

1 Projected effects of climate change on
2 *Pseudo-nitzschia* bloom dynamics in the
3 Gulf of Maine

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4 **Abstract**

5 Worldwide, warming ocean temperatures have contributed to extreme harmful algal bloom
6 events and shifts in phytoplankton species composition. In 2016 in the Gulf of Maine (GOM), an
7 unprecedented *Pseudo-nitzschia* bloom led to the first domoic-acid induced shellfishery closures
8 in the region. Potential links between climate change, warming temperatures, and the GOM
9 *Pseudo-nitzschia* assemblage, however, remain unexplored. In this study, a global climate change
10 projection previously downscaled to 7-km resolution for the Northwest Atlantic was further
11 refined with a 1–3-km resolution simulation of the GOM to investigate the effects of climate
12 change on HAB dynamics. A 25-year time slice of projected conditions at the end of the 21st
13 century (2073–2097) was compared to a 25-year hindcast of contemporary ocean conditions
14 (1994–2018) and analyzed for changes to GOM inflows, transport, and *Pseudo-nitzschia australis*
15 growth potential. On average, climate change is predicted to lead to increased temperatures,
16 decreased salinity, and increased stratification in the GOM, with the largest changes occurring in
17 the late summer. Inflows from the Scotian Shelf are projected to increase, and alongshore
18 transport in the Eastern Maine Coastal Current is projected to intensify. Increasing ocean
19 temperatures will likely make *P. australis* growth conditions less favorable in the southern and
20 western GOM but improve *P. australis* growth conditions in the eastern GOM, including a later
21 growing season in the fall, and a longer growing season in the spring. Combined, these changes
22 suggest that *P. australis* blooms in the eastern GOM could intensify in the 21st century, and that
23 the overall *Pseudo-nitzschia* species assemblage might shift to warmer-adapted species such as
24 *P. plurisecta* or other *Pseudo-nitzschia* species that may be introduced.

25

26 [1 Introduction](#)

27 *Pseudo-nitzschia* is a lightly silicified, pennate diatom genus with at least 52 confirmed species
28 (Bates et al., 2018). Twenty-six species have been confirmed to produce domoic acid (DA), a
29 neurotoxin that can cause amnesic shellfish poisoning. *Pseudo-nitzschia* has been described as a
30 “cosmopolitan” genus (Hasle, 2002), because species exist across a wide range of temperature
31 and salinity conditions and have been observed globally (Bates et al., 2018). The severity and
32 range of harmful algal blooms (HABs) caused by *Pseudo-nitzschia* have both been increasing in
33 recent years, with large-scale blooms leading to millions of dollars in economic losses (Moore et
34 al., 2020), and species blooming in previously unaffected regions (e.g. Bates et al., 2018; Clark et
35 al., 2019; Park et al., 2018).

36 One example of the increasing abundance and extent of *Pseudo-nitzschia* HABs is an
37 unprecedented DA event and subsequent shellfishery closures in the Gulf of Maine (GOM) in
38 2016 (Bates et al., 2018; Clark et al., 2019). Prior to 2016, 14 *Pseudo-nitzschia* species had been
39 identified in the region (Fernandes et al., 2014), including some DA producers, but the 2016
40 bloom was caused primarily by *P. australis*, which had never before been observed in the GOM
41 (Clark et al., 2019). *P. australis* blooms have occurred every year since 2016, reflecting a possible
42 regime shift in *Pseudo-nitzschia* bloom dynamics (Clark et al., 2021).

43 The DA event in 2016 is but one example of recent changes in the GOM. Although the rate of
44 warming in the GOM and its effect on ecosystems is under debate (Palmer et al., 2016; Pershing
45 et al., 2016, 2015), there is no question that sea surface temperatures are warming, and that the
46 warming is strongest in the summer and autumn (Thomas et al., 2017a), the time of year when
47 previous toxic *Pseudo-nitzschia* blooms – including *P. australis* – have occurred. Two marine heat
48 waves have been observed in the region in recent years, one in 2012 and one in 2016 (Pershing
49 et al., 2018, 2015). In addition, the relative importance of different source waters to the GOM
50 may have changed in recent decades: Townsend et al. (2015) provided evidence that the
51 proportion of Scotian Shelf Water flowing into the region has increased relative to Slope Water.
52 Meanwhile, a northward shift in the Gulf Stream may favor inflows of warm slope water along
53 the Gulf of Maine shelf break, and this pattern may strengthen over the 21st century (Saba et al.,

54 2016). Such changes to the inflows to the GOM could affect water mass properties in the interior,
55 and potentially future growth conditions for GOM HABs like *Pseudo-nitzschia*.

56 Changes to the environmental conditions in the GOM and its source waters might affect the
57 existing assemblage of *Pseudo-nitzschia*. Studies in other regions have shown that increasing
58 temperatures might increase *Pseudo-nitzschia* growth rates (Thorel et al., 2014), or favor *Pseudo-*
59 *nitzschia* over other phytoplankton (Zhu et al., 2017). Higher temperatures can also increase DA
60 production, particularly in *P. australis* (McKibben et al., 2017; Thorel et al., 2014; Zhu et al., 2017).
61 Indeed, some changes to *Pseudo-nitzschia* abundance worldwide have already occurred as a
62 result of warming oceans. One illustration is the record-breaking *P. australis* bloom on the U.S.
63 West Coast in 2015 that coincided with the North Pacific Ocean Warm Anomaly and peaked
64 during intermittent upwelling of water with a low silica-to-nitrate ratio (McCabe et al., 2016; Ryan
65 et al., 2017). The response of *P. australis* to climate change in other regions may depend on the
66 environment and *P. australis* population in question (Trainer et al., 2020). Warming ocean
67 temperatures over the 20th Century were correlated with an increase in *Pseudo-nitzschia* species
68 and *P. australis* specifically in the Santa Barbara Basin, (Barron et al., 2013), while increased
69 temperatures along with increased nitrogen loading in Danish sill-fjords may have contributed to
70 a shift in the *Pseudo-nitzschia* species assemblages on decadal time scales (Lundholm et al.,
71 2010).

72 In the context of these global changes, the appearance of *P. australis* in the GOM in 2016, and
73 annual toxic *P. australis* blooms in the GOM since 2016, it is important to project how *Pseudo-*
74 *nitzschia* blooms in the GOM might vary in the future. Clark et al. (2021) outlined how *P. australis*
75 blooms could be a growing concern in the region through persistent introduction, despite
76 insufficient evidence to indicate a regime shift in 2016. Models offer an ideal tool for projections,
77 but a typical Global Climate Model is too coarsely resolved (about 1-degree resolution) to
78 represent the nearshore processes and complex bathymetry that are important to
79 hydrodynamics and HAB dynamics in the GOM. For example, a 1-degree model cannot resolve
80 the Gulf of Maine Coastal Current, which transports HABs from the eastern GOM to the western
81 GOM (Keafer et al., 2005; Li et al., 2009). Coarser models also do not capture slope water inflows
82 through the Northeast Channel (Shin and Alexander, 2020a), which are important for the interior

83 water properties of the GOM and for introducing HAB species to the region (Clark et al., 2021;
84 Hebert et al., 2018).

85 One solution is to downscale a coarse circulation model to a GOM regional model (Drenkard et
86 al., 2021; Ralston and Moore, 2020). This approach was used to model the Northwest Atlantic
87 from the Gulf of Mexico to the Gulf of St. Lawrence at a 7-km horizontal resolution (Alexander et
88 al., 2020). The higher resolution model predicted enhanced bottom warming in the GOM relative
89 to the climate models, because its finer resolution better captured ocean circulation, deep
90 inflows in the Northeast Channel, and altered upstream water mass properties (Shin and
91 Alexander, 2020a).

92 This study will further downscale the 7-km-resolution model (Alexander et al., 2020) to a 1–3-km
93 resolution GOM Regional Ocean Modeling System (ROMS) (He et al., 2008; Li et al., 2009;
94 McGillicuddy et al., 2011) to investigate the effects of climate change on *Pseudo-nitzschia* bloom
95 dynamics in the GOM. The high-resolution GOM ROMS has been shown to capture alongshore
96 transport and hydrographic variability between sub-regions of the Gulf of Maine that are
97 important to regional HAB dynamics (Clark et al., 2021; He et al., 2008; Li et al., 2020, 2015, 2009;
98 McGillicuddy et al., 2011; McGillicuddy et al., 2014). To our knowledge, this is the first study to
99 investigate the effects of climate change on *Pseudo-nitzschia* with a physical circulation model.
100 The following methods section describes the study region, the two ROMS configurations, the
101 downscaling approach, and associated analyses. The results and discussion section will focus on
102 changes to temperature and hydrodynamics, the mechanics thereof, and their consequences for
103 *Pseudo-nitzschia* blooms. Particular attention is given to how *P. australis* bloom dynamics might
104 change in the eastern GOM, a region that has seen shellfishery closures due to DA toxicity nearly
105 every year since 2016.

106 2 Methods

107 2.1 Region of Study

108 2.1.1 Gulf of Maine

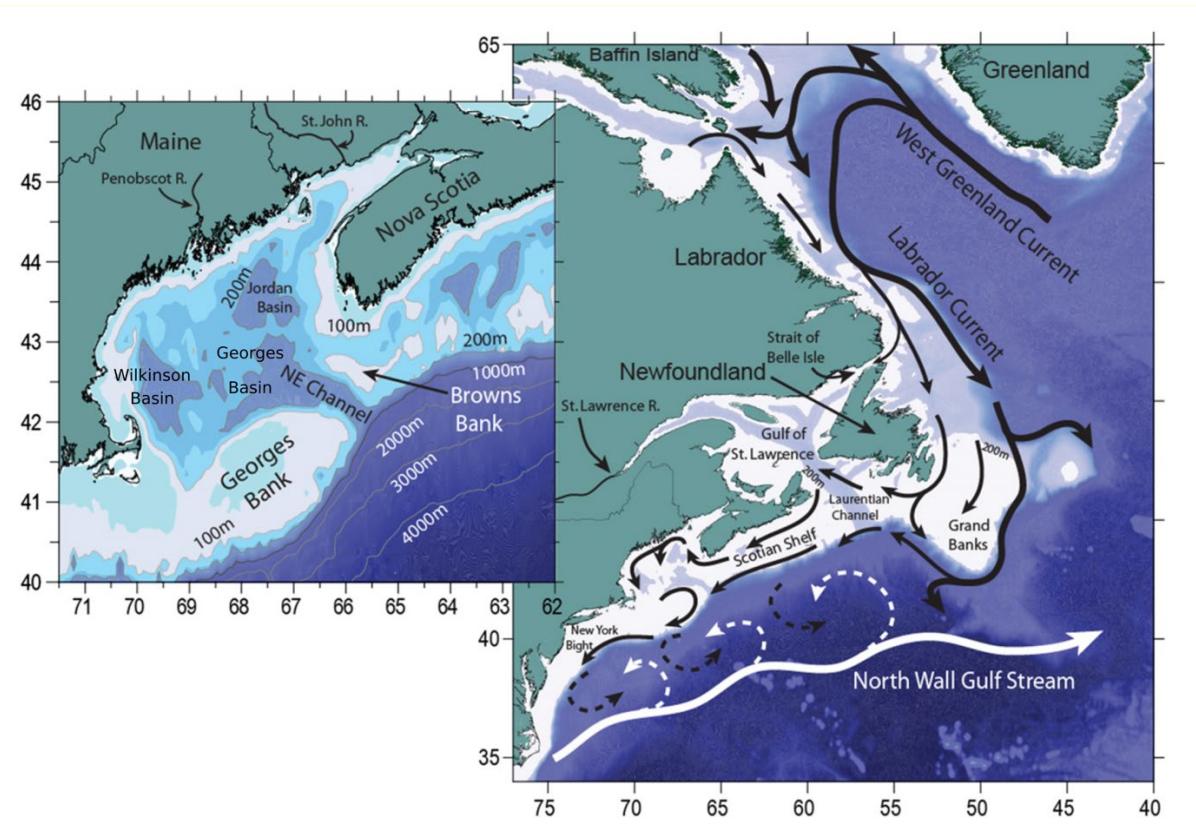
109 The Gulf of Maine is a shelf sea off the coast of the northeast United States and Canada, between
110 42 and 44.5°N and 66 and 71°W (Figure 1). Mean sea surface temperatures (SST) range from 4°C

111 in February to 22.5°C in August, and historical salinity values generally range from 29 to 33.5 PSU
112 (Li et al., 2014). Interior water mass properties are largely driven by inflows, which enter the gulf
113 along the coast south of Nova Scotia and at depth in the Northeast Channel (Townsend et al.,
114 2015). Nova Scotian inflows comprise relatively fresh, cool Scotian Shelf Water (5–7°C, 32.5–33.4
115 PSU), while Northeast Channel inflows are a mixture of Warm Slope Water (11°C, 35 PSU), and
116 Labrador Slope Water (6.5°C, 34.5 PSU) (Townsend et al., 2015, 2014). Portions of the Bay of
117 Fundy, Georges Bank, and northeastern GOM are well-mixed year-round because of the energy
118 imparted by the tides (Townsend et al., 2014). The Gulf of Maine is warming rapidly, at a rate of
119 approximately 0.4°C decade⁻¹ (Chen et al., 2020; Pershing et al., 2015).

120 The interior GOM is comprised of three basins with depths greater than 200m – Georges Basin,
121 Wilkinson Basin, and Jordan Basin – and is separated from the open North Atlantic via offshore
122 banks shallower than 100m – Georges Bank and Browns Bank. The general circulation in the GOM
123 is cyclonic, with anticyclonic circulation around Georges Bank (Bigelow, 1927; Brooks, 1994; Xue
124 et al., 2000). Alongshore flow on the coast of Maine is divided into the buoyancy-driven Maine
125 Coastal Current, and the GOM Coastal Plume (Bisagni et al., 1996; Keafer et al., 2005; Pettigrew
126 et al., 2005), which is fed by the region's five largest rivers, the St. John, Penobscot, Merrimack,
127 Kennebec, and Androscoggin.

128 2.2 Scotian Shelf

129 Upstream of the GOM is the Scotian Shelf, a shelf sea that stretches from 42.5 to 45.5°N and
130 from 57 to 65.5°W. The 30-year (1981–2010) climatological annual mean SST ranges from 7.1°C
131 on the Eastern Scotian Shelf to 8.1°C on the Western Scotian Shelf, and water temperatures have
132 been warming at an average rate of 0.5°C decade⁻¹ (Hebert et al., 2018). The Scotian Shelf is
133 relatively shallow, with depths ranging from 0–200m and several banks shallower than 100m
134 (Hebert et al., 2018). The two main currents, the Nova Scotia Current and the Labrador Current,
135 both flow from the northeast to the southwest, with the Nova Scotia Current along the coast and
136 the Labrador Current along the shelf break (Townsend et al., 2006). The main upstream sources
137 of Scotian Shelf water are the Gulf of St. Lawrence and the Labrador Current.



138

139 *Figure 1. From Townsend et al. (2010)⁸: "Map of the NW Atlantic Ocean, Labrador Sea and Gulf of Maine, showing*
 140 *the major current systems (after Chapman and Beardsley, 1989; Loder et al., 1998) ... Dashed arrows indicate*
 141 *mixing of waters (not currents) in the slope sea (Csanady and Hamilton, 1988). Inset shows location of the*
 142 *Northeast Channel (sill depth ca. 220 m) and the channel between Browns Bank and Nova Scotia (depth ca. 150*
 143 *m)."'*

144 2.3 Models

145 A series of one-way nested models were used to simulate the impact of climate change on the
 146 hydrographic and circulation patterns within the Gulf of Maine that are linked to HAB dynamics:
 147 the Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL-ESM2M), the Northwest
 148 Atlantic ROMS, and the Gulf of Maine ROMS.

149 2.3.1 Climate Model

150 The global earth system model GFDL-ESM2M (Dunne et al., 2013, 2012) was used to force the
 151 Northwest Atlantic ROMS in Alexander et al. (2020). Atmospheric resolution in the GFDL-ESM2M

⁸This figure was published in Continental Shelf Research, Vol 30; Townsend, David W., Rebuck, Nathan D., Thomas, Maura A., Karp-Boss, Lee, Gettings, Rachel M., "A changing nutrient regime in the Gulf of Maine", p. 820–832, Copyright Elsevier (2010).

152 is 2° (lat) $\times 2.5^{\circ}$ (lon) with 24 vertical levels, and the oceanographic resolution is approximately
153 $1^{\circ} \times 1^{\circ}$, with 50 vertical levels (Dunne et al., 2012). The climate simulations that were used in
154 Alexander et al. (2020) were projected with the RCP8.5 emissions pathway, the highest
155 Representative Concentration Pathway defined by the Intergovernmental Panel for Climate
156 Change (IPCC) (IPCC, 2014). Under this scenario, radiative forcing exceeds 8.5 W m^{-2} by 2100.
157 Refer to Dunne et al. (2012, 2013) for more details about the GFDL-ESM2M configuration and
158 Alexander et al. (2020) for comparisons of North Atlantic projections between GFDL-ESM2M and
159 other climate models. The potential effects of climate model selection and differences between
160 climate model projections are discussed more in Section 4.

161 2.3.2 Regional Ocean Modeling System

162 The Regional Ocean Modeling System (ROMS) is a hydrostatic, free surface, split-explicit, terrain-
163 following primitive equation model (Shchepetkin and McWilliams, 2003, 2005). Two different
164 configurations are relevant to this study, the Northwest Atlantic ROMS and the GOM ROMS.

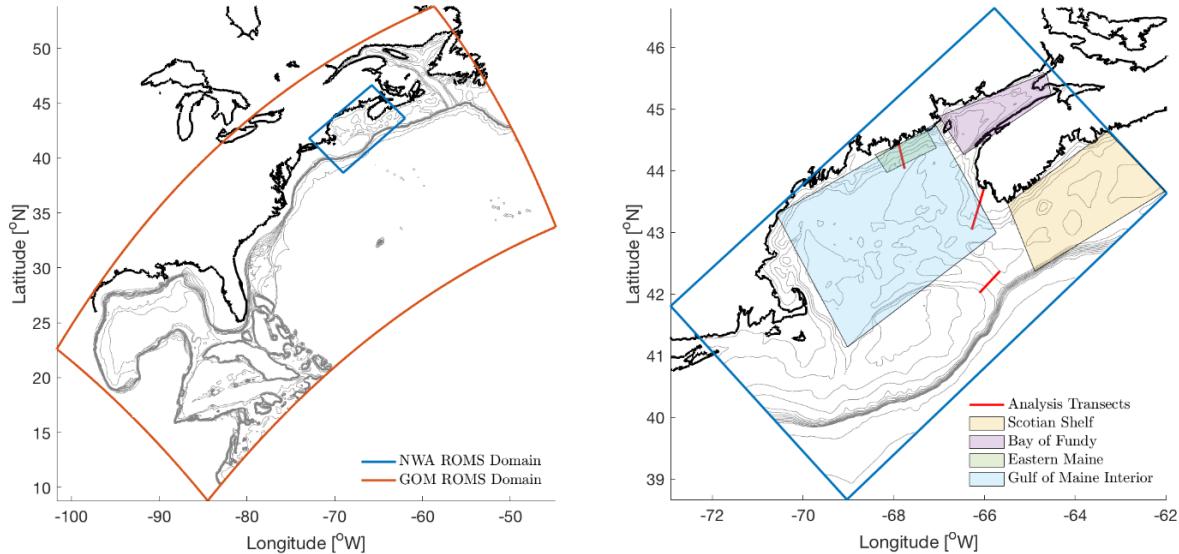
165 2.3.2.1 *Northwest Atlantic ROMS*

166 The Northwest Atlantic ROMS (NWA ROMS) covers the shelf sea and part of the open ocean along
167 the east coast of North America from the Gulf of Mexico to the Gulf of St. Lawrence, between
168 10°N and 50°N (Kang and Curchitser, 2013) (Figure 2). Its horizontal resolution is 7 km and it has
169 40 vertical layers, with higher resolution near the surface. The boundary and initial conditions for
170 the historical run were extracted from the Simple Ocean Data Assimilation (SODA v2.1.6) (Carton
171 and Giese, 2008), which has 0.5° horizontal resolution and 40 vertical layers. Historical surface
172 forcing was taken from the Coordinated Ocean-Ice Reference Experiments (CORE v2), which has
173 a 6-hour temporal resolution and 1.9° spatial resolution (Large and Yeager, 2009). Historical river
174 discharge from the continental discharge database (Dai et al., 2009) was used to implement
175 freshwater fluxes directly into the model's surface grid cells. Results from the control simulation
176 (1976–2005) and the projection (2070–2099) were saved as 5-day averages. The reader is
177 referred to Kang and Curchitser (2013) for more details about the model setup and to Alexander
178 et al. (2020) for specifics about the climate simulations.

179 *2.3.2.2 Gulf of Maine ROMS*

180 The Gulf of Maine ROMS (GOM ROMS) includes the GOM from Georges Bank in the South to the
181 Bay of Fundy in the North (38.7°N to 46.6°N), and from Coastal New England in the West to the
182 Scotian Shelf in the East (72.9°W to 62.0°W) (Figure 2). The horizontal resolution ranges from 1
183 to 3 km, and there are 36 vertical terrain-following layers.

184 The contemporary ocean simulation is based on the system described in He and McGillicuddy
185 (2008), Li et al. (2009), and McGillicuddy et al. (2011). Boundary conditions for temperature,
186 salinity, velocity, and sea surface height for the GOM ROMS were extracted from HYCOM (Hybrid
187 Coordinate Ocean Model) experiment GOFS3.0, which was interpolated to the GOM ROMS grid.
188 HYCOM has a $1/12^{\circ}$ resolution in the horizontal and 40 layers in the vertical, and simulations
189 from GOFS3.0 are available from 1994–2018 at 3-day intervals. HYCOM utilizes hybrid vertical
190 coordinates, with isopycnal vertical layers in the open stratified ocean, terrain-following sigma
191 layers in the coastal ocean, and z-coordinates in unstratified areas. Atmospheric forcing in the
192 GOM ROMS was specified via bulk formulation with data from the North American Regional
193 Reanalysis (NARR), which has 6-hour temporal resolution and $1/6^{\circ}$ spatial resolution (Mesinger
194 et al., 2006). The five largest rivers in the GOM (St. John, Penobscot, Kennebec, Androscoggin,
195 and Merrimack) are included in the GOM ROMS forcing files as daily volume transport ($\text{m}^3 \text{s}^{-1}$) as
196 measured by U.S. Geological Survey river gauges (USGS, 2013). A volumetric adjustment was
197 added to each river to account for drainage area downstream of the gauge. Multi-scale Ultra-
198 High-Resolution Temperature (MUR4.1) from satellites was used for a surface heat flux
199 correction (Chin et al., 2017).



200

201 *Figure 2. (left) The Northwest Atlantic (NWA) ROMS Domain (red outline) and Gulf of Maine (GOM) ROMS Domain*
 202 *(blue outline). Bathymetry is drawn every 100m from 0 to 1000m, at 2000m, and at 3000m according to the*
 203 *bathymetry of the NWA ROMS. The bold black line indicates the coastline. (right) The GOM ROMS domain (blue*
 204 *outline) with transect locations indicated with red lines and important sub-regions indicated with shaded boxes.*
 205 *Bathymetry is drawn every 25m from the surface to 100m, every 100m to 1000m, and at 2000m and 3000m. The*
 206 *bold black line indicates the coastline.*

207 2.4 Experimental Setup

208 The GOM ROMS was run for 25 consecutive years as a hindcast (1994–2018) and projection
 209 (2073–2097). Boundary and initial conditions for the hindcast runs were created from the sources
 210 detailed in Section 2.3.2, while the climate change runs were forced with the Delta Method,
 211 detailed below.

212 2.4.1 Delta Method

213 The NWA ROMS climate projections were downscaled to the GOM ROMS region via the Delta
 214 Method, as described in Alexander et al. (2020) and Shin and Alexander (2020). This method
 215 calculates the long-term (i.e. multi-decadal) mean difference in oceanic and atmospheric
 216 conditions between the projected and contemporary climate states in a lower resolution model
 217 (in this case, the NWA ROMS) and adds this difference (i.e. the Delta) to the initial and boundary
 218 conditions of a higher resolution model (the GOM ROMS). Here the Deltas were calculated
 219 monthly, because climate change impacts are likely to have seasonal variation (Shin and
 220 Alexander, 2020). Because the same Deltas are added to each hindcast year to create the
 221 projection, this method does not account for potential changes in forcing variability as a result of

222 climate change. Rather, forcing variability in the contemporary ocean is preserved, but seasonal
223 means have been shifted in a manner consistent with climate change projections. The sources
224 from which Deltas were calculated and the fields to which they were added are detailed in the
225 Supplementary Material in Table S-3.

226 The Delta Method was implemented as follows:

- 227 1. A 30-year monthly mean for each forcing field at the beginning and the end of the 21st
228 Century was calculated from the sources in Table S-3. Atmospheric Deltas were calculated
229 from the NWA ROMS forcing files, which were created from the GFDL-ESM2M climate
230 simulations.
- 231 2. Twelve Deltas (one for each month) were calculated by subtracting the hindcast means
232 from the climate simulation means.
- 233 3. The hindcast time periods for the NWA ROMS (1976–2005) and the GOM ROMS (1994–
234 2018) were not the same because of the availability of the HYCOM simulations used to
235 provide boundary conditions for the GOM ROMS. As a result – using 2084 as the mid-
236 point of the projection time period – the average time difference between projection and
237 hindcast in the NWA ROMS simulations was 94 years (2084–1990), while the average
238 difference between the projection and hindcast in the GOM ROMS simulations was 78
239 years (2084–2006). Deltas were multiplied by 78/94 to account for the difference,
240 creating a “Fractional Delta”. This assumes that the Deltas increase linearly with time,
241 which is a simplifying assumption.
- 242 4. Fractional Deltas were spatially and temporally interpolated to the required resolution
243 for the GOM ROMS initial and boundary conditions. In this study, this meant that
244 oceanographic Deltas were interpolated to the HYCOM grid, atmospheric Deltas were
245 interpolated to the NARR grid, and SST Deltas were interpolated to the satellite grid.
- 246 5. Interpolated fractional Deltas were added to the appropriate forcing files for the GOM
247 ROMS climate simulations.
- 248 6. The GOM ROMS was run consecutively for 25 years (representing 2073–2097) with the
249 new forcing files.

250 River inputs are implemented differently in the NWA ROMS and GOM ROMS configurations, so
251 the river Deltas were relative: the monthly average percent change between hindcast and
252 projection in the river inputs was calculated from the NWA ROMS input files, and that percent
253 change was applied to the river discharge in the GOM ROMS input files.

254 [2.5 Analysis](#)

255 [2.5.1 Hydrodynamic Analyses](#)

256 Three transects were chosen for transport analysis: across the Northeast Channel (42.02°N,
257 66.11°W to 42.37°N, 65.66°W), perpendicular to Nova Scotia (42.62°N, 66.57°W to 43.69°N,
258 66.02°W), and cross-shore from Mt. Desert Island across the Eastern Maine Coastal Current
259 (EMCC) (44.43°N, 67.89°W to 44.03°N, 67.76°W) (Figure 2). At each transect, velocities were
260 projected in the alongshore direction (along-channel in the Northeast Channel) according to the
261 angle of the coastline (channel) with respect to east (Figure 2) such that positive velocities were
262 toward the GOM. At the EMCC, positive velocities were toward the southwest, the predominant
263 flow direction. Transport toward the GOM was calculated by multiplying the projected velocity
264 in each grid cell where $u > 0$ by the cell's cross-sectional area and summing over the transect.
265 Transport *toward* the GOM was used, rather than *net* transport, because the analysis focused on
266 the ability to carry cells into the GOM. In addition, transport into the GOM in the Northeast
267 Channel is of a similar magnitude as transport out due to strongly sheared flow, and thus the net
268 transport obscures the inflow signal. The GOM inflow ratio was calculated according to Hebert
269 et al. (2018):

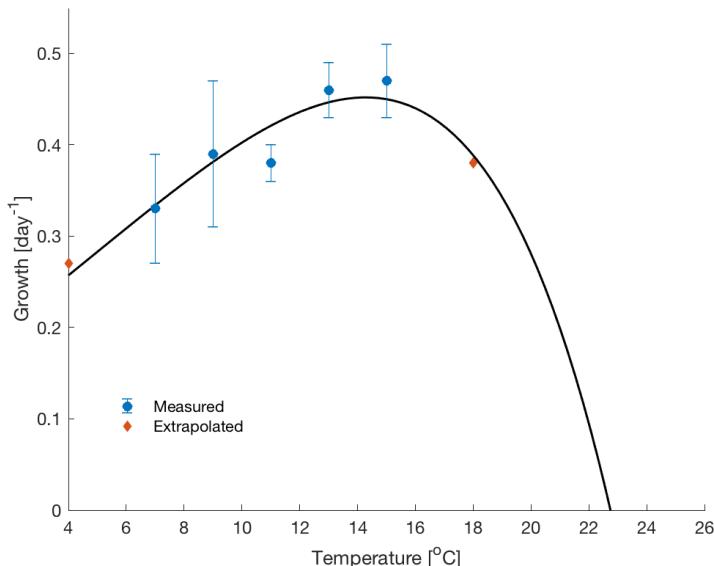
270
$$\text{Inflow Ratio} = \frac{\text{Nova Scotia transport}}{\text{Northeast Channel transport} + \text{Nova Scotia transport}}$$

271 Stratification was defined as the difference in potential density between 100m and the surface
272 (Alexander et al., 2020), except for locations shallower than 100m, where the bottom potential
273 density was used.

274 [2.5.2 Biological Analyses](#)

275 *P. australis* growth potential was estimated according to the method in Clark et al. (2021). In
276 short, growth rates were measured at 7, 9, 11, 13, and 15°C for a *P. australis* isolate from the
277 2016 GOM bloom and extrapolated beyond the 7–15°C temperature range according to a rate of

278 change of growth rate with temperature from short-term exposure experiments ($d\mu/dT = -0.02$
 279 $d^{-1}C^{-1}$ if $T < 7^{\circ}C$ and $-0.03 d^{-1}C^{-1}$ if $T > 15^{\circ}C$). A theoretical curve was fit to the measured and
 280 estimated data points according to equation S.1 in Thomas et al. (2012). The growth curve, which
 281 agrees well with the literature (Thomas et al., 2012), is given in Figure 3, and the reader is referred
 282 to Clark et al. (2021) for more details. For each grid cell at each time step, a temperature-based
 283 potential growth rate was calculated by interpolating the simulated temperature to the growth
 284 curve. Many other factors can affect cellular abundance and growth, such as intraspecific
 285 variability or nutrient and light availability, but this analysis was intended to focus on the effects
 286 of temperature differences on *P. australis* growth. Therefore, the other factors are assumed to
 287 be non-limiting, and hereafter the “temperature-based potential growth rate” will be referred to
 288 as “potential growth rate” for brevity. Potential growth rate was calculated both for SST and for
 289 10m temperatures because *P. australis* and DA have been observed at both depths in the GOM
 290 (Clark et al., 2019).



291
 292 *Figure 3. P. australis growth vs. temperature as described in Clark et al. (2021). Values measured in laboratory*
 293 *experiments are marked with blue circles (error bars indicate standard error), while values that were extrapolated*
 294 *from short-term exposure experiments (see description in text) are indicated with orange diamonds. The black line*
 295 *indicates the growth curve that was fit according to the equation S.1 in Thomas et al. (2012). The growth curve is*
 296 *interpolated only as low as 4°C because laboratory equipment did not allow for measurement of growth rates*
 297 *below that temperature.*

298 The growing season was estimated as the number of days when average noon-time growth rates
299 were greater than 75% of the maximum growth rate (appx 0.47 day⁻¹ see Figure 3), according to
300 Gobler et al. (2017). Surface noon-time growth rates were smoothed over a weekly time period
301 before growing season analysis, because the “composite year” approach and associated
302 averaging used here are more appropriate to assess weekly changes in growth than daily
303 changes. An alternative approach for estimating growing season as a function of temperature is
304 to define the HAB Window of Opportunity, as described for *A. catenella* in Puget Sound (Moore
305 et al., 2011). This was deemed overly simplistic for *Pseudo-nitzschia* because there are multiple
306 species, species might have different sources such as introduction or retention, and the same
307 species has been found to grow in different temperature ranges depending on the location (e.g.
308 *P. australis* in Clark et al. 2019; McCabe et al. 2016; Santiago-Morales and García-Mendoza, 2011;
309 Thorel et al. 2014).

310 2.5.3 Averaging Data Spatially and Temporally

311 Model output was averaged both spatially and temporally to focus the analysis on regions and
312 time periods of interest. A “composite year” is a year in which data were averaged across all 25
313 years from each simulation to represent the average hindcast or projection. Seasonal averages
314 were broken down into winter (December to February), spring (March to May), summer (June to
315 August), and fall (September to November). Regardless of whether data were averaged across
316 the seasons, across the entire year, or averaged into composite years, a “change” in some
317 parameter indicates the projected value minus the hindcast value (not to be confused with
318 “Deltas” for the model forcing). Seasonal averages were calculated for the changes in SST, surface
319 salinity, stratification, and *P. australis* potential growth.

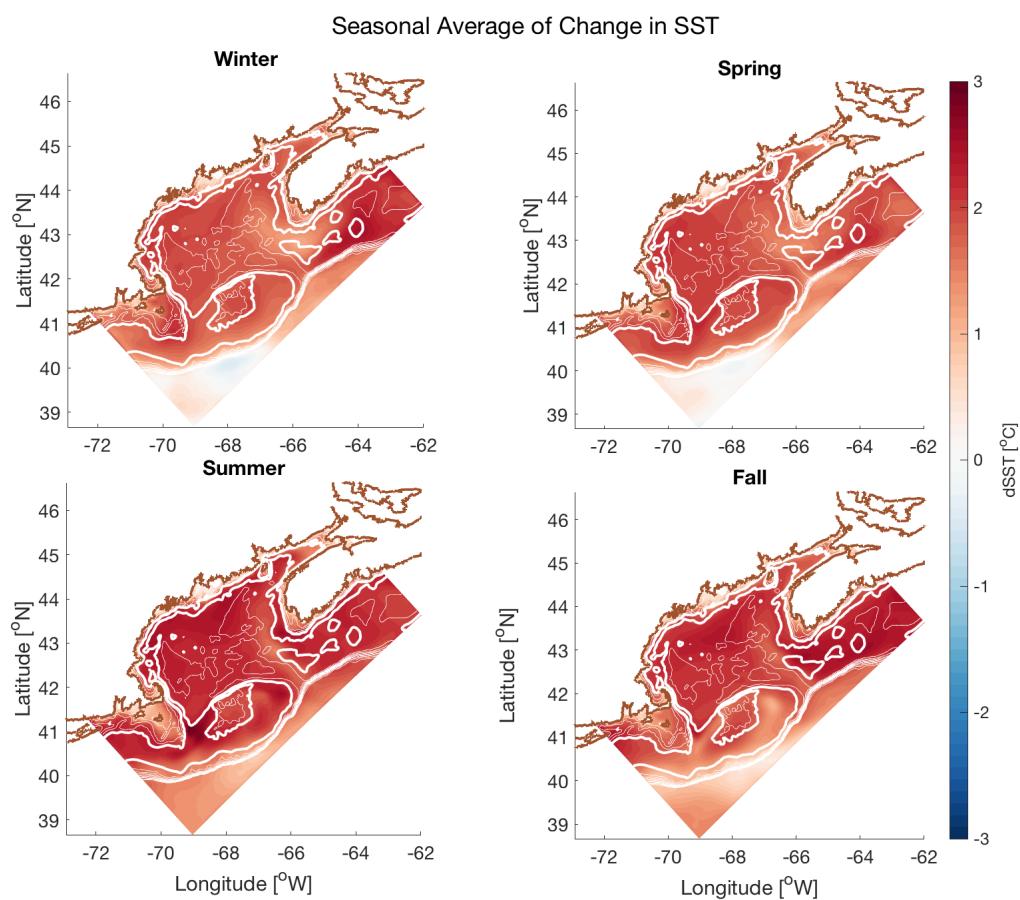
320 To quantify interregional variability within the GOM ROMS domain, four sub-regions (Figure 2)
321 were selected for spatial averaging. The Scotian Shelf was chosen because of its influence on the
322 GOM interior via Scotian Shelf Water inflows, the Bay of Fundy was selected because it is where
323 the 2016 *P. australis* bloom was first observed (Clark et al., 2019), the eastern Maine coast was
324 selected because multiple DA-induced shellfishery closures have occurred here since 2016, and
325 the GOM interior was chosen to assess internal dynamics over the deep basins. Changes in
326 *P. australis* potential growth and growing season were averaged over these sub-regions.

327 3 Results

328 3.1 Hydrodynamics

329 3.1.1 Sea Surface Temperature

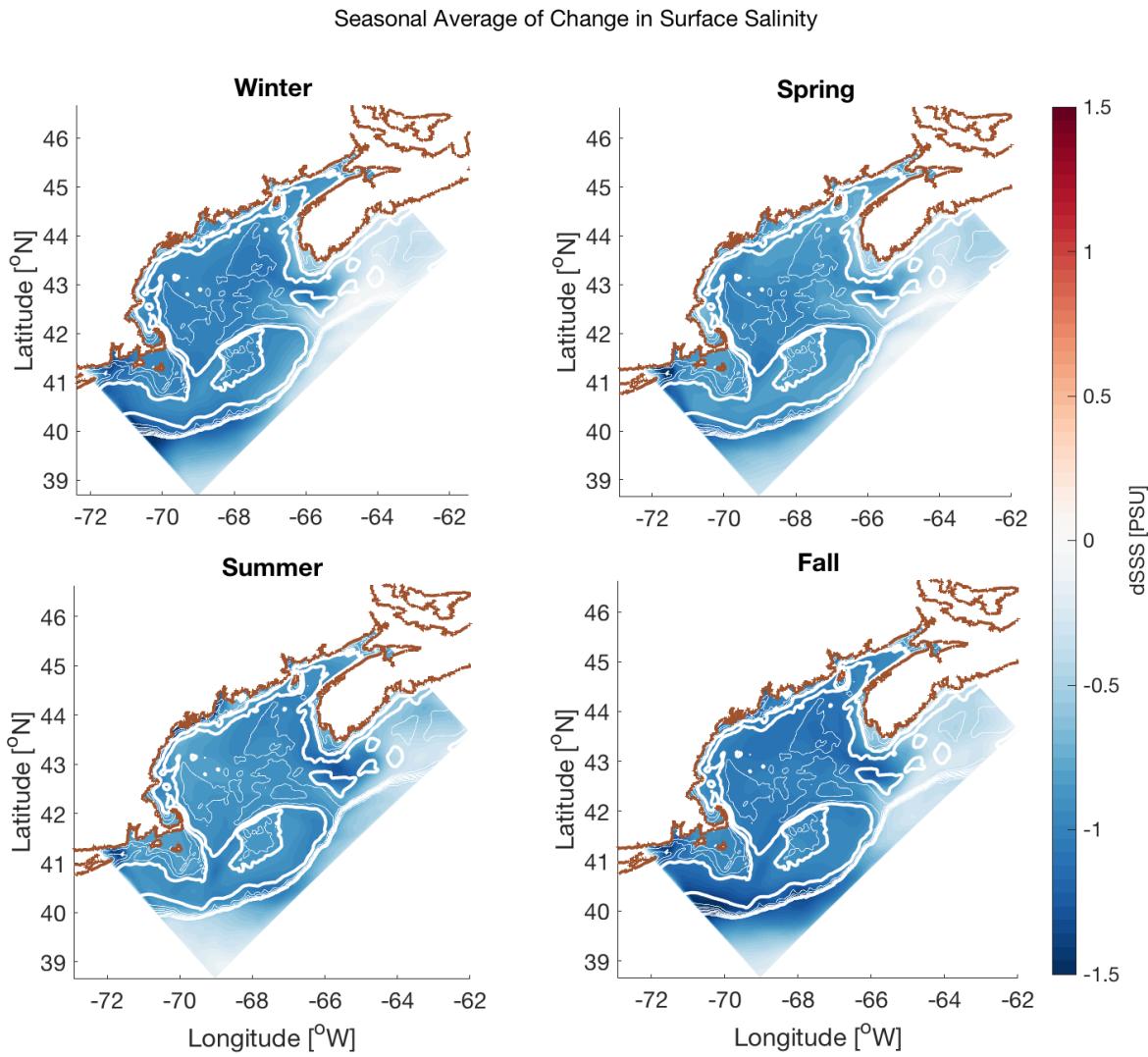
330 In the GOM ROMS projection, across the domain, SST increased by 2°C on average, with the
331 maximum increase in August and September. This agrees with the NWA ROMS projection in
332 magnitude and seasonality. The average increase across the domain was 1.8°C in winter, 1.9°C in
333 spring, 2.2°C in summer, and 2.0°C in fall. The seasonal signal and trend were consistent
334 regardless of sub-region, but the magnitude of warming varied between regions. The Scotian
335 Shelf had the greatest warming (up to 2.7°C in August), while the Bay of Fundy had the least
336 (maximum 1.9°C) (Figure 4). SST in the coastal regions (shallower than 50m) increased less than
337 in the interior, regardless of season.



338

339 *Figure 4. Seasonally-averaged change in SST in the (clockwise from top left) winter, spring, fall, and summer. Color*
 340 *values are defined by the color bar on the right. Bathymetry is drawn every 25m to 100m, every 100m to 1000m,*
 341 *and at 2000m and 3000m.*

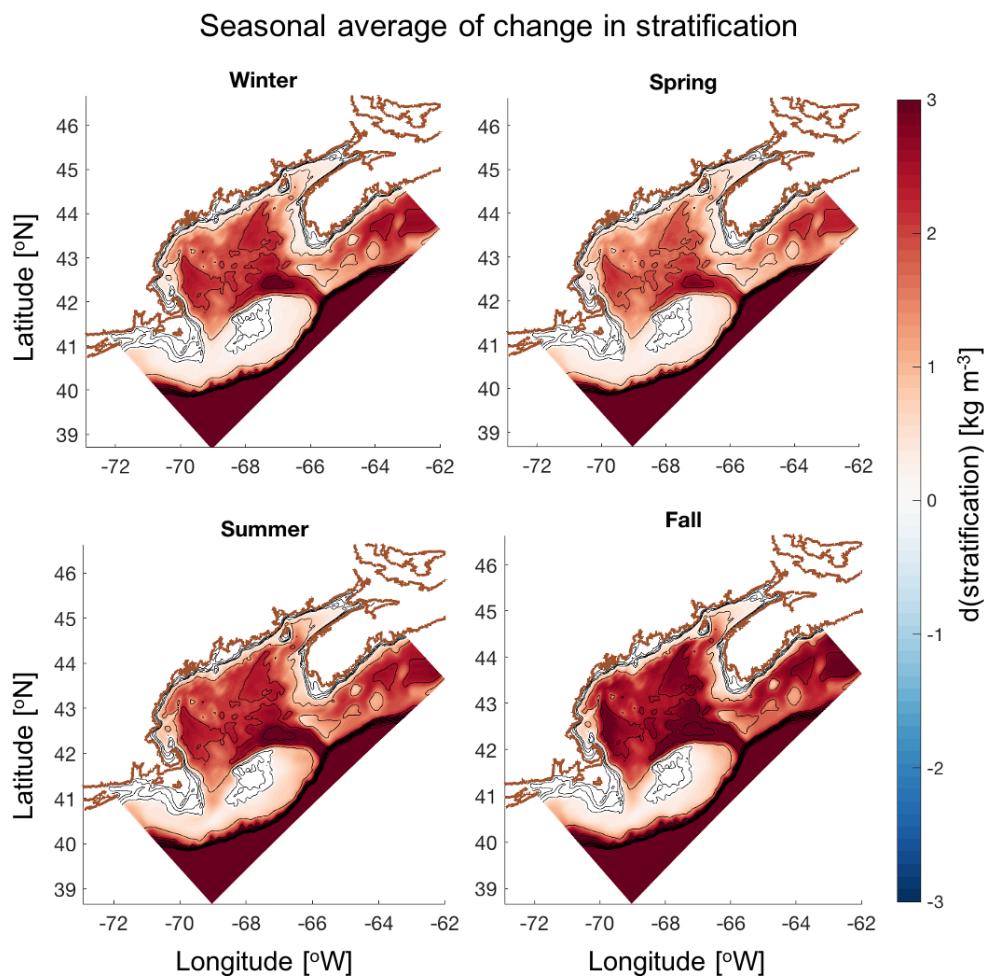
342 3.1.2 Surface Salinity
343 Surface salinity decreased throughout the GOM ROMS domain by 0.9 PSU on average (Figure 5).
344 Although the seasonal signal was largely consistent between sub-regions, the degree of
345 freshening varied. Salinity decreased between 0.8 and 1.1 PSU in the Bay of Fundy, GOM, and
346 eastern Maine sub-regions, with the largest decrease occurring in the fall. On the Scotian Shelf,
347 surface salinity decreased between 0.2 and 0.7 PSU, with the largest decrease in August.



348
349 *Figure 5. Seasonally-averaged change in surface salinity in the (clockwise from top left) winter, spring, fall, and*
350 *summer. Color values are defined by the color bar on the right. Bathymetry is drawn every 25m to 100m, every*
351 *100m to 1000m, and at 2000m and 3000m.*

352 3.1.3 Stratification

353 Stratification largely increased in the GOM ROMS projection throughout the domain, with
354 interregional variability (Figure 6). Near the coast, in the Bay of Fundy, and at the crest of Georges
355 Bank and Browns Bank, stratification increased only slightly, even in the summer. In contrast, in
356 the GOM interior and offshore, stratification increased year-round in the projection by up to 3
357 kg m⁻³. Regardless of interregional variability, the largest stratification increases generally
358 occurred in the summer and fall.

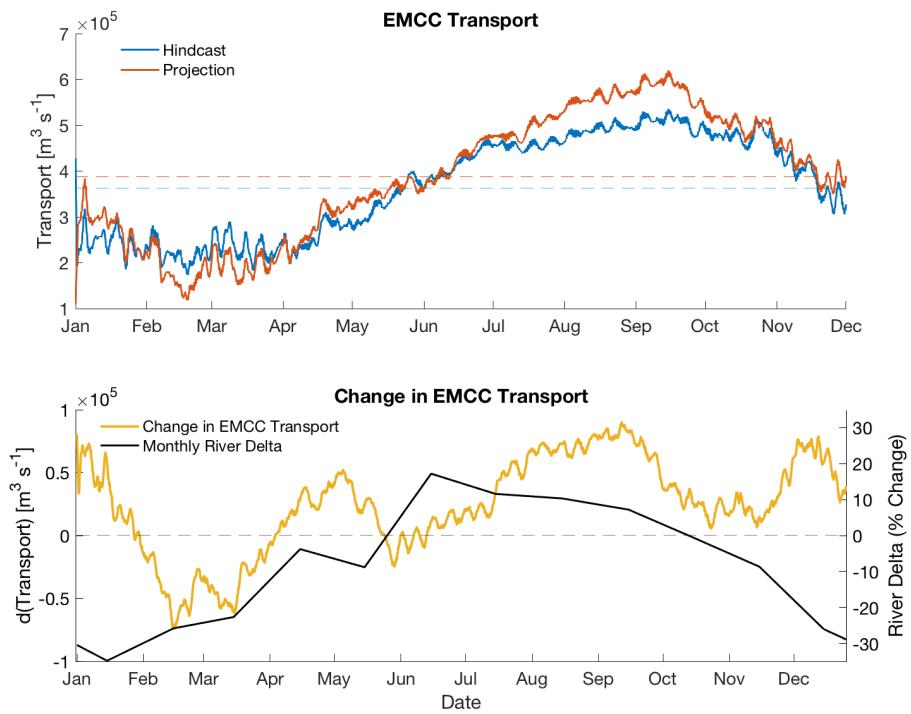


359

360 *Figure 6. Seasonally-averaged change in stratification in the (clockwise from top left) winter, spring, fall, and*
 361 *summer. Color values are defined by the color bar on the right. Bathymetry is drawn every 25m to 100m, every*
 362 *100m to 1000m, and at 2000m and 3000m.*

363 3.1.4 Gulf of Maine Inflow Ratio
364 The Gulf of Maine inflow ratio increased year-round in the GOM ROMS projection, indicating
365 increased inflow through the Scotian Shelf relative to inflows through the Northeast Channel.
366 There was no discernible seasonal variability in this change. In the hindcast the ratio was
367 approximately 0.5 on average, indicating that 50% of the inflows came via the Nova Scotia coastal
368 route, which agrees with the results presented in Hebert et al. (2018). In the projection the inflow
369 ratio increased by 0.1 on average, or 20% of the ratio in the hindcast (Supplementary Material
370 Figure S-1), the drivers of which are discussed in Section 4.1.2. Both the GOM ROMS and the
371 NWA ROMS projected an increase in the GOM inflow ratio (Supplementary Material, Figure S-2).
372 The mean increase in the GOM ROMS was larger than the mean increase in the NWA ROMS, the
373 likely cause of which is discussed in Section 4.1.1.

374 3.1.5 Eastern Maine Coastal Current
375 In the projection, alongshore transport in the EMCC decreased by 5% on average in the winter
376 and spring and increased by 5% on average in the summer and fall (Figure 7). The result of this
377 was an intensified seasonal signal, with the greatest increase (17%) occurring in mid-September.
378 When the increase in total transport peaked, the projected alongshore velocity increased by
379 about 2 cm s^{-1} over the hindcast.



380

381 *Figure 7. (top) Alongshore EMCC transport from the hindcast composite year (blue) and the projected composite year*
 382 *(red) vs. day of the year. Dashed lines in corresponding colors indicate the year-long average. (bottom) Change in*
 383 *alongshore EMCC transport vs. day of the year (yellow, left y axis), and monthly river delta as a percent change for*
 384 *each month (black, right y axis). EMCC data were smoothed over a weekly time period before plotting.*

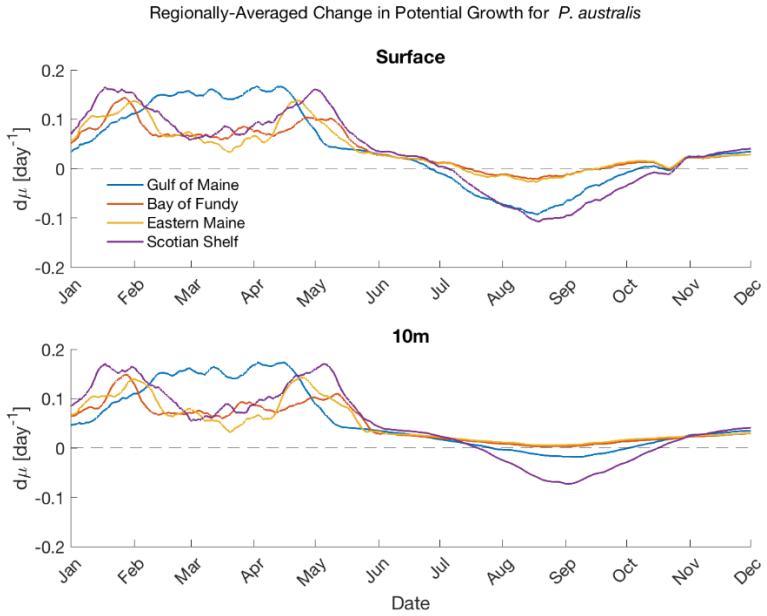
385

386 3.2 Projected Changes to *Pseudo-nitzschia* Growth

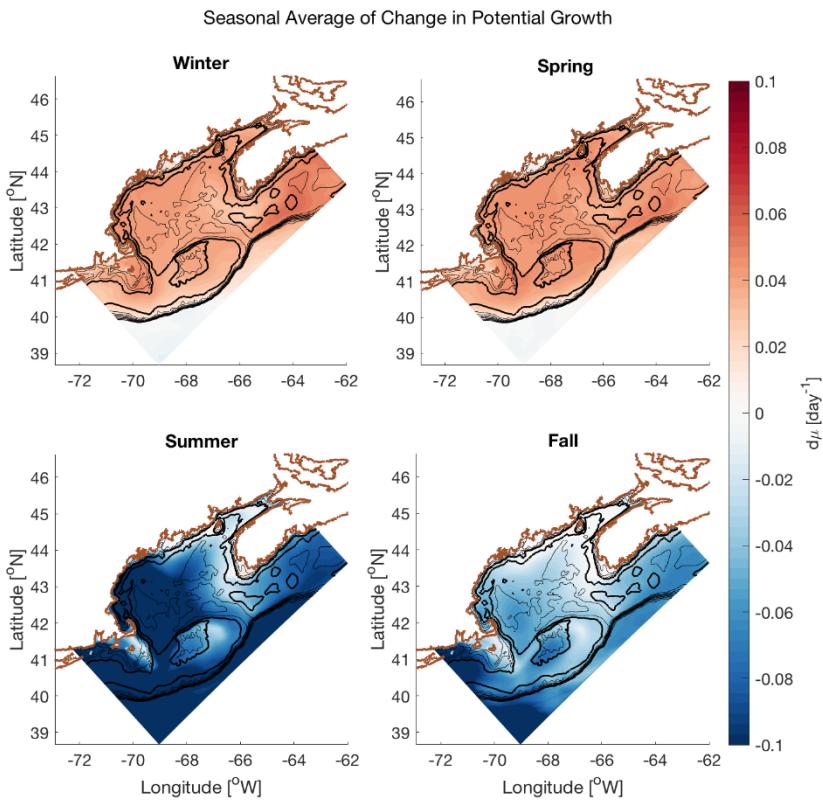
387 3.2.1 Growth Potential

388 In most of the GOM ROMS domain, average *P. australis* potential growth rates increased from
389 November to June and decreased from June to November, with a maximum winter/spring
390 increase of 0.17 day^{-1} in the Bay of Fundy and a maximum summer/fall decrease of 0.07 day^{-1} on
391 the Scotian Shelf (Figure 8). However, there was interregional variability. In the interior GOM sub-
392 region, the springtime increase stretched from February to March, while the Scotian Shelf, Bay
393 of Fundy, and Eastern Maine sub-regions exhibited early and late spring peaks. The summertime
394 decreases were larger in the GOM and Scotian Shelf sub-regions than in the Bay of Fundy and
395 Eastern Maine sub-regions. The seasonal pattern of change in potential growth was similar at
396 10m, but the summertime decrease was less than at the surface, reflecting cooler temperatures
397 at depth. In the Eastern Maine and Bay of Fundy sub-regions, potential growth at 10m did not
398 decrease at any point in the summer (Figure 8).

399 Averaged seasonally, the change in growth potential in most sub-regions was positive in winter
400 and spring and negative in summer and fall (Figure 9). Exceptions to this are found in shallow and
401 tidally energetic regions, including the crest of Georges Bank, the shelf south of Nova Scotia
402 including Browns Bank, the Bay of Fundy, and the eastern coast of Maine, where the spatially
403 and temporally averaged change in growth potential at the surface was greater than zero in the
404 winter and spring and approximately zero in the summer and fall.



406 *Figure 8. Change in potential growth for each of the four sub-regions vs. time at the surface (top) and at 10m*
 407 *(bottom). To see interannual variability in the projected changes in growth potential, refer to Figure S-3 and Figure*
 408 *S-4 in the Appendix.*



410 *Figure 9. Average change in surface *P. australis* potential growth in the GOM ROMS domain in the (clockwise from*
 411 *top left) winter, spring, fall, and summer. Color values are given by the color bar on the right.*

412 3.2.2 Growing Season
413 The number of days in the *P. australis* growing season increased significantly in the projection for
414 the Bay of Fundy by 3 weeks. Changes in growing season averaged over the Eastern Maine Coast,
415 GOM, or Scotian Shelf sub-regions were not significant according to the Wilcoxon rank sum test,
416 which tests the null hypothesis that the data in two samples are from distributions with the same
417 median. When the year was divided into spring and fall growing seasons (i.e. the first half and
418 second half of the year), it became apparent that the growing season increased significantly only
419 in the first half of the year. The spring growing season increased significantly by 4–6 weeks in all
420 sub-regions, while the fall growing season decreased significantly by 6–7 weeks in the GOM and
421 Scotian Shelf sub-regions. Significant changes in growing season for each sub-region are
422 summarized in Table 1.

423 *Table 1. Change in growing season in days averaged over each of the sub-regions. Only numbers that are*
424 *significant at the 95% confidence level are listed. The difference is given in days in the table but rounded to the*
425 *nearest week in the text.*

Sub-Region	Annual Growing Season dt (days)	Spring Growing Season dt (days)	Fall Growing Season dt (days)
Gulf of Maine	--	+40	-43
Scotian Shelf	--	+40	-51
Bay of Fundy	+23	+36	--
Eastern Maine Coast	--	+28	--

426 4 Discussion

427 4.1 Mechanisms Behind Changing Hydrodynamics

428 4.1.1 Sea Surface Temperature, Surface Salinity, and Stratification

429 The general trend in SST – warming overall and enhanced warming in the summer – was also
430 noted in Alexander et al. (2020) and in the GFDL-ESM2M. This is partially explained by a positive
431 feedback between summer warming and stratification: surface warming leads to increased
432 stratification, which leads to reduced mixing with cooler, deeper waters, stronger air-sea
433 temperature coupling, and a shallower layer over which to distribute the heat flux (Alexander et
434 al., 2020, 2018; Thomas et al., 2017b). Warming was stronger on the Scotian Shelf than in other
435 sub-regions (Figure 4), which could be caused both by enhanced warming at northerly latitudes

436 as shown in the GFDL-ESM2M output (Alexander et al., 2020), and by the warming-stratification
437 feedback. In contrast, the Bay of Fundy and Eastern Maine sub-regions, although at similar
438 latitudes to the Scotian Shelf sub-region, had amongst the smallest changes in SST (Figure 4). This
439 is likely the result of strong vertical mixing by the tides, which transports deep, cooler waters to
440 the surface.

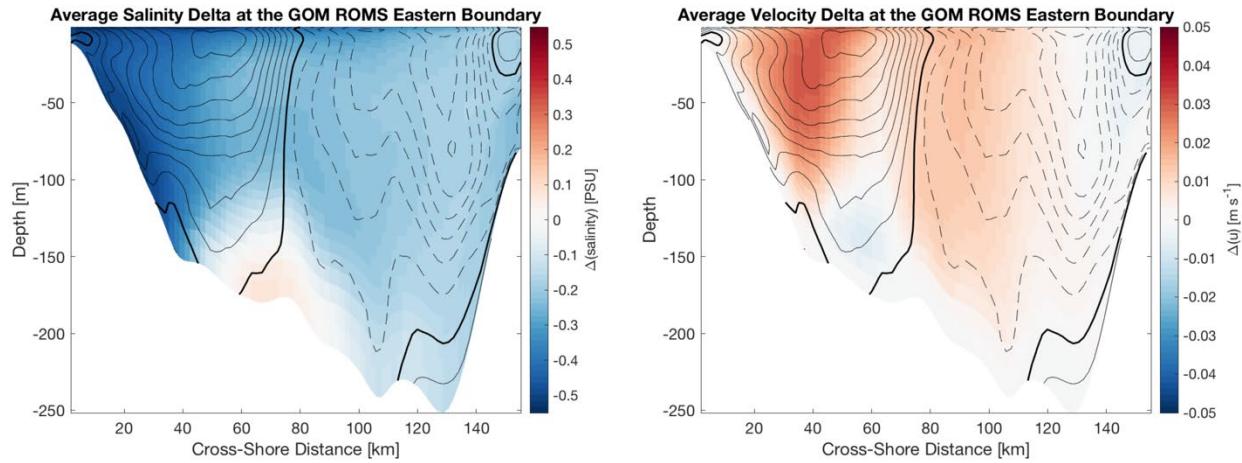
441 Surface salinities decreased throughout the domain in the projection, with the largest decrease
442 in late summer and in the GOM interior (Figure 5). This agrees with projections for the GOM in
443 other studies (Brickman et al., 2021). Decreased salinity was the result of increased freshwater
444 transport into the domain at the eastern and southern boundaries. Freshening north of 40°N
445 occurred in the GFDL-ESM2M, with stronger freshening in summer than in winter (Alexander et
446 al., 2020) because of sea ice melt and an increase in precipitation relative to evaporation
447 ($\Delta(E - P) < 0$) in the Subpolar Gyre and Labrador Sea. This upstream freshwater was likely
448 advected into the GOM (Alexander et al., 2020) via alongshore transport on the Scotian Shelf and
449 shelf break. Some areas saw stronger freshening than average, especially areas of steep
450 bathymetry such as Georges Bank (Figure 5), but this was simulated only by the GOM ROMS.

451 The GOM ROMS and NWA ROMS both projected freshening in the GOM, but they disagreed on
452 the magnitude. Surface salinity decreased by 0.3 PSU on average in the NWA ROMS projection
453 within the GOM ROMS domain, but by 0.9 PSU on average in the GOM ROMS projection
454 (Supplementary Material, Figure S-3). This was largely a result of how the two models resolved
455 alongshore transport at the GOM ROMS eastern boundary on the Scotian Shelf (Figure 10). At
456 this boundary, the average salinity Delta was negative, with stronger freshening nearshore, and
457 the average alongshore velocity Delta was positive (toward the GOM), with a maximum increase
458 of 5 cm s^{-1} nearshore. Nearshore velocities toward the GOM were also, on average, 10 cm s^{-1}
459 faster in the GOM ROMS hindcast than in the NWA ROMS hindcast. The freshwater transport
460 toward the GOM was therefore larger in the GOM ROMS than the NWA ROMS. The enhanced
461 freshening in the GOM ROMS occurred even though the average surface salinity at the GOM
462 ROMS eastern boundary in the hindcast was greater in the GOM ROMS than in the NWA ROMS
463 (Supplementary Material Figure S-4), which highlights the role of freshwater advection
464 throughout the water column.

465 The refined resolution of coastal currents in the GOM ROMS may have amplified the increases in
466 freshwater inflow apparent in the NWA ROMS. Alexander et al. (2020) also noted that salinity
467 decreases were stronger and more spatially extensive in the NWA ROMS compared to the Global
468 Climate Model. On average, freshwater transport at the eastern boundary increased by 11.46
469 mSv ($1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$) in the GOM ROMS and by 2.81 mSv in the NWA ROMS, a difference of 8.65
470 mSv. The Arctic is the primary upstream freshwater source to the Scotian Shelf via the Labrador
471 Sea, and the difference in freshwater transport between the GOM and NWA ROMS is only a small
472 fraction of the projected increase in Arctic freshwater export estimated in the literature. For
473 comparison, Han et al. (2019) projected that freshwater export from the Labrador Sea could
474 increase nearly three-fold, from 110 mSv to 350 mSv, by the end of the 21st Century under a
475 median emissions scenario. The difference between the GOM ROMS and NWA ROMS is only 4%
476 of this increase. In addition, projections for future Arctic freshwater export vary widely, from 130
477 mSv (Haine et al., 2015) to 159 mSv (Vavrus et al., 2012), to 350 mSv (Han et al., 2019), although
478 not all of these projections included present-day estimates for comparison. The difference in
479 freshwater transport between the NWA and GOM ROMS is therefore relatively small compared
480 to the greater uncertainty in the delivery of freshwater from upstream.

481 The difference between the GOM ROMS and NWA ROMS freshwater transport is also only one
482 source of uncertainty in this study. Downscaled model results can vary based on the chosen
483 global model (Alexander et al., 2020; Brickman et al., 2021; Drenkard et al., 2021) and
484 Representative Concentration Pathway (Brickman et al., 2021). Drenkard et al. (2021) suggested
485 downscaling an ensemble of GCMs to mitigate this uncertainty, which this study does not do.
486 However, the changing temperature and salinity signals are robust despite the lack of an
487 ensemble approach, for several reasons. First, the warming signal was consistent across the three
488 models considered by Alexander et al. (2020) and, in the GFDL model, the warming pattern was
489 only weakly impacted by additional resolution refinement. The freshening signal was less
490 consistent across the three models tested in Alexander et al., but freshening on the whole is
491 consistent with recent observational evidence suggesting increased Scotian Shelf Water inflows
492 to the Gulf of Maine because of freshening in the Labrador Sea (Townsend et al., 2015). It also
493 agrees with projected increases in high latitude precipitation in global climate projections (Collins

494 et al., 2013; Knutson and Zeng, 2018; Knutti and Sedláček, 2013). Future efforts with larger
 495 ensembles and downscaled hydrological models are needed to more fully constrain the range of
 496 projected circulation patterns and associated salinity changes.



497
 498 *Figure 10. Colored contours of the average salinity Delta (left) and velocity Delta (right) at the GOM ROMS eastern*
 499 *boundary. Depth in meters is shown on the y axis, and cross-shore distance in km is shown on the x axis, with the*
 500 *coastline to the left. Corresponding color values are given in the color bars on the right. A positive velocity indicates*
 501 *flow toward the GOM. In both plots, contours of the difference in average hindcast velocity between the GOM ROMS*
 502 *and NWA ROMS are overlaid in thin black lines. Solid contours indicate $u_{GOM\ ROMS} - u_{NWA\ ROMS} > 0$ (i.e. GOM ROMS*
 503 *transport toward the GOM is stronger), while dashed contours indicate $u_{GOM\ ROMS} - u_{NWA\ ROMS} < 0$ (i.e. NWA ROMS*
 504 *transport toward the GOM is stronger). Contours are drawn every $0.02\ m\ s^{-1}$, and the zero contour is drawn with a*
 505 *thick black line.*

506 4.1.2 Scotian Shelf Inflows and the Gulf of Maine Inflow Ratio

507 The projected increased velocities (and consequently, transport) at the eastern boundary (Figure
 508 10) help explain several changes downstream. First, they likely caused the increase in the GOM
 509 inflow ratio, because the increase was caused more by increased Scotian Shelf Water inflows
 510 than by decreased Northeast Channel inflows (Supplementary Material, Figure S-2). Second, the
 511 stronger alongshore transport in the GOM ROMS relative to the NWA ROMS (Section 4.1.1)
 512 explains the greater increase in the GOM inflow ratio in the GOM ROMS over the NWA ROMS.
 513 Third, because Scotian Shelf Water inflows are relatively cool compared to Northeast Channel
 514 inflows (Townsend et al., 2015), and because the inflows continue via the coastal current into the
 515 Bay of Fundy, increased Scotian Shelf Water inflows could help explain the relatively small
 516 increases in SST near the coast south of Nova Scotia, in the Bay of Fundy, and along eastern
 517 Maine. In both the hindcast and projected composite years, a mass of cool surface water enters
 518 the domain from the Scotian Shelf, wraps around Nova Scotia, and spreads into the Bay of Fundy,

519 similar to what has been seen in satellite images (Luerssen et al., 2005). In the projected
520 composite year, while the average surface temperature in most of the domain was 16°C, this
521 coastal region remained between 8 and 12°C (Supplementary Material, Figure S-5).

522 4.1.3 Eastern Maine Coastal Current

523 The Eastern Maine Coastal Current (EMCC) has been shown to be an important driver of
524 alongshore HAB dispersal in the GOM (Keafer et al., 2005; Li et al., 2009). The EMCC is driven by
525 a pressure gradient that is influenced by several factors, including river outflow (Bisagni et al.,
526 1996; Brooks, 1994; Keafer et al., 2005), Scotian Shelf inflows (Brooks, 1994; Lynch et al., 1997),
527 and the volume and extent of dense slope water in the Jordan Basin (Brooks, 1994; Lynch et al.,
528 1997). Enhanced Scotian Shelf inflows have been connected to increased EMCC transport
529 (Brooks, 1994). This explanation seems unlikely to explain the presented results, however,
530 because the GOM inflow ratio increased year-round, with no apparent seasonal variability (Figure
531 S-1), while the EMCC transport decreased from February to June and increased from July to
532 November.

533 Increased river discharge can also increase EMCC transport (Pettigrew et al. 2005). As shown in
534 Figure 7, the projected enhancement of river flows associated with climate change (i.e. the
535 Deltas) peaked in June, and was positive from mid-May to mid-September (Figure 7). EMCC
536 transport increased in the projection from mid-July to mid-October. This 60-day lag between
537 enhancement of river flow and enhanced EMCC transport is longer than the 45 day lag between
538 the St. John River and Penobscot Bay that was suggested by Brooks (1994). The lags are of a
539 similar order of magnitude, however, suggesting that river outflow is a reasonable explanation
540 for the increase in transport. An important caveat is that the expected changes in river outflow
541 with climate change are not agreed upon for this region: while most studies find that river
542 discharge is expected to decrease at low latitudes and increase at high latitudes with climate
543 change, they disagree on whether the GOM corresponds to a “high latitude” or “low latitude”
544 regime (e.g. Arnell, 1999; Gosling et al., 2017, 2011; Prudhomme and Davies, 2009).

545 4.2 *P. australis* Potential Growth

546 The temporal and spatial variability in predicted *P. australis* potential growth is driven directly by
547 the variability in ocean temperatures. Temperatures in winter and spring were below the

548 temperature of peak growth (0.45 day^{-1} at approximately 15°C , see Figure 3) in the hindcast and
549 warmed toward peak growth temperatures in the projection. In contrast, temperatures in
550 summer and fall were near to or greater than the peak growth temperature in the hindcast and
551 became too warm in the projection. This happened throughout the domain, as shown in Figure
552 8 and Figure 9. The effects of warming on growth rate were smallest in the Bay of Fundy and
553 Eastern Maine Coast sub-regions because the combination of strong tidal mixing, northerly
554 latitude, and relatively cool inflows from the Scotian Shelf kept temperatures in the species'
555 optimal range of $11\text{--}15^\circ\text{C}$. This explains why seasonally averaged growth potential increased or
556 was unchanged in all seasons in these sub-regions but nowhere else in the domain (Figure 9).

557 Although projected potential growth rates at the surface decreased in every sub-region in
558 summer, the effect diminished with depth. In the Bay of Fundy and Eastern Maine Coast sub-
559 regions, 10m potential growth rate did not change (Figure 8) in the summer. This is logical,
560 because sub-surface waters are typically cooler than surface waters and less affected by
561 atmospheric warming and solar radiation, depending on the mixed layer depth. It is also
562 important, because sub-surface *P. australis* populations have been found to seed *Pseudo-*
563 *nitzschia* blooms off the coasts of Ireland (Cusack et al., 2015), Washington state (Trainer et al.,
564 2000), and Southern California (Seegers et al., 2015). Just because the surface becomes too warm
565 does not mean that the environment will become inhospitable to *P. australis*; sub-surface
566 populations that are deep enough to be in cooler water but shallow enough to be in the euphotic
567 zone may become more prevalent in seeding future blooms.

568 Light and nutrient availability might also affect *P. australis* blooms in the future, but neither of
569 these parameters are addressed by a simple model of growth based on temperature. In the
570 projection, *P. australis* growth potential increased in the spring, when nutrients are typically
571 abundant and light is limiting until March, and the late fall, when nutrients are typically depleted
572 and light is limiting after September. Therefore, a new or extended spring niche for *P. australis*
573 blooms in April or May seems more likely than an expanded fall niche in late October or
574 November. However, *P. australis* has bloomed in October and November in the GOM since 2016,
575 suggesting that limited light and nutrient availability do not prevent its survival; this is also the
576 time frame when conditions become more favorable for growth in the projection.

577 4.3 *P. australis* Domoic Acid Production

578 Domoic Acid production is a complex and poorly understood process. Laboratory studies have
579 shown *Pseudo-nitzschia* toxicity to be affected by copper exposure (Fuentes and Wikfors, 2013;
580 Maldonado et al., 2002), growth phase (Davidson and Fehling, 2006; Tammilehto et al., 2015;
581 Terseleer et al., 2013), pH (Lundholm et al., 2004) and silicate or iron limitation (Maldonado et
582 al., 2002; Terseleer et al., 2013). In the field, DA concentrations have correlated with low silica-
583 to-nitrogen ratios (Marchetti et al., 2004), but many field studies have been inconclusive
584 (Hardardóttir et al., 2015; Tammilehto et al., 2015). In addition, DA production can vary between
585 species (Lema et al., 2017) and species strains (Fehling et al., 2004b). It is thus a difficult process
586 to predict in the present day, let alone at the end of the 21st Century.

587 Despite the ambiguities surrounding DA production, however, some studies have explored the
588 potential effects of a changing climate on *Pseudo-nitzschia* toxicity. Zhu et al. (2017) found that
589 DA production by a *P. australis* isolate from the 2015 bloom on the U.S. West Coast (McCabe et
590 al., 2016; McKibben et al., 2017) increased with temperature, peaking at 30°C. Thorel et al. (2014)
591 found that DA production by a *P. australis* isolate from the English Channel increased with growth
592 rate, which also increased with temperature. There is therefore precedent that increasing
593 temperatures could increase *P. australis* toxicity in the Gulf of Maine as well, as long as the
594 temperatures remain within the preferred range for growth. There are complicating factors,
595 however, because changing temperatures could also shift the timing of DA production. This could
596 affect the influence of nutrient ratios and predatory pressure, both of which have been shown to
597 induce DA production (Lema et al., 2017; Lundholm et al., 2018), thereby negating or
598 exacerbating the effect of changing temperature. These potential changes are purely speculative
599 and warrant future research.

600 4.4 *P. australis* in the Eastern Gulf of Maine

601 The predicted changes to hydrodynamics and *P. australis* growth potential, when combined,
602 suggest that *P. australis* blooms in the eastern GOM may intensify in the latter half of the 21st
603 Century. First, Clark et al. (2021) established that the most likely introduction pathway of *P.*
604 *australis* to the GOM in 2016 was from the inner Scotian Shelf via the coastal current south of
605 Nova Scotia. Assuming an established upstream population of *P. australis*, increased transport
606 from the Scotian Shelf would increase the delivery of cells to the Bay of Fundy. In addition, Scotian

607 Shelf inflows typically have a silica-to-nitrogen ratio greater than 1, which can support a diatom
608 community (Townsend et al., 2010) and increase the likelihood of a bloom in the Bay of Fundy. A
609 greater silica-to-nitrogen ratio might contribute conversely to decreased DA production,
610 however, which is often associated with low silica-to-nitrogen ratios (Lema et al., 2017; Tatters
611 et al., 2012; Terseleer et al., 2013). Second, average potential growth rates increased from fall to
612 early spring in the eastern GOM, the same time and place of past *P. australis* blooms. The seminal
613 2016 DA event, for example, occurred in September and October along the eastern Maine coast
614 (Clark et al., 2019), and, since 2016, *P. australis* cells have bloomed each year in eastern Maine
615 in the late fall (Chadwick, 2021). Finally, increased EMCC transport in the fall might affect a *P.*
616 *australis* bloom's distribution. The EMCC is known to contribute to the alongshore extent of HABs
617 in the GOM (Anderson et al., 2005; Townsend et al., 2001), and strengthened alongshore
618 transport might carry *P. australis* cells from the eastern GOM to the west. This hypothesis should
619 be the subject of future monitoring efforts and research.

620 4.5 *Pseudo-nitzschia* Community Composition

621 *P. australis* is not the only *Pseudo-nitzschia* species in the GOM: there are currently 15 known
622 species in the region (Clark et al., 2019; Fernandes et al., 2014), some of which (such as
623 *P. plurisecta* and *P. seriata*) are known DA producers. There are several examples of shifts in
624 species composition in response to changing environmental factors on event (Schnetzer et al.,
625 2013, 2007), seasonal (Chadwick, 2021; Fehling et al., 2006; Thessen and Stoecker, 2008),
626 interannual (Clark et al., 2019), and decadal (Lundholm et al., 2010; Parsons et al., 2002) time
627 scales, so it is important to consider how the species assemblage might change as a result of
628 climate change.

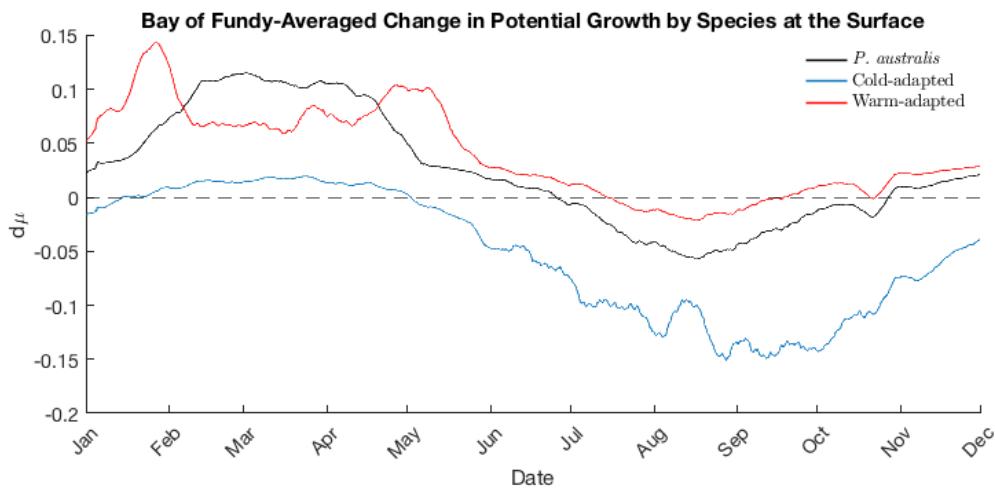
629 To consider an envelope of variability, *P. australis* was compared to a representative “cold-
630 adapted” species and a representative “warm-adapted” species, both of which already exist in
631 the GOM *Pseudo-nitzschia* species assemblage. *P. seriata* has been shown to grow in -2 to 12°C,
632 with a lethal limit between 12–15°C (Smith et al., 1994), and is the representative cold-adapted
633 species. *P. plurisecta* is the representative warm-adapted species because it typically blooms in
634 the GOM in July and August and dominated the species assemblage at 15.5–16°C in 2013 (see
635 Figure 3 in Clark et al., 2019). To estimate changes in these species’ potential growth in the

636 projected GOM, the *P. australis* growth curve was shifted such that growth approached zero at
637 15°C for *P. seriata* and peaked at 17°C for *P. plurisecta* (Supplementary Material, Figure S-6). The
638 same analyses of potential growth and growing season were then calculated. This approach does
639 not seek to understand how all species in the *Pseudo-nitzschia* assemblage might change, but
640 rather to represent an envelope of variability. The full growth rates as a function of temperature
641 for the GOM strains of *P. plurisecta* and *P. seriata* are not known, so this is only an approximation
642 for species whose growth curves peak at higher or lower temperatures. Measured growth rates
643 for *P. seriata* isolated from 15°C Scottish waters were approximately 0.55–0.58 day⁻¹ in a study
644 by Fehling et al. (2004), which is similar to the maximum growth rate for *P. australis* (0.47 day⁻¹)
645 described in Clark et al. (2021). Growth rates for *P. plurisecta* are not currently available in the
646 literature.

647 In the projection, the cold-adapted species' growth potential decreased from May through
648 January, with a slight increase from February through April (Figure 11), and its growing season
649 contracted significantly by 3–6 weeks in each sub-region (Table 2). This is because the projected
650 GOM became too warm for the cold-adapted species, decreasing its ability to grow without
651 further adaptation. Meanwhile, time periods previously too cold for the warm-adapted species
652 became more hospitable, its potential growth increased in parts of the summer (Figure 11), and
653 its growing season in the Bay of Fundy and Eastern Maine Coast sub-regions increased
654 significantly by 4 weeks (Table 2). Average temperatures increased into the warm-adapted
655 species' growing window, and its growing season lengthened by moving into the spring and fall.
656 In the eastern GOM, *P. australis*' projected growing season shifted to replace the cold-adapted
657 species, while it was replaced by the warm-adapted species in its present bloom periods. This
658 suggests that niches might open in both spring and early fall for blooms of species that previously
659 only bloomed in the summer in the GOM, while niches may close for cold-adapted species.

660 These predictions all rely on a growth curve for a single isolate of *P. australis*, which was shown
661 to be similar to other growth curves from the literature (Clark et al., 2021). However, different
662 *Pseudo-nitzschia* species in the GOM and their intraspecific variants might thrive in a variety of
663 temperatures, and new species or strains may be introduced over time. As temperatures
664 increase, it is possible that populations more suited to the warmer temperatures could out-

665 compete cold-adapted ones, such that shifts occur primarily between strains instead of – or in
 666 addition to – between species. For example, a warm-adapted strain of *P. australis* might bloom
 667 in the future, rather than *P. plurisecta*. These predictions should therefore be treated with
 668 caution as an example of what might happen in the future.



669

670 *Figure 11. Change in growth potential at the surface averaged over the Bay of Fundy vs. time for (black) *P. australis*,*

671 (blue) the cold-adapted species, and (red) the warm-adapted species. The Bay of Fundy was chosen as an

672 illustrative sub-region because of its relevance to *P. australis* blooms in the GOM and because it was one of only

673 two sub-regions where change in growing season was significant for all three species.

674

675 *Table 2. Change in growing season (days) for *P. australis* and the representative cold-adapted and warm-adapted*

676 *species. Only numbers that were significant at the 95% confidence level are shown. Note that values are given in days*

677 *in the table and listed as weeks in the text.*

Sub-Region	<i>P. australis</i> Season dt (days)	Cold Species Season dt (days)	Warm Species Season dt (days)
Gulf of Maine	--	-37	--
Scotian Shelf	--	-27	--
Bay of Fundy	+24	-31	+28
Eastern Maine	+19	-39	+26

678

679 4.6 Effects of Physical Changes on Phytoplankton Functional Groups

680 *Pseudo-nitzschia* species are not the only phytoplankton present in the GOM, and any projected
 681 changes, such as to stratification strength and timing, will likely affect other planktonic functional
 682 groups as well. Early stratification onset could lead to an earlier spring bloom (Song et al., 2011;

683 Sverdrup, 1953), which could affect DA production or deplete nutrients before *Pseudo-nitzschia*
684 can grow. This phenomenon has occurred in the GOM and partly explains the suppression of the
685 annual *A. catenella* bloom in 2010 (McGillicuddy et al., 2011, see Section 4.6). Increases in
686 stratification may also be unfavorable to diatoms (Bopp et al., 2005; John et al., 2015), despite
687 the fact that long-term warming has been shown to contribute to shifts in the phytoplankton
688 assemblage toward diatoms and away from dinoflagellates (Hinder et al., 2012). Diatoms
689 (including *Pseudo-nitzschia*) are typically competitive in turbulent, eutrophic waters because they
690 have faster growth rates under high nutrient concentrations (Miller and Wheeler, 2012), but their
691 inability to swim and their hard silica shells necessitate a physical transport process to return
692 them to the surface (Miller and Wheeler, 2012).

693 Increased stratification might suppress wind-induced vertical mixing and reduce the introduction
694 of new nutrients from deeper waters, which presents a challenge to the entire phytoplankton
695 community (Doney, 2006). Dinoflagellates might be more competitive than diatoms in this
696 environment because they can migrate vertically to access nutrients. *Pseudo-nitzschia* might
697 have an advantage relative to other diatoms, however, because they are smaller and lightly
698 silicified, so do not require as much silica (Marchetti et al., 2004; Parsons et al., 2002). Whether
699 that advantage is enough to overcome the disadvantages of negative buoyancy and immobility
700 remains to be seen, especially considering the strong tidally induced mixing in the nearshore
701 GOM. Increased stratification with climate change in the global oceans will have different
702 consequences depending on the latitude and phytoplankton in question (Anderson, 2014;
703 Hallegraeff, 2010; Moore et al., 2008; Wells et al., 2020), and a complete understanding of *P.*
704 *australis* bloom dynamics in the future will require a deeper investigation of how it interacts with
705 the planktonic ecosystem in which it is embedded, including top-down controls (Banse, 1992).

706 4.7 Variability and Episodic Events in the Context of Long-Term Change

707 This study has focused on mean changes in hydrodynamics, temperature, and *Pseudo-nitzschia*
708 potential growth, but variability and episodic events superimposed on the mean change are also
709 important. Events such as the Warm Blob on the U.S. West Coast (McCabe et al., 2016; Ryan et
710 al., 2017; Trainer et al., 2020) and marine heat waves in the GOM (Pershing et al., 2018, 2015)
711 have caused extreme *Pseudo-nitzschia* blooms and fisheries collapses, respectively. In 2010 in

712 the GOM, because of several simultaneous departures from typical conditions, the annual
713 *A. catenella* bloom did not occur despite large cyst abundance portending a large bloom
714 (McGillicuddy et al., 2011). First, abnormally warm and fresh surface waters led to early onset of
715 stratification, an early spring bloom, and depletion of nutrients in surface waters. The resulting
716 mismatch in nutrient availability and *A. catenella* germination suppressed the bloom. Second,
717 strong upwelling-favorable winds reduced alongshore transport via the Maine Coastal Current,
718 limiting the downcoast transport of cells (McGillicuddy et al., 2011). These simultaneous changes
719 in hydrodynamics are an example of how the mean shift alone might not tell the whole story;
720 concurrent changes in multiple factors can alter bloom dynamics or suppress a bloom entirely.
721 Some of the factors that suppressed the 2010 *A. catenella* bloom, such as warm, fresh surface
722 waters and earlier stratification onset, are predicted to increase with climate change, potentially
723 increasing the occurrence of such events in the future.

724 5 Conclusions

725 In this study, the Delta Method was used to downscale climate simulations to a 1–3-km-
726 resolution GOM ROMS and to simulate the effects of climate change on *Pseudo-nitzschia* growth
727 potential in the GOM. Output was analyzed for changes to SST, surface salinity, stratification,
728 inflows, transport, and *P. australis* potential growth and growing season. On average, the GOM
729 is projected to warm by 2°C, freshen by 0.9 PSU, and become more stratified by 3 kg m⁻³. The
730 relative strength of Scotian Shelf inflows to the GOM may increase by as much as 20% in the
731 future, and autumnal transport in the Eastern Maine Coastal Current may strengthen by up to
732 20%. In the climate simulations, as a result of increased SST, *P. australis* surface potential growth
733 increased throughout the domain from November to June and decreased in most of the domain
734 from June to November, due to warming that exceeded the optimal temperature for growth.
735 Sub-surface growth rates did not decrease as much as surface growth rates in the projection due
736 to more moderate temperature increases. As a result of changing potential growth rates, blooms
737 are likely to shift later in the fall and are more likely to persist through winter into spring. As the
738 timing and duration of *P. australis* blooms change, so might the GOM *Pseudo-nitzschia*
739 community composition: cold-adapted species and populations are likely to become less
740 prevalent, while warm-adapted species and populations might fill the seasonal niche previously

741 dominated by *P. australis* and species in the same temperature range. A more complete
742 assessment of *Pseudo-nitzschia* bloom dynamics will require explicit treatment of both bottom-
743 up and top-down controls on these populations, as well as interactions with the plankton
744 ecosystem of which they are a part.

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750 **6 Bibliography**

751 Alexander, M.A., Scott, J.D., Friedland, K.D., Mills, K.E., Nye, J.A., Pershing, A.J., Thomas, A.C.,
752 2018. Projected sea surface temperatures over the 21st century: Changes in the mean,
753 variability and extremes for large marine ecosystem regions of Northern Oceans. *Elem. Sci.
754 Anthr.* 6.

755 Alexander, M.A., Shin, S.-I., Scott, J.D., Curchitser, E., Stock, C., 2020. The Response of the
756 Northwest Atlantic Ocean to Climate Change. *J. Clim.* 33, 405–428.
757 <https://doi.org/10.1175/JCLI-D-19-0117.1>

758 Anderson, D., 2014. HABs in a changing world: a perspective on harmful algal blooms, their
759 impacts, and research and management in a dynamic era of climactic and environmental
760 change. *Harmful Algae* 3–17.

761 Anderson, D.M., Keafer, B.A., McGillicuddy, D.J., Mickelson, M.J., Keay, K.E., Scott Libby, P.,
762 Manning, J.P., Mayo, C.A., Whittaker, D.K., Michael Hickey, J., He, R., Lynch, D.R., Smith,
763 K.W., 2005. Initial observations of the 2005 *Alexandrium fundyense* bloom in southern
764 New England: General patterns and mechanisms. *Deep. Res. Part II Top. Stud. Oceanogr.*
765 52, 2856–2876. <https://doi.org/10.1016/j.dsr2.2005.09.004>

766 Arnell, N.W., 1999. Climate change and global water resources. *Glob. Environ. Chang.* S31–S49.
767 <https://doi.org/10.1507/endocrj.42.83>

768 Banse, K., 1992. Grazing, temporal changes of phytoplankton concentrations, and the microbial
769 loop in the open sea., in: Primary Productivity and Biogeochemical Cycles in the Sea.
770 Springer US, pp. 409–440.

771 Barron, J.A., Bukry, D., Field, D.B., Finney, B., 2013. Response of diatoms and silicoflagellates to
772 climate change and warming in the California Current during the past 250 years and the
773 recent rise of the toxic diatom *Pseudo-nitzschia australis*. *Quat. Int.* 310, 140–154.
774 <https://doi.org/10.1016/j.quaint.2012.07.002>

775 Bates, S.S., Hubbard, K.A., Lundholm, N., Montresor, M., Leaw, C.P., 2018. *Pseudo-nitzschia*,
776 *Nitzschia*, and domoic acid: New research since 2011. *Harmful Algae* 79, 3–43.
777 <https://doi.org/10.1016/j.hal.2018.06.001>

778 Bigelow, H., 1927. Dynamic oceanography of the Gulf of Maine. *Trans. Am. Geophys. Union*
779 206–211. <https://doi.org/10.1063/1.3058361>

780 Bisagni, J.J., Gifford, D.J., Ruhsam, C.M., 1996. The spatial and temporal distribution of the
781 Maine Coastal Current during 1982. *Cont. Shelf Res.* 16, 1–24.

782 Bopp, L., Aumont, O., Cadule, P., Alvain, S., Gehlen, M., 2005. Response of diatoms distribution
783 to global warming and potential implications: A global model study. *Geophys. Res. Lett.* 32,
784 1–4. <https://doi.org/10.1029/2005GL023653>

785 Brickman, D., Alexander, M.A., Pershing, A., Scott, J.D., Wang, Z., 2021. Projections of physical
786 conditions in the Gulf of Maine in 2050. *Elem. Sci. Anthr.* 9, 1–15.
787 <https://doi.org/https://doi.org/10.1525/elementa.2020.20.00055>

788 Brooks, D.A., 1994. A model study of the buoyancy-driven circulation in the Gulf of Maine. *Am.
789 Meteorol. Soc.* 2387–2412.

790 Carton, J.A., Giese, B.S., 2008. A reanalysis of ocean climate using Simple Ocean Data
791 Assimilation (SODA). *Mon. Weather Rev.* 136, 2999–3017.
792 <https://doi.org/10.1175/2007MWR1978.1>

793 Chadwick, C., 2021. Pseudo-nitzschia in the GOM, in: Gulf of Maine Stakeholders' Meeting.

794 Chapman, D.C., Beardsley, R.C., 1989. On the origin of shelf water in the Middle Atlantic Bight.

795 *J. Phys. Oceanogr.* 19, 1–8.

796 Chen, Z., Kwon, Y.O., Chen, K., Fratantoni, P., Gawarkiewicz, G., Joyce, T.M., 2020. Long-Term

797 SST variability on the Northwest Atlantic continental shelf and slope. *Geophys. Res. Lett.*

798 47, 1–11. <https://doi.org/10.1029/2019GL085455>

799 Chin, T.M., Vazquez-Cuervo, J., Armstrong, E.M., 2017. A multi-scale high-resolution analysis of

800 global sea surface temperature. *Remote Sens. Environ.* 200, 154–169.

801 <https://doi.org/10.1016/j.rse.2017.07.029>

802 Clark, S., Hubbard, K.A., Anderson, D.M., McGillicuddy, D.J.J., Ralston, D.K., Townsend, D.W.,

803 2019. Pseudo-nitzschia bloom dynamics in the Gulf of Maine : 2012 – 2016. *Harmful Algae*

804 88, 101656. <https://doi.org/10.1016/j.hal.2019.101656>

805 Clark, S., Hubbard, K.A., McGillicuddy, D.J., Ralston, D.K., Shankar, S., 2021. Investigating

806 Pseudo-nitzschia australis introduction to the Gulf of Maine with observations and models.

807 *Cont. Shelf Res.* 104493. <https://doi.org/10.1016/j.csr.2021.104493>

808 Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Ficheft, T., Friedlingstein, P., Gao, X.,

809 Gutowski, W., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J., Wehner, M.,

810 Allen, M., Andrews, T., Beyerle, U., Bitz, C., Bony, S., Booth, B., Brooks, H., Brovkin, V.,

811 Browne, O., Brutel-Vuilmet, C., Cane, M., Chadwick, R., Cook, E., Cook, K., Eby, M., Fasullo,

812 J., Fischer, E., Forest, C., Forster, P., Good, P., Goosse, H., Gregory, J., Hegerl, G., Hezel, P.,

813 Hodges, K., Holland, M., Huber, M., Huybrechts, P., Joshi, M., Kharin, V., Kushnir, Y.,

814 Larence, D., Lee, R., Liddicoat, S., Lucas, C., Lucht, W., Marotzke, J., Massonnet, F.,

815 Matthews, H.D., Meinshausen, M., Morice, C., Otto, A., Patricola, C., Philippon-Berthier, G.,

816 Prabhat, Rahmstorf, S., Riley, W., Rogelj, J., Saenko, O., Seager, R., Sedlacek, J., Shaffrey, L.,

817 Shindell, D., Sillmann, J., Slater, A., Stevens, B., Stott, P., Webb, R., Zappa, G., Zickfeld, K.,

818 2013. Long-term climate change: Projections, commitments and irreversibility, in: Long-

819 Term Climate Change: Projections, Commitments and Irreversibility. pp. 1029–1136.

820 <https://doi.org/10.1017/CBO9781107415324.024>

821 Csanady, G.T., Hamilton, P., 1988. Circulation of slopewater. *Cont. Shelf Res.* 8, 565–624.

822 [https://doi.org/10.1016/0278-4343\(88\)90068-4](https://doi.org/10.1016/0278-4343(88)90068-4)

823 Cusack, C., Mouríño, H., Moita, M.T., Silke, J., 2015. Modelling Pseudo-nitzschia events off

824 southwest Ireland. *J. Sea Res.* 105, 30–41. <https://doi.org/10.1016/j.seares.2015.06.012>

825 Dai, A., Qian, T., Trenberth, K.E., Milliman, J.D., 2009. Changes in continental freshwater

826 discharge from 1948 to 2004. *Am. Meteorol. Soc.* 22, 2773–2792.

827 <https://doi.org/10.1175/2008JCLI2592.1>

828 Davidson, K., Fehling, J., 2006. Modelling the influence of silicon and phosphorus limitation on

829 the growth and toxicity of Pseudo-nitzschia seriata. *African J. Mar. Sci.* 28, 357–360.

830 <https://doi.org/10.2989/18142320609504177>

831 Doney, S.C., 2006. Plankton in a warmer world. *Nature* 444.

832 Drenkard, E.J., Stock, C., Ross, A.C., Dixon, K.W., Adcroft, A., Alexander, M., Balaji, V., Bograd,

833 S.J., Butenschön, M., Cheng, W., Curchitser, E., Lorenzo, E. Di, Dussin, R., Haynie, A.C.,

834 Harrison, M., Hermann, A., Hollowed, A., Holsman, K., Holt, J., Jacox, M.G., Jang, C.J.,

835 Kearney, K.A., Muhling, B.A., Buil, M.P., Saba, V., Sandø, A.B., Tommasi, D., Wang, M.,

836 2021. Next-generation regional ocean projections for living marine resource management

837 in a changing climate. ICES J. Mar. Sci. <https://doi.org/10.1093/icesjms/fsab100>

838 Dunne, J.P., John, J.G., Adcroft, A.J., Griffies, S.M., Hallberg, R.W., Shevliakova, E., Stouffer, R.J.,
839 Cooke, W., Dunne, K.A., Harrison, M.J., Krasting, J.P., Malyshov, S.L., Milly, P.C.D., Phillipps,
840 P.J., Sentman, L.T., Samuels, B.L., Spelman, M.J., Winton, M., Wittenberg, A.T., Zadeh, N.,
841 2012. GFDL's ESM2 global coupled climate-carbon earth system models. Part I: Physical
842 formulation and baseline simulation characteristics. J. Clim. 25, 6646–6665.
843 <https://doi.org/10.1175/JCLI-D-11-00560.1>

844 Dunne, J.P., John, J.G., Shevliakova, S., Stouffer, R.J., Krasting, J.P., Malyshov, S.L., Milly, P.C.D.,
845 Sentman, L.T., Adcroft, A.J., Cooke, W., Dunne, K.A., Griffies, S.M., Hallberg, R.W., Harrison,
846 M.J., Levy, H., Wittenberg, A.T., Phillips, P.J., Zadeh, N., 2013. GFDL's ESM2 global coupled
847 climate-carbon earth system models. Part II: Carbon system formulation and baseline
848 simulation characteristics. J. Clim. 26, 2247–2267. <https://doi.org/10.1175/JCLI-D-12-00150.1>

849 Fehling, J., Davidson, K., Bolch, C., Tett, P., 2006. Seasonality of *Pseudo-nitzschia*
850 spp. (Bacillariophyceae) in western Scottish waters. Mar. Ecol. Prog. Ser. 323, 91–105.

851 Fehling, J., Davidson, K., Bolch, C.J., Bates, S.S., 2004a. Growth and domoic acid production by
852 *Pseudo-nitzschia seriata* (Bacillariophyceae) under phosphate and silicate limitation. J.
853 Phycol. 40, 674–683. <https://doi.org/10.1111/j.1529-8817.2004.03213.x>

854 Fehling, J., Green, D.H., Davidson, K., Botch, C.J., Bates, S.S., 2004b. Domoic acid production by
855 *Pseudo-nitzschia seriata* (bacillariophyceae) in Scottish waters. J. Phycol. 40, 622–630.
856 <https://doi.org/10.1111/j.1529-8817.2004.03200.x>

857 Fernandes, L.F., Hubbard, K.A., Richlen, M.L., Smith, J., Bates, S.S., Ehrman, J., Léger, C., Mafra,
858 L.L., Kulis, D., Quilliam, M., Libera, K., McCauley, L., Anderson, D.M., 2014. Diversity and
859 toxicity of the diatom *Pseudo-nitzschia Peragallo* in the Gulf of Maine, Northwestern
860 Atlantic Ocean. Deep. Res. Part II Top. Stud. Oceanogr. 103, 139–162.
861 <https://doi.org/10.1016/j.dsr2.2013.06.022>

862 Fuentes, M.S., Wikfors, G.H., 2013. Control of domoic acid toxin expression in *Pseudo-nitzschia*
863 multiseries by copper and silica: Relevance to mussel aquaculture in New England (USA).
864 Mar. Environ. Res. 83, 23–28. <https://doi.org/10.1016/j.marenvres.2012.10.005>

865 Gobler, C.J., Doherty, O.M., Hattenrath-Lehmann, T.K., Griffith, A.W., Kang, Y., Litaker, R.W.,
866 2017. Ocean warming since 1982 has expanded the niche of toxic algal blooms in the
867 North Atlantic and North Pacific oceans. Proc. Natl. Acad. Sci. 114, 4975–4980.
868 <https://doi.org/10.1073/pnas.1619575114>

869 Gosling, S.N., Taylor, R.G., Arnell, N.W., Todd, M.C., 2011. A comparative analysis of projected
870 impacts of climate change on river runoff from global and catchment-scale hydrological
871 models. Hydrol. Earth Syst. Sci. 15, 279–294. <https://doi.org/10.5194/hess-15-279-2011>

872 Gosling, S.N., Zaherpour, J., Mount, N.J., Hattermann, F.F., Dankers, R., Arheimer, B., Breuer, L.,
873 Ding, J., Haddeland, I., Kumar, R., Kundu, D., Liu, J., van Griensven, A., Veldkamp, T.I.E.,
874 Vetter, T., Wang, X., Zhang, X., 2017. A comparison of changes in river runoff from multiple
875 global and catchment-scale hydrological models under global warming scenarios of 1 °C, 2
876 °C and 3 °C. Clim. Change 141, 577–595. <https://doi.org/10.1007/s10584-016-1773-3>

877 Haine, T.W.N., Curry, B., Gerdes, R., Hansen, E., Karcher, M., Lee, C., Rudels, B., Spreen, G., de
878 Steur, L., Stewart, K.D., Woodgate, R., 2015. Arctic freshwater export: Status, mechanisms,
879 and prospects. Glob. Planet. Change 125, 13–35.

880

881 https://doi.org/10.1016/j.gloplacha.2014.11.013
882 Hallegraeff, G.M., 2010. Ocean climate change, phytoplankton community responses, and
883 harmful algal blooms: A formidable predictive challenge. *J. Phycol.* 46, 220–235.
884 https://doi.org/10.1111/j.1529-8817.2010.00815.x
885 Han, G., Ma, Z., Long, Z., Perrie, W., Chassé, J., 2019. Climate Change on Newfoundland and
886 Labrador Shelves: Results from a regional downscaled ocean and sea-ice model under an
887 A1B forcing scenario 2011–2069. *Atmos. - Ocean* 57, 3–17.
888 https://doi.org/10.1080/07055900.2017.1417110
889 Hardardóttir, S., Pančić, M., Tammilehto, A., Krock, B., Møller, E.F., Nielsen, T.G., Lundholm, N.,
890 2015. Dangerous relations in the arctic marine food web: Interactions between toxin
891 producing *Pseudo-nitzschia* diatoms and *Calanus* copepodites. *Mar. Drugs* 13, 3809–3835.
892 https://doi.org/10.3390/md13063809
893 Hasle, G.R., 2002. Are most of the domoic acid-producing species of the diatom genus *Pseudo-*
894 *nitzschia* *cosmopolites*? *Harmful Algae* 1, 137–146. https://doi.org/10.1016/S1568-
895 9883(02)00014-8
896 He, R., McGillicuddy, D.J., 2008. Historic 2005 toxic bloom of *Alexandrium fundyense* in the
897 west Gulf of Maine: 1. In situ observations of coastal hydrography and circulation. *J.*
898 *Geophys. Res. Ocean.* 113, 1–12. https://doi.org/10.1029/2007JC004601
899 He, R., McGillicuddy, D.J., Keafer, B.A., Anderson, D.M., 2008. Historic 2005 toxic bloom of
900 *Alexandrium fundyense* in the western Gulf of Maine: 2. Coupled biophysical numerical
901 modeling. *J. Geophys. Res. Ocean.* 113, 1–12. https://doi.org/10.1029/2007JC004602
902 Hebert, D., Pettipas, R., Brickman, D., Dever, M., 2018. Meteorological, sea ice and physical
903 oceanographic conditions on the Scotian Shelf and in the Gulf of Maine during 2016.
904 Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W., Gravenor, M.B., 2012. Changes
905 in marine dinoflagellate and diatom abundance under climate change. *Nat. Clim. Chang.* 2,
906 271–275. https://doi.org/10.1038/nclimate1388
907 IPCC, Pachauri, R.K., Meyer, L.A., 2014. Climate Change 2014: Synthesis Report. Contribution of
908 Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel
909 on Climate Change. Geneva, Switzerland.
910 John, J.G., Stock, C.A., Dunne, J.P., 2015. A more productive, but different, ocean after
911 mitigation. *Geophys. Res. Lett.* 42, 9836–9845. https://doi.org/10.1002/2015GL066160
912 Kang, D., Curchitser, E.N., 2013. Gulf Stream eddy characteristics in a high-resolution ocean
913 model. *J. Geophys. Res. Ocean.* 118, 4474–4487. https://doi.org/10.1002/jgrc.20318
914 Keafer, B.A., Churchill, J.H., McGillicuddy, D.J., Anderson, D.M., 2005. Bloom development and
915 transport of toxic *Alexandrium fundyense* populations within a coastal plume in the Gulf of
916 Maine. *Deep. Res. Part II Top. Stud. Oceanogr.* 52, 2674–2697.
917 https://doi.org/10.1016/j.dsr2.2005.06.016
918 Knutson, T.R., Zeng, F., 2018. Model assessment of observed precipitation trends over land
919 regions: Detectable human influences and possible low bias in model trends. *J. Clim.* 31,
920 4617–4637. https://doi.org/10.1175/JCLI-D-17-0672.1
921 Knutti, R., Sedláček, J., 2013. Robustness and uncertainties in the new CMIP5 climate model
922 projections. *Nat. Clim. Chang.* 3, 369–373. https://doi.org/10.1038/nclimate1716
923 Large, W.G., Yeager, S.G., 2009. The global climatology of an interannually varying air - sea flux
924 data set. *Clim. Dyn.* 33, 341–364. https://doi.org/10.1007/s00382-008-0441-3

925 Lema, K.A., Latimier, M., Nézan, É., Fauchot, J., Le Gac, M., 2017. Inter and intra-specific growth
926 and domoic acid production in relation to nutrient ratios and concentrations in *Pseudo-*
927 *nitzschia*: phosphate an important factor. *Harmful Algae* 64, 11–19.
928 <https://doi.org/10.1016/j.hal.2017.03.001>

929 Li, Y., He, R., Chen, K., McGillicuddy, D.J., 2015. Variational data assimilative modeling of the
930 Gulf of Maine in spring and summer 2010. *J. Geophys. Res. Ocean.* 132, 1–17.
931 <https://doi.org/10.1002/2014JC010320>.Received

932 Li, Y., He, R., McGillicuddy, D.J., 2014. Seasonal and interannual variability in Gulf of Maine
933 hydrodynamics: 2002–2011. *Deep. Res. Part II Top. Stud. Oceanogr.* 103, 210–222.
934 <https://doi.org/10.1016/j.dsr2.2013.03.001>

935 Li, Y., He, R., McGillicuddy, D.J., Anderson, D.M., Keafer, B.A., 2009. Investigation of the 2006
936 *Alexandrium fundyense* bloom in the Gulf of Maine: In-situ observations and numerical
937 modeling. *Cont. Shelf Res.* 29, 2069–2082. <https://doi.org/10.1016/j.csr.2009.07.012>

938 Li, Y., Stumpf, R.P., McGillicuddy, D.J., He, R., 2020. Dynamics of an intense *Alexandrium*
939 *catenella* red tide in the Gulf of Maine: satellite observations and numerical modeling.
940 *Harmful Algae* 99, 101927. <https://doi.org/10.1016/j.hal.2020.101927>

941 Loder, J.W., Petrie, B., Gawarkiewicz, G., 1998. The coastal ocean off northwestern North
942 America: a large-scale view., in: *The Sea*, Vol 11. pp. 105–133.

943 Luerssen, R.M., Thomas, A.C., Hurst, J., 2005. Relationships between satellite-measured thermal
944 features and *Alexandrium*-imposed toxicity in the Gulf of Maine. *Deep. Res. Part II Top.*
945 *Stud. Oceanogr.* 52, 2656–2673. <https://doi.org/10.1016/j.dsr2.2005.06.025>

946 Lundholm, N., Clarke, A., Ellegaard, M., 2010. A 100-year record of changing *Pseudo-nitzschia*
947 species in a sill-fjord in Denmark related to nitrogen loading and temperature. *Harmful*
948 *Algae* 9, 449–457. <https://doi.org/10.1016/j.hal.2010.03.001>

949 Lundholm, N., Hansen, P.J., Kotaki, Y., 2004. Effect of pH on growth and domoic acid production
950 by potentially toxic diatoms of the genera *Pseudo-nitzschia* and *Nitzschia*. *Mar. Ecol. Prog. Ser.* 273, 1–15. <https://doi.org/10.3354/meps273001>

951 Lundholm, N., Krock, B., John, U., Skov, J., Cheng, J., Pančić, M., Wohlrab, S., Rigby, K., Nielsen,
952 T.G., Selander, E., Harðardóttir, S., 2018. Induction of domoic acid production in diatoms—
953 Types of grazers and diatoms are important. *Harmful Algae*.
954 <https://doi.org/10.1016/j.hal.2018.06.005>

955 Lynch, D.R., Holboke, M.J., Naimie, C.E., 1997. The Maine coastal current: Spring climatological
956 circulation. *Cont. Shelf Res.* 17, 605–634. [https://doi.org/10.1016/S0278-4343\(96\)00055-6](https://doi.org/10.1016/S0278-4343(96)00055-6)

957 Maldonado, M.T., Hughes, M.P., Rue, E.L., Wells, M.L., 2002. The effect of Fe and Cu on growth
958 and domoic acid production by *Pseudo-nitzschia* multiseries and *Pseudo-nitzschia*
959 *australis*. *Limnol. Oceanogr.* 47, 515–526. <https://doi.org/10.4319/lo.2002.47.2.0515>

960 Marchetti, A., Trainer, V.L., Harrison, P.J., 2004. Environmental conditions and phytoplankton
961 dynamics associated with *Pseudo-nitzschia* abundance and domoic acid in the Juan de
962 Fuca eddy. *Mar. Ecol. Prog. Ser.* 281, 1–12. <https://doi.org/10.3354/meps281001>

963 McCabe, R.M., Hickey, B.M., Kudela, R.M., Lefebvre, K.A., Adams, N.G., Bill, B.D., Gulland,
964 F.M.D., Thomson, R.E., Cochlan, W.P., Trainer, V.L., 2016. An unprecedented coastwide
965 toxic algal bloom linked to anomalous ocean conditions. *Geophys. Res. Lett.* 43, 10,366–
966 10,376. <https://doi.org/10.1002/2016GL070023>

967 McGillicuddy, D. J., Townsend, D.W., He, R., Keafer, B.A., Kleindinst, J.L., Li, Y., Manning, J.P.,

969 Mountain, D.G., Thomas, M.A., Anderson, D.M., 2011. Suppression of the 2010
970 *Alexandrium fundyense* bloom by changes in physical, biological, and chemical properties
971 of the Gulf of Maine. *Limnol. Oceanogr.* 56, 2411–2426.
972 <https://doi.org/10.4319/lo.2011.56.6.2411>

973 McGillicuddy, D.J., Townsend, D.W., He, R., Keafer, B.A., Kleindinst, J.L., Li, Y., Manning, J.P.,
974 Mountain, D.G., Thomas, M.A., Anderson, D.M., 2011. Suppression of the 2010
975 *Alexandrium fundyense* bloom by changes in physical, biological, and chemical properties
976 of the Gulf of Maine. *Limnol. Oceanogr.* 56, 2411–2426.
977 <https://doi.org/10.4319/lo.2011.56.6.2411>

978 McGillicuddy, D.J., Townsend, D.W., Keafer, B.A., Thomas, M.A., Anderson, D.M., 2014. Georges
979 Bank: A leaky incubator of *Alexandrium fundyense* blooms. *Deep. Res. Part II Top. Stud.*
980 *Oceanogr.* 103, 163–173. <https://doi.org/10.1016/j.dsr2.2012.11.002>

981 McKibben, S.M., Peterson, W., Wood, A.M., Trainer, V.L., Hunter, M., White, A.E., 2017. Climatic
982 regulation of the neurotoxin domoic acid. *Proc. Natl. Acad. Sci.* 114, 239–244.
983 <https://doi.org/10.1073/pnas.1606798114>

984 Mesinger, F., DiMego, G., Kalnay, E., Mitchell, K., 2006. North American Regional Reanalysis.
985 *Bull. Am. Meteorol. Soc.* 87, 343–360. <https://doi.org/10.1175/BAMS-87-3-343>

986 Miller, C.B., Wheeler, P.A., 2012. *Biological Oceanography*.

987 Moore, S.K., Dreyer, S.J., Ekstrom, J.A., Moore, K., Norman, K., Klinger, T., Allison, E.H., Jardine,
988 S.L., 2020. Harmful algal blooms and coastal communities: Socioeconomic impacts and
989 actions taken to cope with the 2015 U.S. West Coast domoic acid event. *Harmful Algae* 96,
990 101799. <https://doi.org/10.1016/j.hal.2020.101799>

991 Moore, S.K., Mantua, N.J., Salathé, E.P., 2011. Past trends and future scenarios for
992 environmental conditions favoring the accumulation of paralytic shellfish toxins in Puget
993 Sound shellfish. *Harmful Algae* 10, 521–529. <https://doi.org/10.1016/j.hal.2011.04.004>

994 Moore, S.K., Trainer, V.L., Mantua, N.J., Parker, M.S., Laws, E.A., Backer, L.C., Fleming, L.E.,
995 2008. Impacts of climate variability and future climate change on harmful algal blooms and
996 human health. *Environ. Heal.* 12, 1–12. <https://doi.org/10.1186/1476-069X-7-S2-S4>

997 Palmer, M.C., Deroba, J.J., Legault, C.M., Brooks, E.N., 2016. Comment on “Slow adaptation in
998 the face of rapid warming leads to collapse of the Gulf of Maine cod fishery.” *Science* (80-
999). 352, 423. <https://doi.org/10.1126/science.aae0463>

1000 Park, J.M., Archer, S.D., Hubbard, K.A., Poulton, N., Countway, P.D., 2018. Effects of phosphate
1001 limitation on cell growth and toxin production in *Pseudo-nitzschia* in the Gulf of Maine, in:
1002 Oral Presentation at the AGU Ocean Sciences Meeting. American Geophysical Union,
1003 Portland, Oregon.

1004 Parsons, M.L., Dortch, Q., Turner, R.E., 2002. Sedimentological evidence of an increase in
1005 *Pseudo-nitzschia* (Bacillariophyceae) abundance in response to coastal eutrophication.
1006 *Limnol. Oceanogr.* 47, 551–558. <https://doi.org/10.4319/lo.2002.47.2.00551>

1007 Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Bris, A., Le, Mills, K.E., Nye, J.A.,
1008 Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., Thomas, A.C., 2016. Response to
1009 comments on “Slow adaptation in the face of rapid warming leads to collapse of the Gulf
1010 of Maine cod fishery. *Science* (80-). 352, 423. <https://doi.org/10.1126/science.aae0463>

1011 Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A.,
1012 Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., Thomas, A.C., 2015. Slow

1013 adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery.
1014 *Science* (80-). 350, 809–812. <https://doi.org/10.1126/science.aac9819>

1015 Pershing, A.J., Mills, K.E., Dayton, A.M., Franklin, B.S., Kennedy, B.T., 2018. Evidence for
1016 adaptation from the 2016 marine heatwave in the Northwest Atlantic Ocean.
1017 *Oceanography* 31. [https://doi.org/https://doi.org/10.5670/oceanog.2018.213](https://doi.org/10.5670/oceanog.2018.213)

1018 Pettigrew, N.R., Churchill, J.H., Janzen, C.D., Mangum, L.J., Signell, R.P., Thomas, A.C.,
1019 Townsend, D.W., Wallinga, J.P., Xue, H., 2005. The kinematic and hydrographic structure of
1020 the Gulf of Maine Coastal Current. *Deep. Res. Part II Top. Stud. Oceanogr.* 52, 2369–2391.
1021 <https://doi.org/10.1016/j.dsr2.2005.06.033>

1022 Prudhomme, C., Davies, H., 2009. Assessing uncertainties in climate change impact analyses on
1023 the river flow regimes in the UK. Part 1: Baseline climate. *Clim. Change* 93, 177–195.
1024 <https://doi.org/10.1007/s10584-008-9464-3>

1025 Ralston, D.K., Moore, S.K., 2020. Modeling harmful algal blooms in a changing climate. *Harmful
1026 Algae* 91, 101729. <https://doi.org/10.1016/j.hal.2019.101729>

1027 Ryan, J.P., Kudela, R.M., Birch, J.M., Blum, M., Bowers, H.A., Chavez, F.P., Doucette, G.J.,
1028 Hayashi, K., Marin, R., Mikulski, C.M., Pennington, J.T., Scholin, C.A., Smith, G.J., Woods, A.,
1029 Zhang, Y., 2017. Causality of an extreme harmful algal bloom in Monterey Bay, California,
1030 during the 2014–2016 northeast Pacific warm anomaly. *Geophys. Res. Lett.* 44, 5571–
1031 5579. <https://doi.org/10.1002/2017GL072637>

1032 Saba, V.S., Griffies, S.M., Anderson, W.G., Winton, M., Alexander, M.A., Delworth, T.L., Hare,
1033 J.A., Harrison, M.J., Rosati, A., Vecchi, G.A., Zhang, R., 2016. Enhanced warming of the
1034 Northwest Atlantic Ocean under climate change. *J. Geophys. Res. Ocean.* 121, 118–132.
1035 <https://doi.org/10.1002/2015JC011346>

1036 Santiago-Morales, I.S., García-Mendoza, E., 2011. Growth and domoic acid content of *Pseudo-*
1037 *nitzschia australis* isolated from northwestern Baja California, Mexico, cultured under
1038 batch conditions at different temperatures and two Si:NO₃ ratios. *Harmful Algae* 12, 82–
1039 94. <https://doi.org/10.1016/j.hal.2011.09.004>

1040 Schnetzer, A., Jones, B.H., Schaffner, R.A., Cetinic, I., Fitzpatrick, E., Miller, P.E., Seubert, E.L.,
1041 Caron, D.A., 2013. Coastal upwelling linked to toxic *Pseudo-nitzschia australis* blooms in
1042 Los Angeles coastal waters, 2005–2007. *J. Plankton Res.* 35, 1080–1092.
1043 <https://doi.org/10.1093/plankt/fbt051>

1044 Schnetzer, A., Miller, P.E., Schaffner, R.A., Stauffer, B.A., Jones, B.H., Weisberg, S.B., DiGiacomo,
1045 P.M., Berelson, W.M., Caron, D.A., 2007. Blooms of *Pseudo-nitzschia* and domoic acid in
1046 the San Pedro Channel and Los Angeles harbor areas of the Southern California Bight,
1047 2003–2004. *Harmful Algae* 6, 372–387. <https://doi.org/10.1016/j.hal.2006.11.004>

1048 Seegers, B.N., Birch, J.M., Marin, R., Scholin, C.A., Caron, D.A., Seubert, E.L., Howard, M.D.A.,
1049 Robertson, G.L., Jones, B.H., 2015. Subsurface seeding of surface harmful algal blooms
1050 observed through the integration of autonomous gliders, moored environmental sample
1051 processors, and satellite remote sensing in southern California. *Limnol. Oceanogr.* 60, 754–
1052 764. <https://doi.org/10.1002/1no.10082>

1053 Shchepetkin, A., McWilliams, J.C., 2005. The regional oceanic modeling system (ROMS): A split-
1054 explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model.* 9,
1055 347–404.

1056 Shchepetkin, A.F., McWilliams, J.C., 2003. A method for computing horizontal pressure-gradient

1057 force in an oceanic model with a nonaligned vertical coordinate. *J. Geophys. Res.* 108,
1058 3090.

1059 Shin, S.-I., Alexander, M.A., 2020a. Dynamical downscaling of future hydrographic changes over
1060 the Northwest Atlantic Ocean. *Am. Meteorol. Soc.* 33, 2871–2890.
1061 <https://doi.org/10.1175/JCLI-D-19-0483.1>

1062 Shin, S.-I., Alexander, M.A., 2020b. Dynamical downscaling of future hydrographic changes over
1063 the Northwest Atlantic Ocean. *J. Clim.* 33, 2871–2890. <https://doi.org/10.1175/jcli-d-19-0483.1>

1065 Smith, R.E.H., Stapleford, L.C., Ridings, R.S., 1994. The acclimate response of growth,
1066 photosynthesis, composition, and carbon balance to temperature in the psychrophilic ice
1067 diatom *Nitzschia seriata*. *J. Phycol.* 30, 8–16.
1068 <https://doi.org/https://doi.org/10.1111/j.0022-3646.1994.00008.x>

1069 Song, H., Ji, R., Stock, C., Kearney, K., Wang, Z., 2011. Interannual variability in phytoplankton
1070 blooms and plankton productivity over the Nova Scotian Shelf and in the Gulf of Maine.
1071 *Mar. Ecol. Prog. Ser.* 426, 105–118. <https://doi.org/10.3354/meps09002>

1072 Sverdrup, H.U., 1953. On conditions for the vernal bloom of phytoplankton.
1073 *J.Cons.Perm.Int.Explor.Mer* 18, 287–295.

1074 Tammilehto, A., Nielsen, T.G., Krock, B., Møller, E.F., Lundholm, N., 2015. Induction of domoic
1075 acid production in the toxic diatom *Pseudo-nitzschia seriata* by calanoid copepods. *Aquat.*
1076 *Toxicol.* 159, 52–61. <https://doi.org/10.1016/j.aquatox.2014.11.026>

1077 Tatters, A.O., Fu, F.X., Hutchins, D.A., 2012. High CO₂ and silicate limitation synergistically
1078 increase the toxicity of *Pseudo-nitzschia fraudulenta*. *PLoS One* 7.
1079 <https://doi.org/10.1371/journal.pone.0032116>

1080 Terseleer, N., Gypens, N., Lancelot, C., 2013. Factors controlling the production of domoic acid
1081 by *Pseudo-nitzschia* (Bacillariophyceae): A model study. *Harmful Algae* 24, 45–53.
1082 <https://doi.org/10.1016/j.hal.2013.01.004>

1083 Thessen, A.E., Stoecker, D.K., 2008. Distribution, abundance and domoic acid analysis of the
1084 toxic diatom genus *Pseudo-nitzschia* from the Chesapeake Bay. *Estuaries and Coasts* 31,
1085 664–672. <https://doi.org/10.1007/s12237-008-9053-8>

1086 Thomas, A.C., Pershing, A.J., Friedland, K.D., Nye, J.A., Mills, K.E., Alexander, M.A., Record, N.R.,
1087 Weatherbee, R., Elisabeth Henderson, M., 2017a. Seasonal trends and phenology shifts in
1088 sea surface temperature on the North American northeastern continental shelf. *Elementa*
1089 5. <https://doi.org/10.1525/elementa.240>

1090 Thomas, A.C., Pershing, A.J., Friedland, K.D., Nye, J.A., Mills, K.E., Alexander, M.A., Record, N.R.,
1091 Weatherbee, R., Elisabeth Henderson, M., 2017b. Seasonal trends and phenology shifts in
1092 sea surface temperature on the North American northeastern continental shelf. *Elementa*
1093 5, 1–17. <https://doi.org/10.1525/elementa.240>

1094 Thomas, M.K., Kremer, C.T., Klausmeier, C.A., Litchman, E., 2012. A global pattern of thermal
1095 adaptation in marine phytoplankton. *Science* (80-). 338, 1085–1088.
1096 <https://doi.org/10.1126/science.1224836>

1097 Thorel, M., Fauchot, J., Morelle, J., Raimbault, V., Le Roy, B., Miossec, C., Kientz-Bouchart, V.,
1098 Clauquin, P., 2014. Interactive effects of irradiance and temperature on growth and domoic
1099 acid production of the toxic diatom *Pseudo-nitzschia australis* (Bacillariophyceae). *Harmful*
1100 *Algae* 39, 232–241. <https://doi.org/10.1016/j.hal.2014.07.010>

1101 Townsend, D.W., McGillicuddy, D.J., Thomas, M.A., Rebuck, N.D., 2014. Nutrients and water
1102 masses in the Gulf of Maine-Georges Bank region: Variability and importance to blooms of
1103 the toxic dinoflagellate *Alexandrium fundyense*. Deep. Res. Part II Top. Stud. Oceanogr.
1104 103, 238–263. <https://doi.org/10.1016/j.dsr2.2013.08.003>

1105 Townsend, D.W., Pettigrew, N.R., Thomas, A.C., 2001. Offshore blooms of the red tide
1106 dinoflagellate, *Alexandrium* sp., in the Gulf of Maine. Cont. Shelf Res. 21, 347–369.
1107 [https://doi.org/10.1016/S0278-4343\(00\)00093-5](https://doi.org/10.1016/S0278-4343(00)00093-5)

1108 Townsend, D.W., Pettigrew, N.R., Thomas, M.A., Neary, M.G., McGillicuddy, D.J., Donnell, J.O.,
1109 2015. Water masses and nutrient sources to the Gulf of Maine. J. Mar. Res. 141, 93–122.
1110 <https://doi.org/10.1038/141548c0>

1111 Townsend, D.W., Rebuck, N.D., Thomas, M.A., Karp-Boss, L., Gettings, R.M., 2010. A changing
1112 nutrient regime in the Gulf of Maine. Cont. Shelf Res. 30, 820–832.
1113 <https://doi.org/10.1016/j.csr.2010.01.019>

1114 Townsend, D.W., Thomas, A.C., Mayer, L.M., Thomas, M.A., Quinlan, J.A., 2006. Oceanography
1115 of the Northwest Atlantic Shelf (1, W), in: The Sea: The Global Coastal Ocean:
1116 Interdisciplinary Regional Studies and Syntheses. Harvard University Press, pp. 119–168.

1117 Trainer, V.L., Adams, N.G., Bill, B.D., Stehr, C.M., Wekell, J.C., Moeller, P., Busman, M.,
1118 Woodruff, D., 2000. Domoic acid production near California coastal upwelling zones, June
1119 1998. Limnol. Oceanogr. 45, 1818–1833. <https://doi.org/10.4319/lo.2000.45.8.1818>

1120 Trainer, V.L., Moore, S.K., Hallegraeff, G., Kudela, R.M., Clement, A., Mardones, J.I., Cochlan,
1121 W.P., 2020. Pelagic harmful algal blooms and climate change: Lessons from nature's
1122 experiments with extremes. Harmful Algae 91, 101591.
1123 <https://doi.org/10.1016/j.hal.2019.03.009>

1124 USGS, 2013. Water Data for the Nation [WWW Document]. URL
1125 <https://waterdata.usgs.gov/nwis>

1126 Vavrus, S.J., Holland, M.M., Jahn, A., Bailey, D.A., Blazey, B.A., 2012. Twenty-first-century arctic
1127 climate change in CCSM4. J. Clim. 25, 2696–2710. <https://doi.org/10.1175/JCLI-D-11-00220.1>

1129 Wells, M.L., Karlson, B., Wulff, A., Kudela, R., Trick, C., Asnaghi, V., Berdalet, E., Cochlan, W.,
1130 Davidson, K., De Rijcke, M., Dutkiewicz, S., Hallegraeff, G., Flynn, K.J., Legrand, C., Paerl, H.,
1131 Silke, J., Suikkanen, S., Thompson, P., Trainer, V.L., 2020. Future HAB science: Directions
1132 and challenges in a changing climate. Harmful Algae 91.
1133 <https://doi.org/10.1016/j.hal.2019.101632>

1134 Xue, H., Chai, F., Pettigrew, N.R., 2000. A model study of the seasonal circulation in the Gulf of
1135 Maine. J. Phys. Oceanogr. 30, 1111–1135. [https://doi.org/10.1175/1520-0485\(2000\)030<1111:AMSOTS>2.0.CO;2](https://doi.org/10.1175/1520-0485(2000)030<1111:AMSOTS>2.0.CO;2)

1137 Zhu, Z., Qu, P., Fu, F., Tennenbaum, N., Tatters, A.O., Hutchins, D.A., 2017. Understanding the
1138 blob bloom: Warming increases toxicity and abundance of the harmful bloom diatom
1139 *Pseudo-nitzschia* in California coastal waters. Harmful Algae 67, 36–43.
1140 <https://doi.org/10.1016/j.hal.2017.06.004>

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1145 7 Supplementary Material

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1147 7.1 Additional Information Regarding the Delta Method and Boundary Conditions

1148 Delta method sources and application:

1149

1150 *Table S-3 - Model fields to which Deltas were added, and the source from which Deltas were calculated. Note that*
 1151 *ROMS can read humidity as either relative humidity (%) or specific humidity (g kg⁻¹)*

Description	ROMS Variable	Units	Source
3D salinity	salt	PSU	
3D temperature	temp	°C	
3D velocity	u/v	m/s	NWA ROMS output
2D sea surface height	zeta	m	
Sea level air pressure	P _{air}	mbar	
Surface relative humidity	Q _{air}	%	
Surface air temperature	T _{air}	°C	
10m wind velocity	U _{wind} /V _{wind}	m s ⁻¹	
Rainfall rate	rain	kg (m ⁻² s ⁻¹)	GFDL-ESM2M
Downwelling longwave radiation	lwradiad	W m ⁻²	
Downwelling shortwave radiation	swrad	W m ⁻²	
River runoff	River transport	m ³ s ⁻¹	GFDL-ESM2M

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1156 GOM ROMS Boundary Conditions:

Variable	Boundary Type
Free-surface (eta)	Chapman implicit
2-D (depth-averaged) velocity (u/v)	Flather
3-D velocity (u/v)	Radiation
Temperature/Salinity	Radiation-Nudging

1157

1158 More details about how the Delta Method was implemented:

1159 1. Monthly Deltas were calculated from the variables on the NWA ROMS grid.

1160 2. The result from step 1 was interpolated from the NWA ROMS grid to the GOM ROMS grid

1161 with the Rutgers toolbox function, roms2roms.m (This uses the Matlab function

1162 TriScatteredInterp, which in turn uses a Delaunay triangulation of the variable to generate a

1163 function that goes through the input points and can be queried at any 3-D point.)

1164 3. The interpolated Delta value was extracted at the correct indices for each boundary. Depth-

1165 integrated velocities were calculated at all grid cells and then extracted at the boundaries.

1166 4. The result of #3 was added to the hindcast boundary conditions.

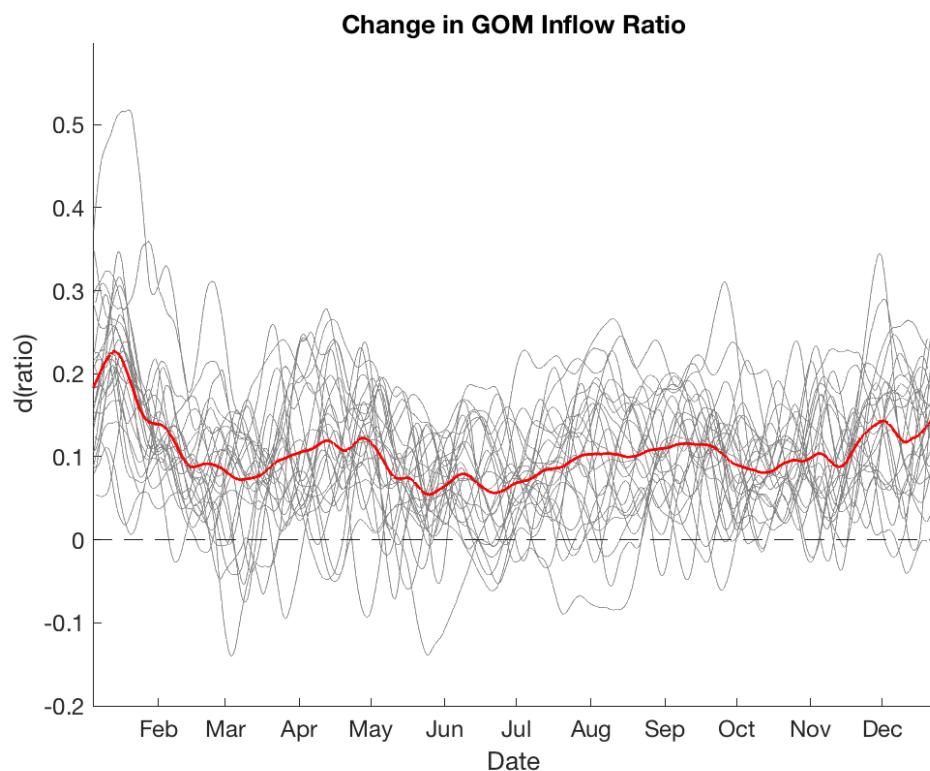
1167 5. The model was re-run with the same setup as the hindcast but with the new initial and

1168 boundary conditions.

1169

1170 7.2 Results

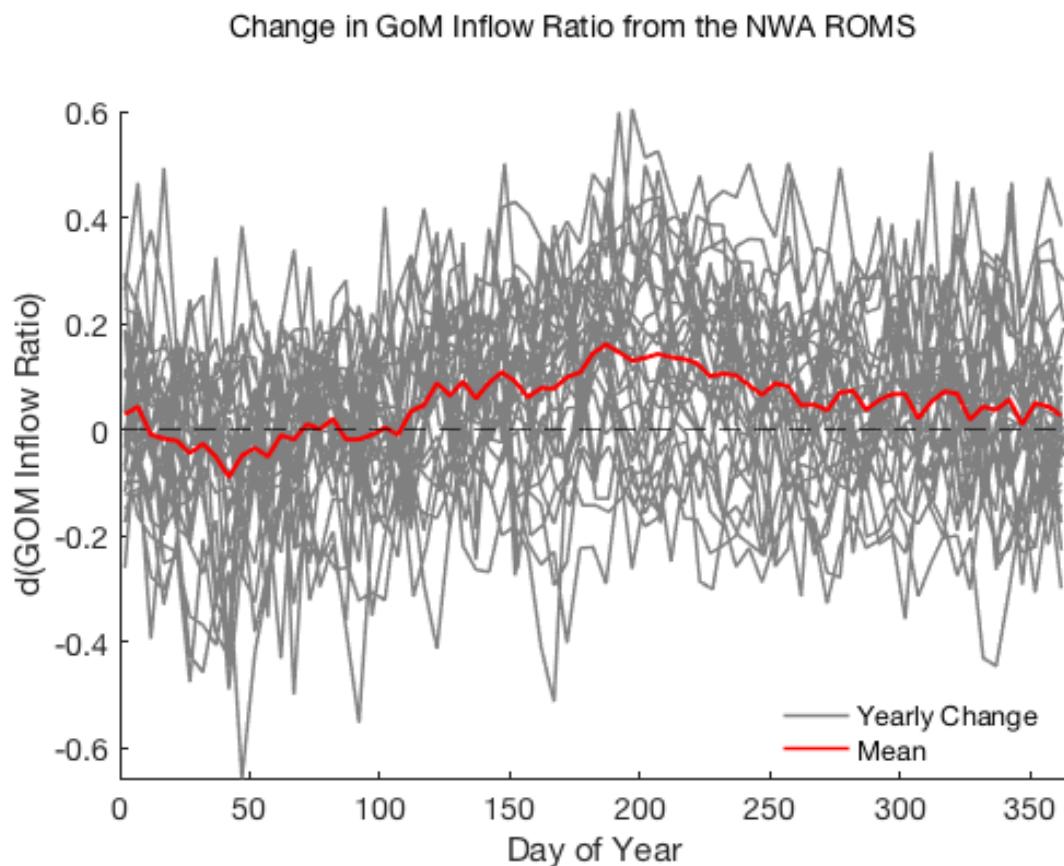
1171 In the projection the inflow ratio increased by 0.1 on average, or 20% of the hindcast ratio.



1172

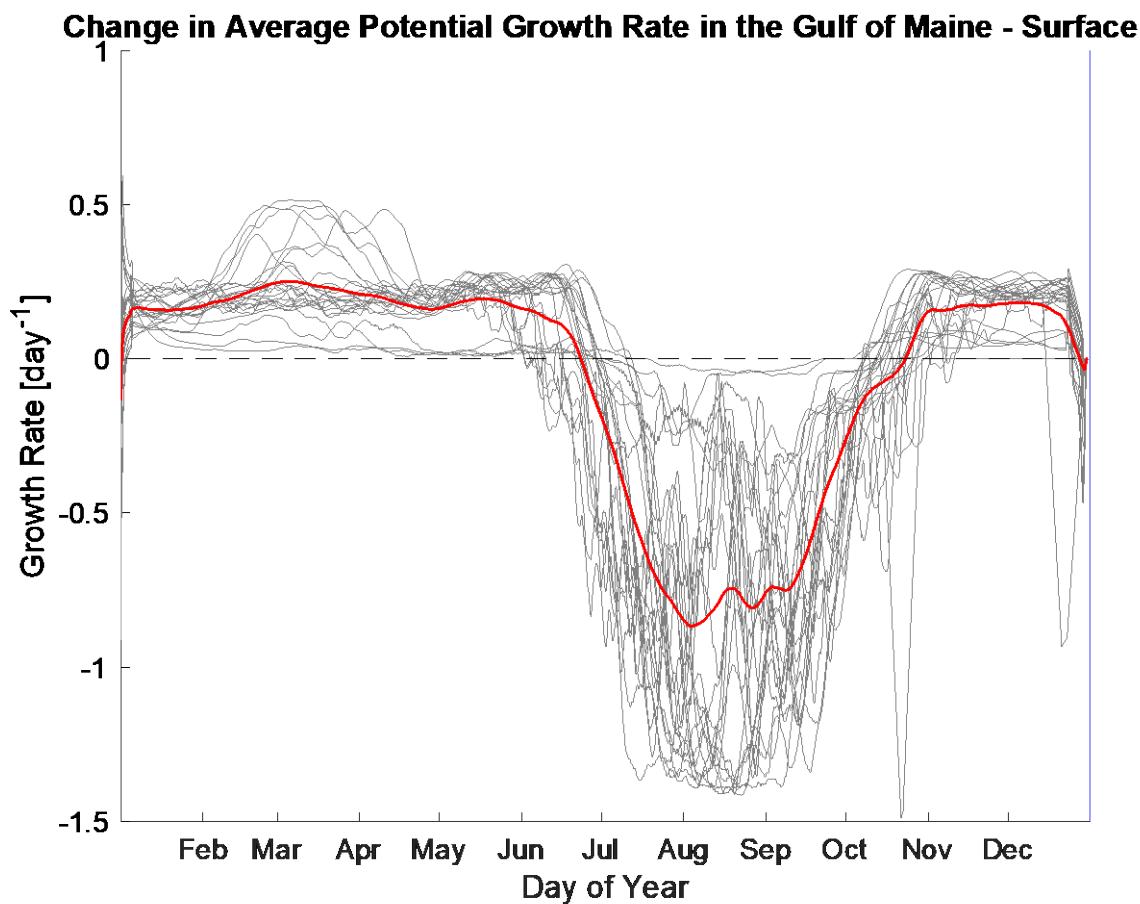
1173 *Figure S-1 – Change in GOM inflow ratio vs. day of the year. The differences between individual projections and*
1174 *hindcasts for each year are plotted in grey. The difference between the projected composite year and the hindcast*
1175 *composite year is plotted in red. Data were smoothed over a weekly time scale before plotting.*

1176 Both models projected an increase in the GOM inflow ratio.



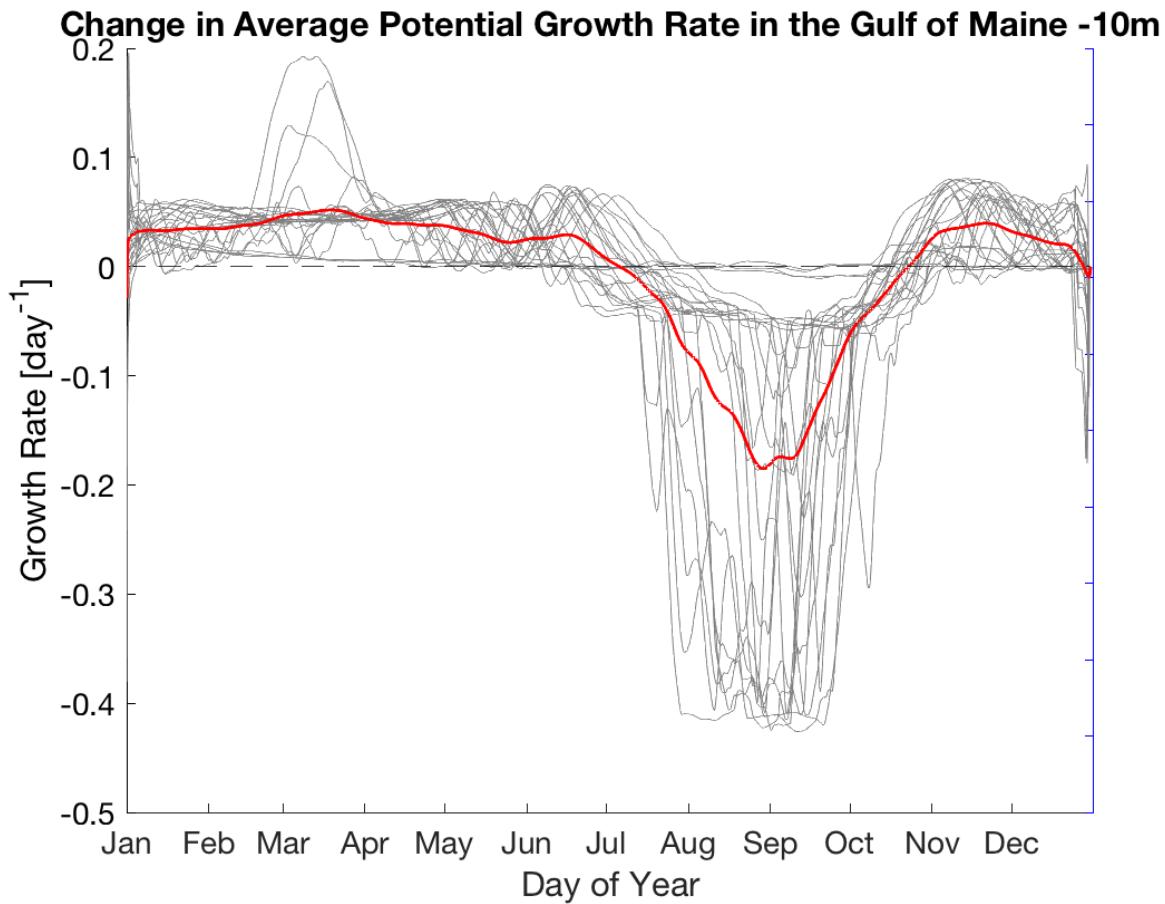
1177
1178 *Figure S-2 - Change in the GOM inflow ratio vs. day of the year as calculated from NWA ROMS output. The*
1179 *differences between individual projections and hindcasts for each year are plotted in grey. The difference between*
1180 *the projected composite year and the hindcast composite year is plotted in red. The ratio was calculated and*
1181 *plotted at the 3-day output resolution of the NWA ROMS.*

1182



1183

1184 *Figure S-3 – Change in *P. australis* potential growth at the surface vs. day of the year. The differences between*
1185 *individual projections and hindcasts for each year are plotted in grey. The difference between the projected*
1186 *composite year and the hindcast composite year is plotted in red. Data were averaged over the Gulf of Maine*
1187 *before plotting.*



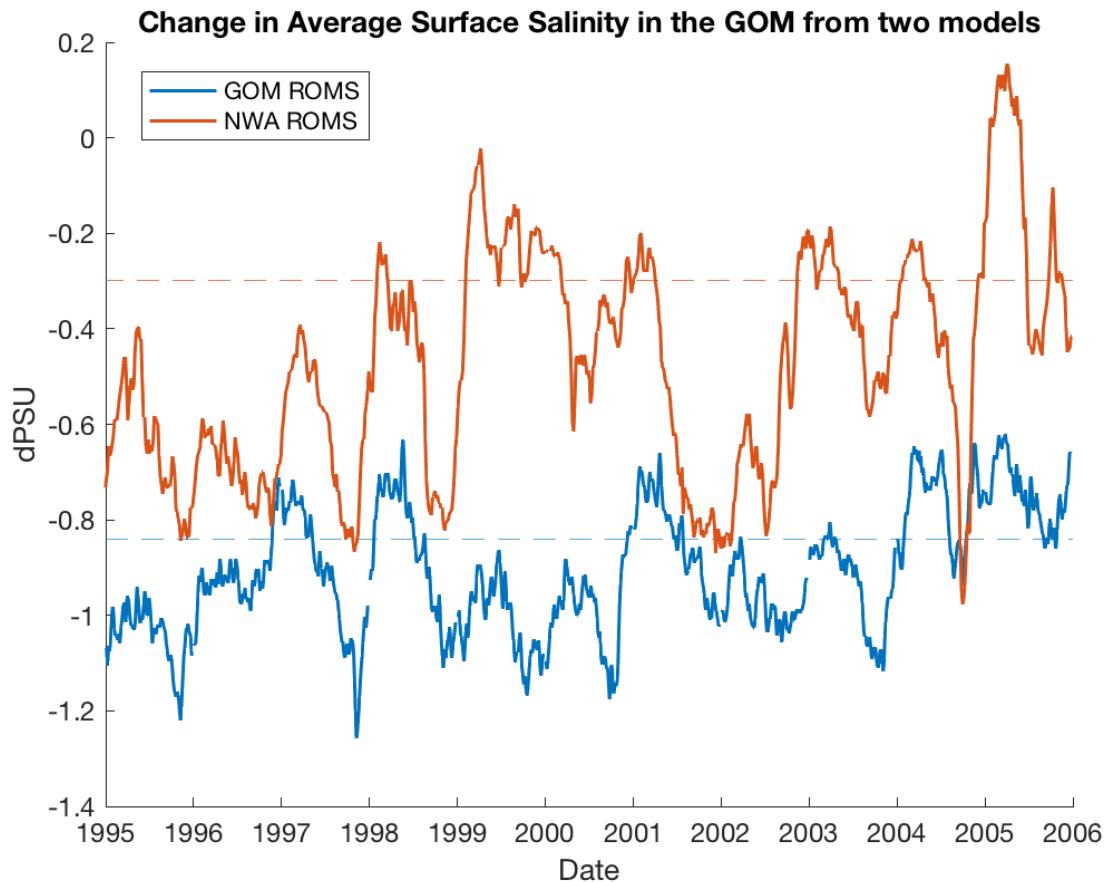
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Figure S-4 - Change in *P. australis* potential growth at the surface vs. day of the year. The differences between individual projections and hindcasts for each year are plotted in grey. The difference between the projected composite year and the hindcast composite year is plotted in red. Data were averaged over the Gulf of Maine before plotting

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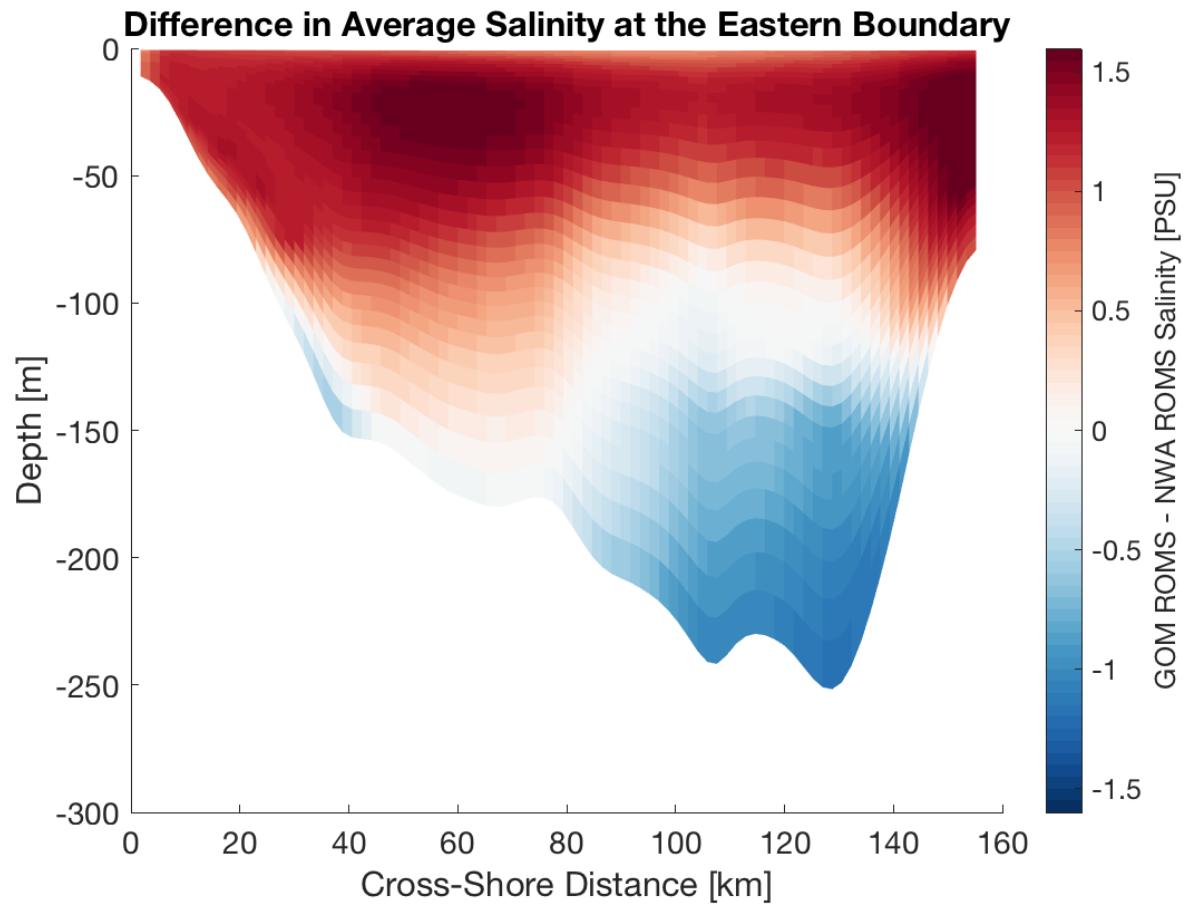
1194 7.3 Discussion

1195 Surface salinity decreased by 0.3 PSU on average in the NWA ROMS projection within the GOM
1196 ROMS domain, but by 0.9 PSU on average in the GOM ROMS projection.



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Figure S-5 - Change in average surface salinity in the GOM ROMS domain vs. time from (blue) the GOM ROMS and (red) the NWA ROMS. NWA ROMS data were interpolated to the GOM ROMS grid before plotting. Data are only plotted for the time period when the two model simulations overlap.

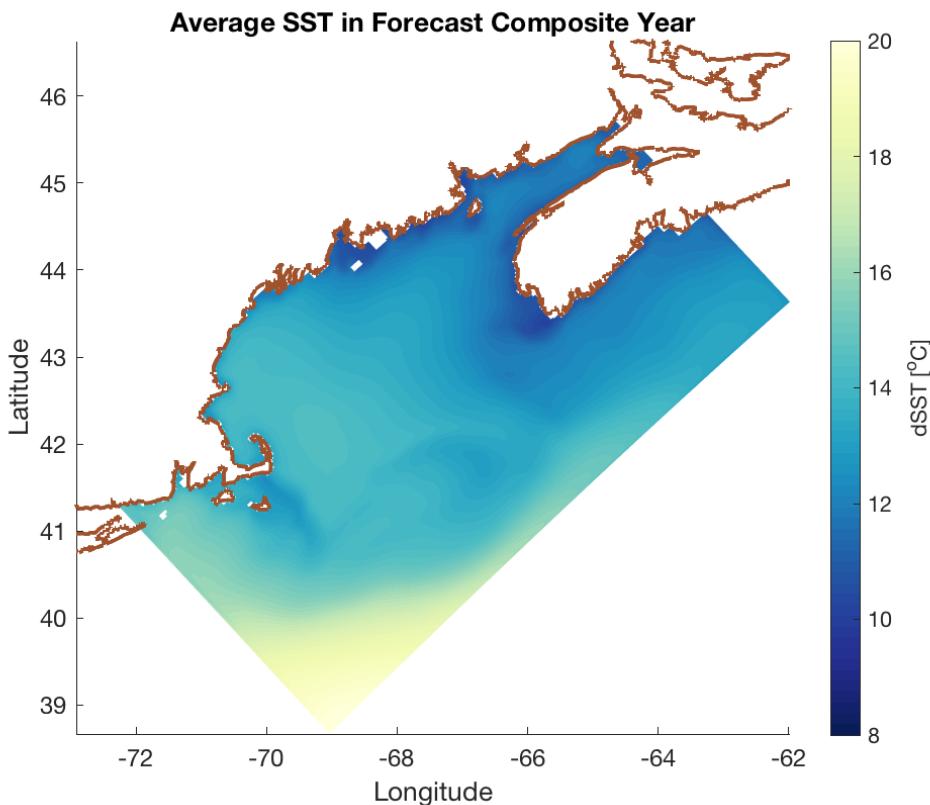


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Figure S-6 - Contours of the difference in average salinity between the GOM ROMS and the NWA ROMS at the GOM ROMS eastern boundary. Depth in meters is shown on the y axis, and cross-shore distance in km is shown on the x axis, with the coastline to the left. Corresponding color values are given in the color bars on the right.

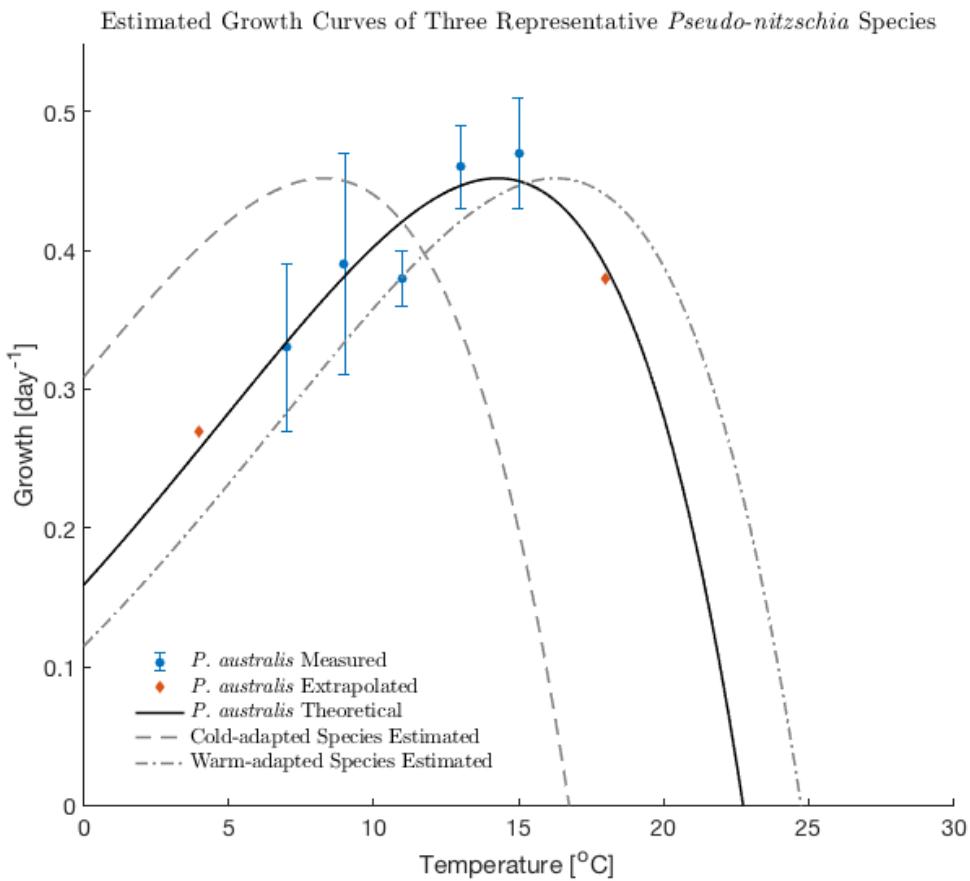
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1209 In the projected composite year, while the average surface temperature in most of the domain
1210 was 16°C, this water mass remained between 8 and 12°C.



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1212 *Figure S-7 - Average SST in the projected composite year. Color scale is defined by the color bar on the right.*

1213 To assess how these species' growth might change as a result of warming temperatures, the *P.*
1214 *australis* growth curve was shifted to their corresponding temperature ranges such that the curve
1215 approached zero at 15°C for *P. seriata* and growth peaked at 17°C for *P. plurisecta*.



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1217 *Figure S-8 – Same as Figure 3, but with growth curves for a hypothetical cold-adapted species (dashed line) and*
1218 *warm-adapted species (dotted line) included for reference*

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