski et al., 1992; Friedrichs and Scully, 2007). Thus, the simplified settling velocity scheme used in both the biological model and the scallop SFG model might result in uncertainties in food concentrations at the bottom. Additionally, the resuspension of detritus on the seabed was estimated using current–induced bottom shear stress, whereas both field observations and models suggested strong wave–induced resuspension during energetic events (e.g., winter storms and hurricanes; Miles et al., 2015). Given the important role of resuspension in scallop food quality and quantity (Grant et al., 1997; Cranford et al., 1998; Witbaard et al., 2001), future modelling efforts should better resolve particulate matter resuspension and its influence on scallop feeding behavior via coupling with wave models.

Second, the variations of clearance and respiration rates with temperature in our SFG model were parameterized based on the previous laboratory experiments. However, these experiments were conducted below the optimal temperature range. The lack of measurements at higher temperatures made the physiological responses to thermal stress weakly constrained, and model uncertainties could increase at higher bottom temperatures. Given the importance of temperature in shaping the boundaries of scallop habitats and SFG estimations, future lab experiments should focus more on the thermal stress by measuring clearance and respiration rates at higher temperatures that include the entire optimal range.

A high potential SFG does not always correlate with high scallop abundance. This is evident from the discrepancies between the SFG model results and the spatial distribution of scallops based on the dredge survey data over central GB and southern New England Shelf, where the SFG is positive in our simulation but scallops are largely absent (Figs. 1 and 8). The discrepancies suggest that there are factors beyond food and temperature that control the scallop population dynamics in these two regions. One possible reason for the low scallop abundance over the center of GB and the southern New England Shelf could be the instability of substrate. The estimation of sediment stability index suggests that central GB with bottom depth < 60 m is very unstable due to strong disturbance associated with tidal currents (Harris et al., 2012, 2018). There is a substantial portion of the southern New England Shelf with fine grained sediment, which is unfavorable for the settlement of scallop larvae (Dalyander et al., 2013). Scallop larvae may delay settlement for several days until suitable substrates are encountered (Culliney, 1974). Other factors, such as predation and fishing pressure, could also significantly affect scallop abundance (e.g., Hart, 2006; Shank et al., 2012). Thus, model-based estimation of scallop distributions needs to include multiple biotic and abiotic factors that impact sea scallops at different life stages.

5. Conclusions

An Atlantic sea scallop SFG model was developed and applied to the NES to explore the spatiotemporal variability of energy balance at a seasonal scale. The thermal stress based on the Arrhenius relationship and the food limitation depending on the simulated phytoplankton and detritus concentrations were included to examine their joint effects on the SFG. The results indicated that the overall SFG was highest in May-June, and relatively low in January-February. The SFG in the MAB showed different seasonality with negative values from July to October due to the substantial thermal stress. Phytoplankton alone was insufficient to meet the energy demands of sea scallops. Detritus was an important food source for scallops, and its contribution to energy gain was more important under colder temperatures. The suitability of scallop habitats represented by the SFG was more susceptible to the variations of temperature and food supply in the MAB than that in GB. The sensitivity of SFG to food availability increased with temperature from 0 to 15 ºC, and the SFG of large scallops was more sensitive to the changing environments than that of small scallops. Given the important role of food and thermal conditions in assessing the scallop energy balance and growth potential, future studies and the development of fisheries management strategies should consider multi-stressor effects (e.g., warming, food supply, and OA) on different time scales to address the changing scallop biogeography and population dynamics under climate change.

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Conflict of interest: There is no conflict of interest to state in this research.

Author contributions: Z.Z. and R.J. developed the idea and the SFG model. C.C. and L.Z. analyzed the physical model results. Z.Z. and R.J. developed the marine food web model and processed its results. D.R.H. and C.S.D. assisted with the conceptualization of this study. All authors contributed to drafting and improving the manuscript.

Data availability statement: The data that support the findings of this study can be shared upon request to the corresponding author.

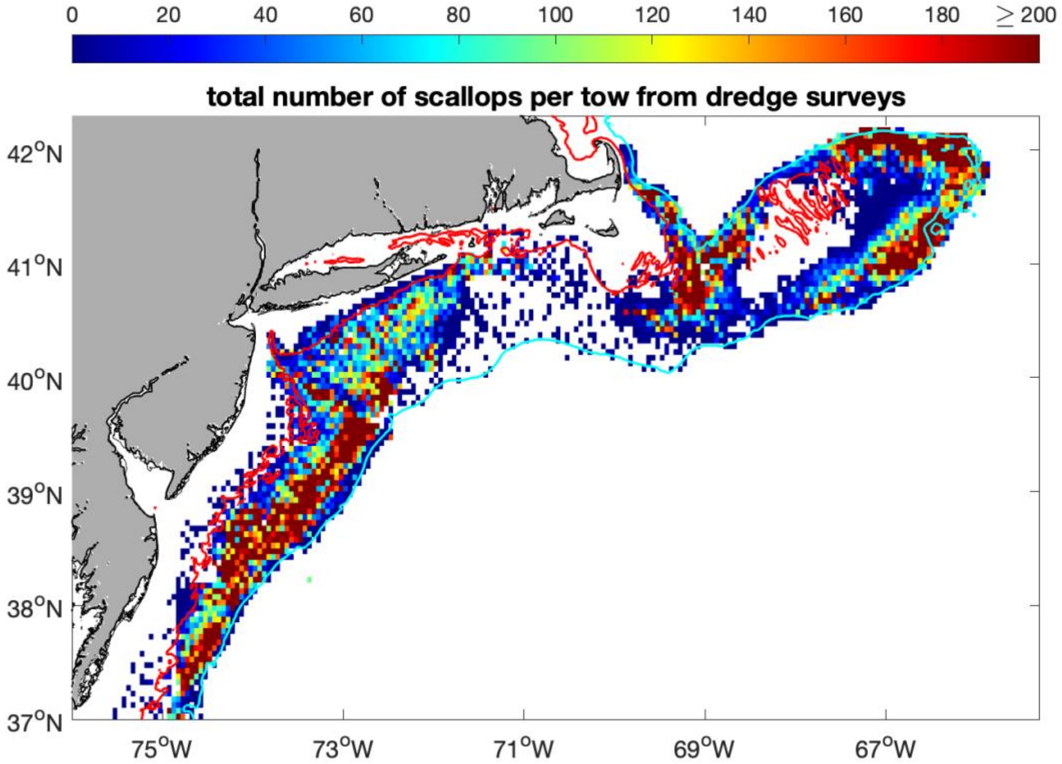

Fig. 1. The climatology of Atlantic sea scallop density (unit: number of scallops per tow) over the Northeast U.S. Shelf from Georges Bank to the Mid-Atlantic Bight from 1978 to 2017 (data source: dredge survey data provided by NOAA and Canadian scallop survey data provided by the Department of Fisheries and Oceans, Canada). The original dredge survey data are projected onto a grid with 0.05°×0.05° resolution. The color in each grid represents the mean scallop density based on all the survey data in the grid. The red and blue lines are 35 and 100 m isobaths, respectively.

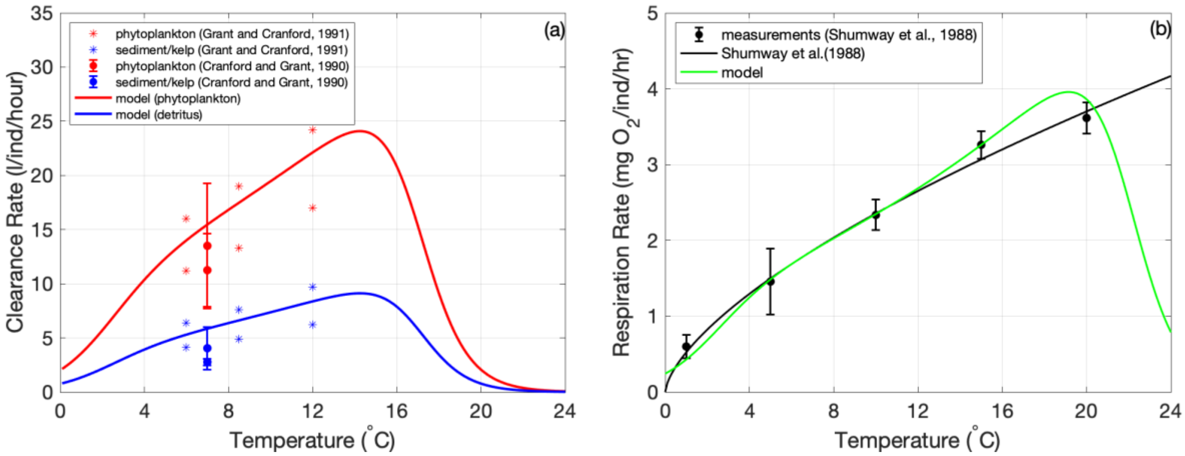

Fig. 2. The variations of clearance rate (left) and respiration rate (right) with temperature for a standard scallop individual (DTW = 6.3 g; Grant and Cranford, (1991)). In the left panel, the red and blue lines represent the clearance rate for phytoplankton and detritus, respectively. Asterisks and dots are the measured clearance rate in Grant and Cranford (1991) and Cranford and Grant (1990). In the right panel, the black line is the fitting curve based on the measurements (black dots) in Shumway et al. (1988). The green line is the respiration rate of Atlantic sea scallop used in the SFG model. Error bars in the figure represent one standard deviation.

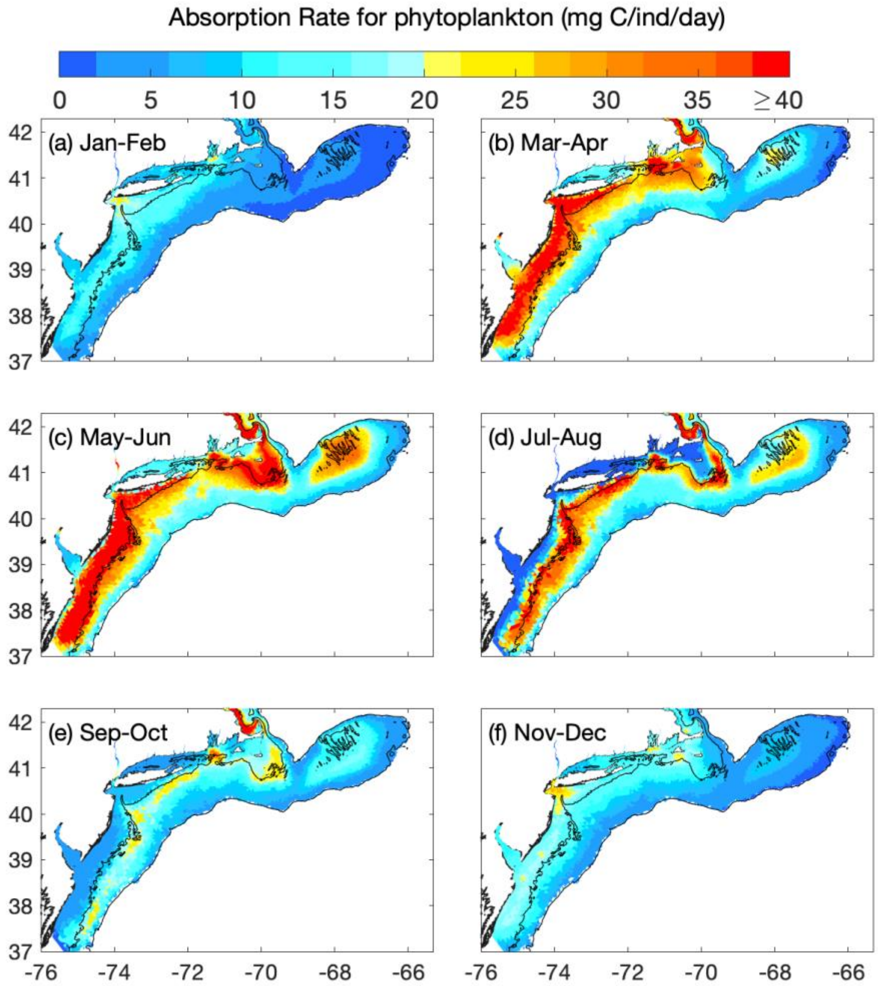

Fig. 3. Bimonthly sea scallop absorption rate for phytoplankton (SP+LP) over the NES (scallop DTW = 5 g).

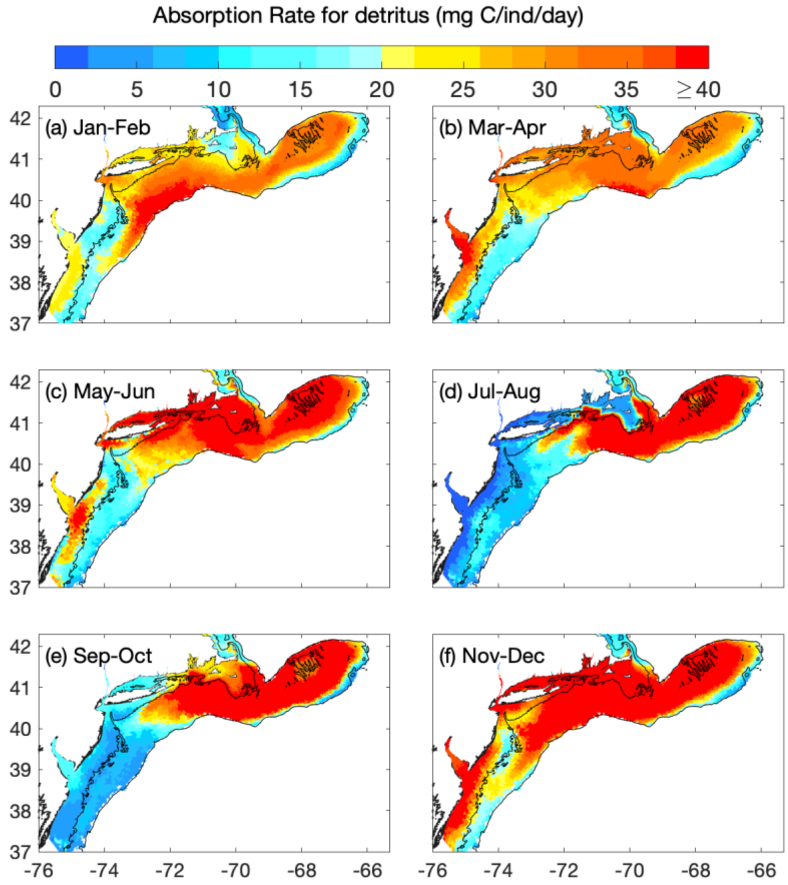

Fig. 4. Bimonthly sea scallop absorption rate for detritus over the NES (scallop DTW = 5 g).

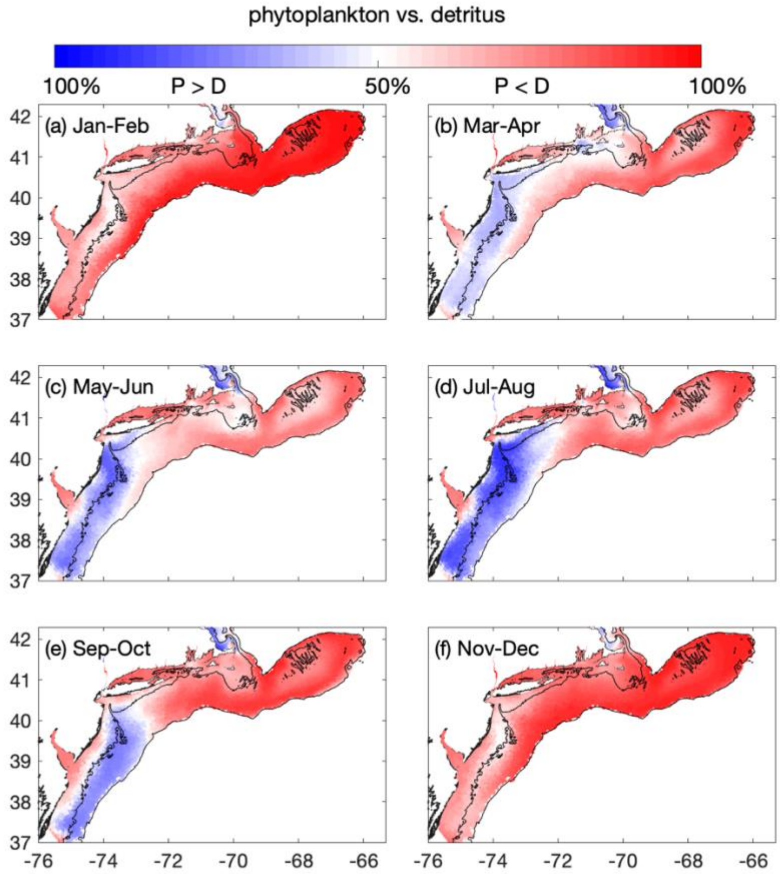

Fig. 5. Bimonthly comparison between absorption rate for phytoplankton and detritus over the NES. Blue/red color indicates that phytoplankton/detritus is more important (higher absorption rate).

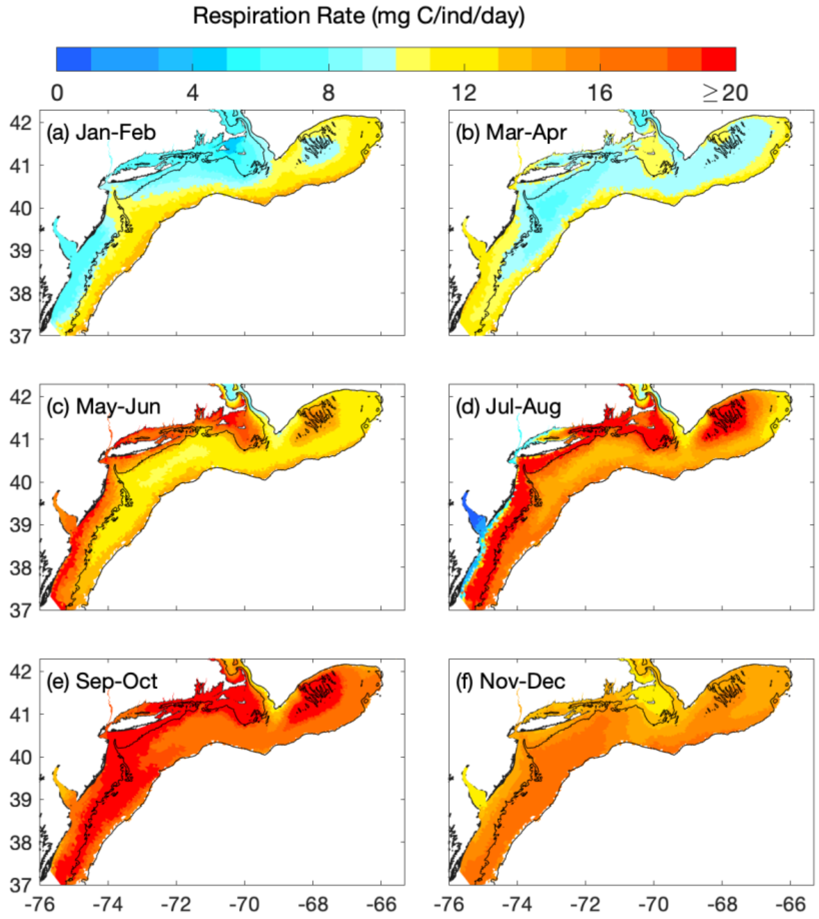

Fig. 6. Bimonthly sea scallop respiration rate over the NES (scallop DTW = 5 g).

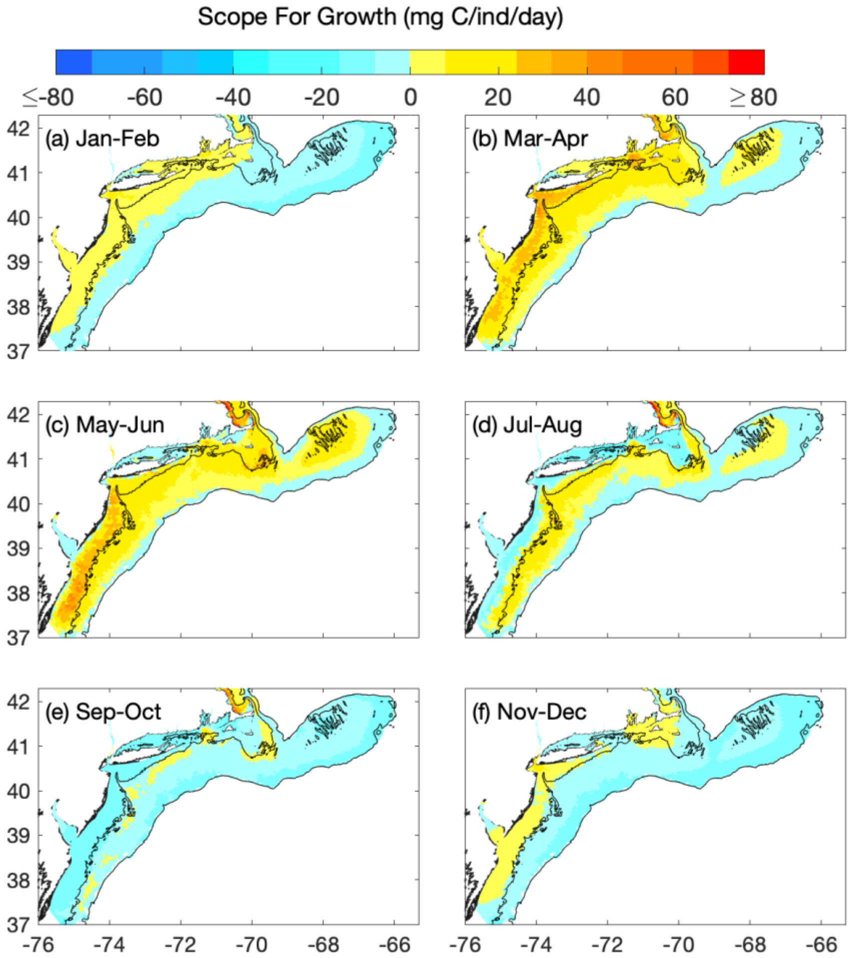

Fig. 7. Bimonthly sea scallop SFG over the NES feeding only on phytoplankton (warm color: SFG > 0 mg C/ind/day; cold color: SFG < 0 mg C/ind/day).

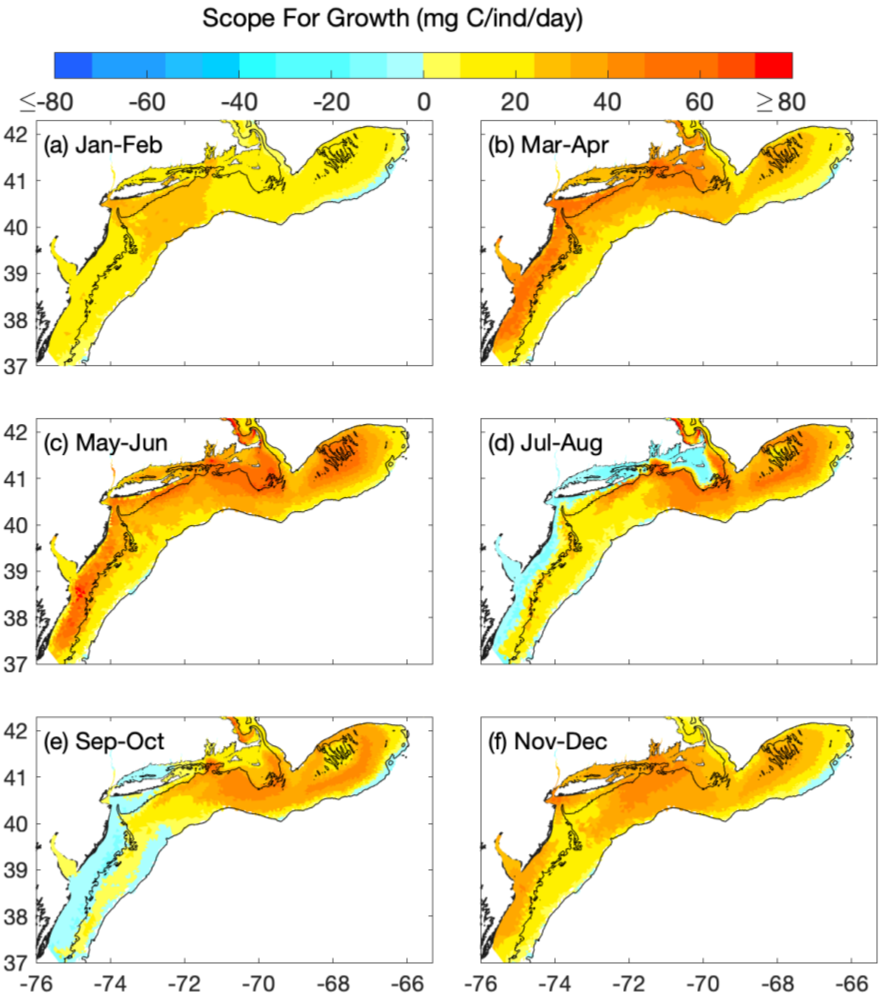

Fig. 8. Bimonthly sea scallop SFG over the NES feeding on both phytoplankton and detritus (warm color: SFG > 0 mg C/ind/day; cold color: SFG < 0 mg C/ind/day).

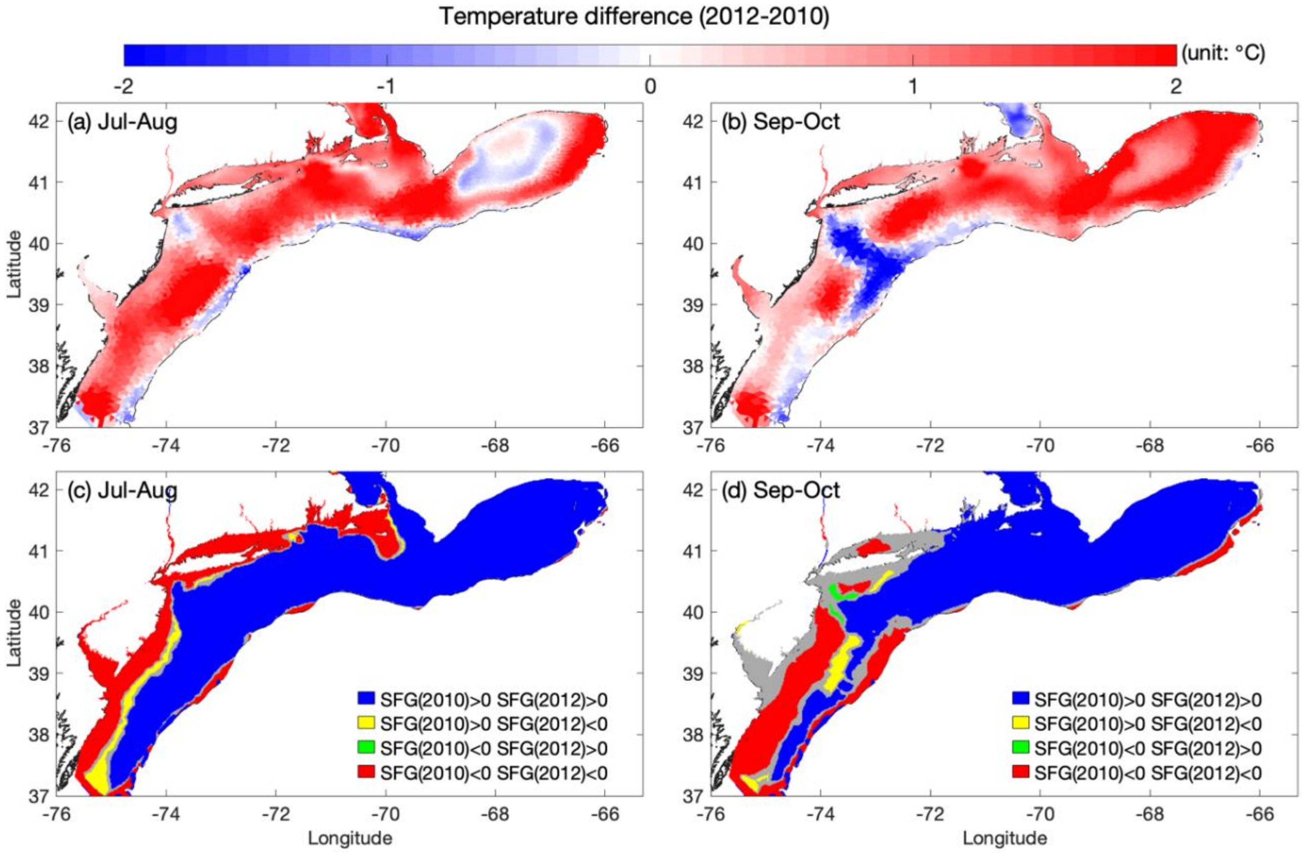

Fig. 9. The upper two panels represent the bimonthly mean bottom temperature difference between 2010 and 2012 in July-August (a) and September-October (b) (red: 2012 > 2010; blue: 2010 > 2012). The lower two panels show the spatial distribution of bimonthly mean SFG difference between 2010 and 2012 (blue: SFG > 0 in both years; yellow: SFG > 0 only in 2010; green: SFG > 0 only in 2012; red: SFG < 0 in both years). The one-tailed z-test was applied to the daily SFG at each location in July-August (panel c) and September-October (panel d) to examine the statistical significance. Grey color in panels c and d represents those regions where SFG > 0 or SFG < 0 is not statistically significant in 2010 or 2012.

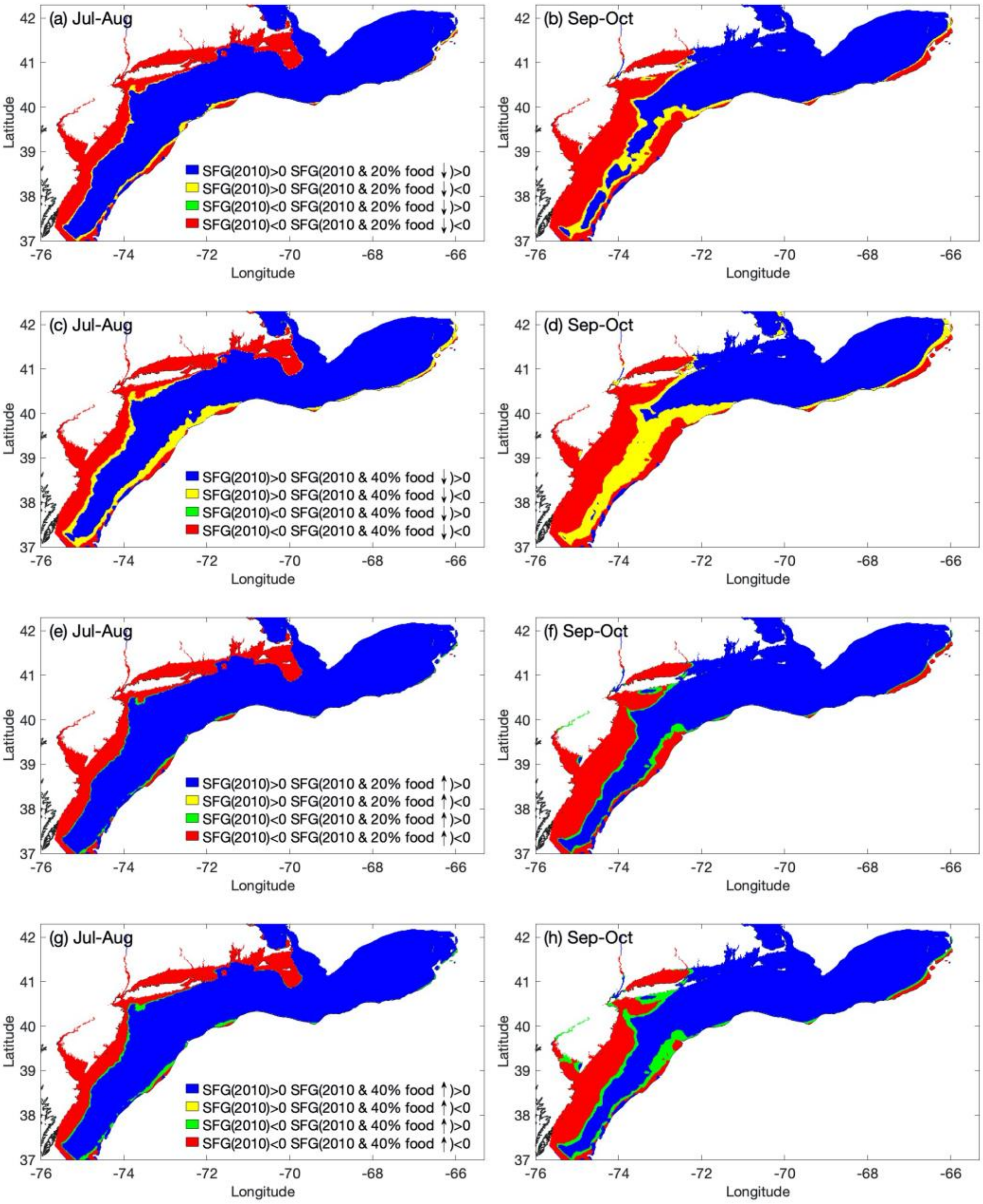

Fig. 10. The SFG difference between the benchmark run and the sensitivity tests on the NES with 20% food decrease (a and b), 40% food decrease (c and d), 20% food increase (e and f), and 40% food increase (g and h). The left panels represent the results in July-August, and the right panels represent the results in September-October.

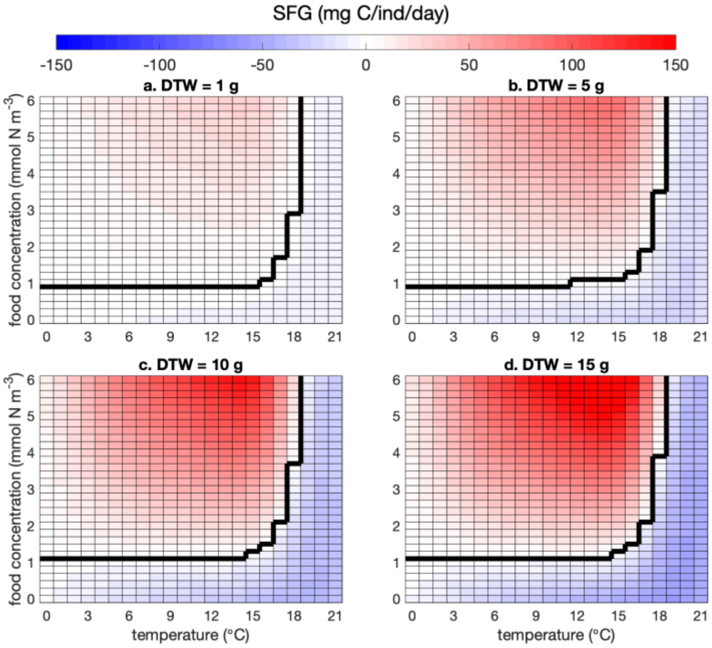

Fig. 11. The variations of SFG with temperature and food concentration. The four panels represent scallops with different dry tissue weights (panel a: DTW=1 g; panel b: DTW=5 g; panel c: DTW=10 g; panel d: DTW=15 g). Red/blue color represents positive/negative SFG. The solid black lines are the boundaries between positive and negative SFG.

Table. 1. SFG model parameters used in this study and related references

Parameters	Symbol	Units	Value	References
Clearance rate of a standard scallop for phytoplankton at reference temperature	$CR_{std,Phy}$	l/ind/hr	14.0	Grant and Cranford, (1991)
Clearance rate of a standard scallop for detritus at reference temperature	$CR_{std,Det}$	l/ind/hr	5.3	Grant and Cranford, (1991)
Respiration rate of a standard scallop at reference temperature	RR_{std}	mg O_2/ind/hr	1.69	Shumway et al. (1988)
Absorption efficiency for phytoplankton	AE_{Phy}	%	80	Grant and Cranford, (1991)
Absorption efficiency for detritus	AE_{det}	%	50	Grant and Cranford, (1991)
Dry tissue weight of a standard scallop	DTW_{std}	g	6.3	Grant and Cranford, (1991)
Weight exponent for clearance	b_{CR}	-	0.7	(MacDonald and Thompson, 1986)
Weight exponent for respiration	b_{RR}	-	0.8	Shumway et al. (1988)
Reference temperature	T_{ref}	K	279	Grant and Cranford, (1991)
Arrhenius temperature	T_A	K	5290	Van der Veer et al. (2006)
Rate of decrease at lower boundary	T_{AL}	K	51154	Van der Veer et al. (2006)
Rate of decrease at upper boundary	T_{AH}	K	47126	Van der Veer et al. (2006)
Lower boundary of tolerance range for clearance	T_{L_CR}	K	275	Van der Veer et al. (2006)
Lower boundary of tolerance range for respiration	T_{L_RR}	K	275	Van der Veer et al. (2006)
Upper boundary of tolerance range for clearance	T_{H_CR}	K	292	Van der Veer et al. (2006)
Upper boundary of tolerance range for respiration	T_{H_RR}	K	297	This study

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