

1 **Temperature and residence time controls on an estuarine harmful algal bloom: Modeling**
2 **hydrodynamics and *Alexandrium fundyense* in Nauset estuary**

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15 **ABSTRACT**

16 A highly resolved, 3-d model of hydrodynamics and *Alexandrium fundyense* in an estuarine embayment
17 has been developed to investigate the physical and biological controls on a recurrent harmful algal bloom.
18 Nauset estuary on Cape Cod (MA, USA) consists of three salt ponds connected to the ocean through a
19 shallow marsh and network of tidal channels. The model is evaluated using quantitative skill metrics
20 against observations of physical and biological conditions during three spring blooms. The *A. fundyense*
21 model is based on prior model applications for the nearby Gulf of Maine, but notable modifications were
22 made to be consistent with the Nauset observations. The dominant factors controlling the *A. fundyense*
23 bloom in Nauset were the water temperature, which regulates organism growth rates, and the efficient
24 retention of cells due to bathymetric constraints, stratification, and cell behavior (diel vertical migration).
25 Spring-neap variability in exchange altered residence times, but for cell retention to be substantially
26 longer than the cell doubling time required both active vertical migration and stratification that inhibits
27 mixing of cells into the surface layer by wind and tidal currents. Unlike in the Gulf of Maine, the model
28 results were relatively insensitive to cyst distributions or germination rates. Instead, in Nauset, high
29 apparent rates of vegetative cell division by retained populations dictated bloom development. Cyst
30 germination occurred earlier in the year than in the Gulf of Maine, suggesting that Nauset cysts have
31 different controls on germination timing. The model results were relatively insensitive to nutrient
32 concentrations, due to eutrophic conditions in the highly impacted estuary or due to limitations in the
33 spatial and temporal resolution of nutrient sampling. Cell loss rates were inferred to be extremely low
34 during the growth phase of the bloom, but increased rapidly during the final phase due to processes that
35 remain uncertain. The validated model allows a quantitative assessment of the factors that contribute to
36 the development of a recurrent harmful algal bloom and provides a framework for assessing similarly
37 impacted coastal systems.

38 1. INTRODUCTION

39 Harmful algal blooms (HABs) are a global issue, causing significant public health, economic, and
40 ecological problems (Hallegraeff, 1993; Anderson et al., 2012). Paralytic shellfish poisoning (PSP),
41 caused by blooms of the dinoflagellate *Alexandrium fundyense*, is one example of a HAB human
42 poisoning syndrome that frequently impacts the northeastern United States. *A. fundyense* blooms
43 regularly occur over large regions of the Gulf of Maine and separately in embayments and estuaries along
44 the coast (Anderson, 1997). Coastal states maintain extensive monitoring networks to minimize public
45 health impacts, but contaminated and quarantined shellfish resources have significant negative impacts on
46 local and regional economies (Shumway, 1990; Hoagland and Scatasta, 2006). Understanding the
47 fundamental processes governing the development of *A. fundyense* blooms will allow more informed
48 management of the public health risks and better predictive capabilities for how HABs may respond
49 under changing climate conditions and anthropogenic inputs.

50 Previous studies of the physical and biological processes controlling the *A. fundyense* bloom in
51 the Gulf of Maine led to the development of a physical-biological model (Franks and Anderson, 1992;
52 Anderson, Keafer, et al., 2005; McGillicuddy et al., 2005; Stock et al., 2005; He et al., 2008). In turn, this
53 model has been used to evaluate processes that influence bloom development, including basin-scale
54 circulation, wind and river discharge patterns, and cyst and nutrient distributions (McGillicuddy et al.,
55 2005, 2011; Li et al., 2009). The model has undergone continuous refinement and skill assessment as part
56 of an effort to produce weekly and annual forecasts of HAB intensity in the region, and planning is
57 underway to make the Gulf of Maine forecast model operational (McGillicuddy et al., 2011; R. He pers.
58 comm.).

59 In addition to the large-scale Gulf of Maine bloom, independent blooms of *A. fundyense* occur in
60 estuaries and bays along the northeast coast (Anderson, 1997; Anderson and Rengefors, 2006; Hattenrath
61 et al., 2010; Borkman et al., 2014). One example is Nauset estuary on Cape Cod, MA, an area that
62 experiences recurrent *A. fundyense* blooms and PSP toxicity (Anderson and Stolzenbach, 1985; Crespo et
63 al., 2011; Ralston et al., 2014). Major blooms in Nauset led to shellfishing closures in 21 of 23 years from
64 1992 to 2014 (Massachusetts Division of Marine Fisheries). These blooms tend to occur earlier in the
65 year than those in the Gulf of Maine and are localized around three ponds that form the uppermost termini
66 of the estuary (Anderson, 1997; Crespo et al., 2011). Thus, Nauset frequently hosts multiple, concurrent
67 but independent *A. fundyense* blooms each year, making it a natural laboratory for the investigation of *A.*
68 *fundyense* bloom dynamics. Observations and model development from Nauset can inform predictive
69 models of similar blooms occurring in shallow, stratified coastal environments around the world (Ralston
70 et al., 2014; Raine, 2014).

71 Accurate modeling of HABs remains a significant challenge. Some HAB forecast models have
72 demonstrated skill at categorical predictions of impacts on human health (Stumpf et al., 2009), but
73 predictive skill of organism abundance is difficult. Bloom development depends on both physical and
74 biological processes, so model uncertainties in water properties or circulation limit the ability to predict
75 cell concentrations. For example, the *A. fundyense* model for the Gulf of Maine demonstrated skill in
76 hindcasts of several years of blooms (He et al., 2008; Li et al., 2009), but uncertainties in water properties
77 at the open boundaries led to overprediction of a bloom in 2010, a year when no significant
78 concentrations of *A. fundyense* were observed (McGillicuddy et al., 2011). Similarly, concentrations of *A.*
79 *tamarensis* in the St. Lawrence estuary were not simulated accurately because they depended on plume
80 advection processes that were poorly constrained by the model (Fauchot et al., 2008).

81 In this work, we develop, evaluate, and analyze a physical-biological model of *A. fundyense* in
82 Nauset estuary. The aims are to use the model to better understand processes contributing to bloom
83 development in Nauset and to use observations to evaluate and modify the *A. fundyense* model
84 formulation so that it may be useful in similar coastal settings. Observational studies in Nauset in recent
85 years (Crespo et al., 2011; Ralston et al., 2014; D. Anderson, unpub. data) provide extensive data to help
86 constrain uncertainties in both physical and biological parameters. The *A. fundyense* component of the
87 model builds off work in the Gulf of Maine (Stock et al., 2005; He et al., 2008), but is modified in
88 accordance with observations from Nauset. The approach develops a single set of model parameters that
89 are applied to conditions in multiple years, thereby minimizing over-fitting of the model to observations.
90 Similarly, we strive to reduce model complexity that it is not supported by observational data. The model
91 results are used to quantify factors controlling bloom development, including retention of cells due to
92 physical processes and organism behavior, dependence on the distribution and emergence rate of cysts,
93 and scaling with loss rates at bloom termination using a growing degree-day approach.

94 **2. METHODS**

95 **2.1 Study location: Nauset estuary**

96 Nauset estuary is a complex of marshes and submerged tidal kettle ponds on Cape Cod,
97 Massachusetts connected by an inlet through a dynamic barrier beach to the Atlantic Ocean (Fig. 1). The
98 central estuary has a network of tidal channels through a vegetated marsh platform. Three tidal kettle
99 ponds (or salt ponds) - Salt Pond, Town Cove, and Mill Pond (north-to-south) - form the uppermost
100 termini of the estuary and are connected to the central marsh by tidal channels. The maximum depths of
101 the salt ponds range from 6 to 11 m, while the marsh tidal channels are typically 1 to 3 m deep. Tidal
102 forcing is mainly semidiurnal with a range from 1 to 2 m.

103 Nauset estuary has no river input, so the primary sources of freshwater are groundwater and direct
104 precipitation. Groundwater discharge from the Nauset and Monomoy lenses also provides a major source
105 of nutrient loading to the estuary from a densely residential watershed with septic wastewater inputs
106 (Giblin and Gaines, 1990; Portnoy et al., 1998; Colman and Masterson, 2008). Mean monthly
107 precipitation from February to May is about 10 cm (National Climate Data Center (NCDC), Chatham
108 Municipal Airport). The freshwater input and solar heating are sufficient to create stratification in the salt
109 ponds due to both salinity and temperature gradients. Surface-to-bottom salinity gradients in the ponds
110 were typically ~1-2 psu, and thermal stratification ranged from about 1 °C at the beginning of the bloom
111 to greater than 10 °C toward the end (Crespo et al., 2011; Ralston et al., 2014).

112 **2.2 Physical-biological model**

113 *2.2.1 Hydrodynamic model*

114 The hydrodynamic model was developed using the Finite Volume Coastal Ocean Model
115 (FVCOM) (Chen et al., 2003). FVCOM is discretized horizontally with an unstructured grid that allows
116 variable resolution through the domain to resolve bathymetric complexity. The Nauset grid had node
117 spacing ranging from a minimum of less than 10 m in the estuary to 4 km on the open boundary (Fig. 1).
118 The model grid extends about 25 km north and south of Nauset inlet and 25 km offshore. FVCOM uses
119 sigma layers vertically. The results presented here use 21 sigma layers; a 31 layer model was also tested
120 but did not yield substantively different results. FVCOM incorporates surface heat fluxes using the
121 TOGA-COARE bulk air-sea flux algorithm (Fairall et al., 1996, 2003). Turbulence closure is with the
122 General Ocean Turbulence Model (Umlauf and Burchard, 2005), in these simulations using the k- ϵ model
123 (Rodi, 1987; Burchard and Baumert, 1995).

124 In shallow estuarine flows, the hydrodynamic processes are extremely sensitive to bathymetry.
125 High-resolution bathymetry was incorporated into the Nauset model from lidar-derived topographic maps
126 of Cape Cod National Seashore from the U.S. Geological Survey (USGS) (Brock et al., 2007).
127 Bathymetry in subtidal regions too deep for lidar penetration was based on acoustic surveys during this
128 study and from previous observations by investigators from the USGS (Cross et al., 2006) and Woods
129 Hole Oceanographic Institution (WHOI) (Aubrey et al., 1997).

130 Model boundary conditions were based primarily on observations. Water level at the open
131 boundary was taken from the NOAA station at Chatham (#8447435), located 15 km south of Nauset Inlet.
132 Salinity and temperature in the coastal ocean were based on buoy data in Massachusetts Bay from the
133 Gulf of Maine Ocean Observing System (part of the Northeastern Regional Association of Coastal Ocean
134 Observing Systems). Meteorological conditions, including wind speed and direction, air temperature,

135 irradiance, and relative humidity, were from the Massachusetts Department of Environmental Quality
136 monitoring station in Truro (17 km north of Nauset) and, when Truro data were unavailable, the Martha's
137 Vineyard Coastal Observatory (WHOI). Groundwater fluxes were from a groundwater model developed
138 by the USGS that covered the northern half of the estuary (Colman and Masterson, 2008); fluxes into the
139 southern half of the estuary were based on the average groundwater flux in the northern half but made
140 proportional to watershed area. Direct precipitation was added at the surface based on observations from
141 the Chatham Municipal Airport (NCDC, #725069, 3 km east of the tidal station).

142 2.2.2 *A. fundyense* model

143 Although the physical and biological models are described separately, they were run as a single,
144 integrated system. The *A. fundyense* model was based substantially on models previously developed for
145 the Gulf of Maine (Stock et al., 2005; He et al., 2008). The biological model calculates germination and
146 growth rates of *A. fundyense* as a function of environmental conditions including temperature, nutrients,
147 and light based on laboratory experiments (Stock et al., 2005). To adapt the Gulf of Maine model
148 framework to Nauset, the basic approach was to simplify and adjust the model to the extent consistent
149 with observations. Model parameters from the calibration to Nauset observations are listed in Table 1, and
150 others not listed are as described in Stock et al. (2005).

151 Several important modifications were made to the *A. fundyense* model. For cyst germination, an
152 endogenous clock places a rigid constraint on the timing of bloom initiation in the Gulf of Maine
153 (Anderson and Keafer, 1987; Matrai et al., 2005). Peak germination rates in the Gulf of Maine occur
154 April through June, but in Nauset the blooms are often well underway by mid-March (Crespo et al., 2011;
155 Ralston et al., 2014). Observations of cysts from Perch Pond, a coastal embayment similar to Nauset,
156 found that cyst germination was not controlled by an endogenous clock, and that instead cysts could
157 germinate any time of year provided a suitable temperature regime (Anderson and Keafer, 1985;
158 Anderson, 1997). Similarly, excystment experiments on *A. minutum* and *A. tamarensis* cysts from Cork
159 Harbor found no evidence of an endogenous clock, but that temperature did affect germination rate (Ní
160 Rathaille and Raine, 2011). Given the absence of evidence of an endogenous clock for cysts in inshore
161 systems like Nauset, that component was removed from the model. Temperature dependence of cyst
162 germination was retained as in the Gulf of Maine model (Stock et al., 2005). Cyst distributions from
163 benthic surveys of Nauset estuary were mapped in the falls of 2008, 2009, and 2011 (Crespo et al., 2011)
164 and used to force the bottom boundary condition. Model sensitivities to the cyst germination rate and
165 benthic cyst distribution are addressed in the results section.

166 As the water column is seeded by germinating cysts, additional *A. fundyense* cell concentration
167 increases occur through vegetative cell division. Maximum growth rates depend on water temperature,

168 irradiance, and nutrient availability, as in the Gulf of Maine model. The nutrient dependence was assumed
169 to be only on the combined nitrate and nitrite concentration, and concentrations were specified based on
170 observations from the weekly surveys. Nauset estuary is highly impacted by anthropogenic inputs, so
171 nutrient concentrations are generally high (Giblin and Gaines, 1990; Colman and Masterson, 2008; S. Fox
172 unpublished). Simulations were run using a range of half-saturation constants for nitrate (k_N) from the
173 literature. Model results using relatively low k_N (< 0.5 M) were most consistent with observed cell
174 concentrations, but skill did not differ significantly between low k_N and removing the nutrient dependence
175 entirely by setting $k_N=0$.

176 Incorporating the daily variation in irradiance and associated diel vertical migration of *A.*
177 *fundyense* was another important modification from the Gulf of Maine model. Observations have found
178 that diel vertical migration substantially alters the vertical distribution of cells in Salt Pond (Anderson and
179 Stolzenbach, 1985; Crespo et al., 2011). Vertical migration is incorporated through a time-varying
180 vertical advection of cells, with upward velocities during the early morning and downward velocities in
181 the afternoon, as in observations. During daylight hours, maximum cell concentrations typically were 2-3
182 m below the surface, while at night the maximum concentrations descended to 5-6 m. The environmental
183 cues that are driving the observed vertical migration remain uncertain, but in the model we assume that it
184 depends on solar irradiance. Specifically, cells in the model swim up during the day ($I_0 > 75$ W m²) and
185 down at night, with the top of the ambit at $1/k_w$ and the bottom at $2/k_w$. The values for k_w were based on
186 fits to measured profiles of photosynthetically active radiation (PAR), described below. Typical values for
187 k_w were 0.3-0.5 m⁻¹, leading to upper and lower migration limits consistent with the observed cell
188 distributions (Anderson and Stolzenbach, 1985; Crespo et al., 2011). The migration in the model is in
189 phase with the solar cycle rather than beginning ascent before sunrise and descent before sunset
190 (Kamykowski, 1981), a simplification that could be refined. The daily variation in irradiance is also used
191 to calculate cell growth rates, so maximum instantaneous growth rates (μ_{max}) in the Nauset model are
192 greater than growth rates in the Gulf of Maine model that use continuous, daily averaged irradiance.
193 Averaged over the diel cycle, the maximum growth rates in the two models are similar.

194 The decline of *A. fundyense* blooms in the Gulf of Maine has been found to best match
195 observations using a Q_{10} formulation that imposes a strong temperature dependence on cell loss (He et al.,
196 2008). The Q_{10} formulation increases mortality exponentially with temperature and encompasses many
197 potential loss terms including predation, parasitism, and encystment. A similar Q_{10} approach can be used
198 to match observations in Nauset in any single year, but no one formulation simulated the decline of the
199 bloom over the multiple years with different temperature histories. Instead of depending on water
200 temperature, the decline tended to occur at a consistent phase of the bloom that could be described by a

201 degree-day calculation (Ralston et al., 2014). The mechanisms behind the bloom decline in Nauset remain
 202 unresolved, as it may represent loss due to encystment, parasitism by *Amoebophrya* (Velo-Suárez et al.,
 203 2013), or some other process. In the results presented here, the mortality rate increased from 0 to the
 204 maximum value over degree days 500 to 550. The approach is highly empirical, and uses a local, Eulerian
 205 calculation of cumulative degree day (at each grid cell) to represent Lagrangian processes associated with
 206 advecting cells (Ralston et al., 2014). However, as shown in the results, this empirical approach more
 207 effectively represented the decline of blooms over multiple years than any single Q_{10} formulation. The
 208 degree day approach is not causatively linked to specific mechanisms driving the decline of the bloom.

209 2.2.3 Model skill assessment

210 To quantify model performance, we compared results with observations of physical variables
 211 from moored sensors (water level, temperature, salinity) and of *A. fundyense* concentrations from weekly
 212 surveys. For metrics, we focus on the correlation coefficient (r) and a skill score (SS). The correlation
 213 coefficient is the covariance between the model and the observations, while the skill score is the mean
 214 square error normalized by the standard deviation of the observations:

$$215 \quad SS = 1 - \sigma_o^{-2} \frac{1}{N} \sum_{i=1}^N (X_m - X_o)^2 \quad (1)$$

216 where X is the variable of interest, σ is the standard deviation, N is the number of samples, and subscripts
 217 m and o represent the model and observations (Murphy, 1988). The skill score compares the model
 218 prediction to the mean of the observations, and is also described as a modeling efficiency (Stow et al.,
 219 2009). The skill score can be related to the correlation coefficient and two additional terms:

$$220 \quad SS = r^2 - \left(r - \frac{\sigma_m}{\sigma_o} \right)^2 - \left(\frac{\overline{X_m} - \overline{X_o}}{\sigma_o} \right)^2 \quad (2)$$

221 where an overbar represents a time average. The second term is the difference in variance between the
 222 model and the observations, which vanishes when the slope of the regression line is equal to 1. The last
 223 term is the mismatch of the means, and is equal to the intercept of the linear regression. The maximum
 224 skill score is 1, and a skill of 0 represents a mean square error equal to the variance of the observations.

225 Most of the model-data comparisons shown here are from the spring of 2011, which has the most
 226 extensive set of physical and biological observations. Similar, less extensive, observations were made in
 227 2009 and 2012. For consistency, model parameters were developed for the 2011 case and applied to all 3
 228 years rather than tuning coefficients to match each year separately.

229 2.3 Observations

230 2.3.1 Large-scale weekly and high-resolution tidal-cycle surveys

231 Approximately weekly during the spring months of 2009, 2011, and 2012, large-scale surveys
232 were made of Nauset estuary, with sampling at about 30 stations throughout the estuary (Fig. 1): 12
233 surveys from 24 March to 17 June 2009, 13 surveys from 23 March to 16 June 2011, and 11 surveys from
234 15 February to 8 May 2012 (Crespo et al., 2011; Ralston et al., 2014). Surveys occurred around daytime
235 high tides to maximize navigability of the central marsh. Continuous vertical profiles of salinity and
236 temperature were measured with a conductivity-temperature-depth (CTD, SeaBird Electronics SBE
237 19plus) sensor at each station, and in 2011 and 2012, instruments also measured chlorophyll fluorescence
238 (470 nm excitation, 685 nm emission, SeaPoint Sensors) and photosynthetic active radiation (PAR, 400-
239 700 nm, scalar detector, Biospherical Instruments). Water samples for *A. fundyense* cell counts and
240 nutrient concentrations were collected at each station with 2.5 L Niskin bottles. Samples were taken at the
241 surface and, where possible, at 3, 5, 7, and 10 m depths. Details on the sample processing are provided in
242 Crespo et al. (2011) and Ralston et al. (2014).

243 The weekly surveys provided snapshots of Nauset estuary and captured large-scale spatial
244 variability and seasonal trends. To complement the weekly surveys, a series of higher-resolution, higher-
245 frequency surveys around the peak of the *A. fundyense* bloom were conducted in Mill Pond and Salt Pond
246 in 2011 and 2012. These surveys had additional sampling stations to increase the horizontal resolution,
247 and were repeated every 30 to 60 minutes through a tidal cycle. Sampling from a small-boat included the
248 CTD and fluorescence profiles as above, with Niskin bottle samples collected for a subset of the stations
249 at regular depths (surface, 2-3 m, 5 m, 7 m and 10 m, depending on water depth). Representative data
250 from a high-resolution tidal-cycle survey in Salt Pond on 9 May 2011 are used below to illustrate the
251 spatial structure of water properties and *A. fundyense* in the ponds.

252 The chlorophyll fluorometer with the CTD was calibrated in the laboratory using serial dilutions
253 of *A. fundyense* in culture from 16 to 0.5×10^6 cell L^{-1} . Regressions to convert from fluorometer voltage to
254 cell concentration were developed based on the lab tests. Water column profiles from the fluorometer
255 were also compared with cell counts from Niskin bottle samples (Fig. 2). Fluorometer values were
256 extracted from the depth of the water sample, averaging over a depth range equal to the length of the
257 bottle. The fluorometer compared well with the bottle samples when concentrations of *A. fundyense* were
258 greater than about 10^4 cell L^{-1} ; at lower concentrations the chlorophyll signal likely was dominated by
259 other phytoplankton species. The vertical structure in the fluorometer data when *A. fundyense*
260 concentrations were high corresponded with the vertical structure from the bottle sampling profiles, albeit
261 at much higher resolution. Concentrations derived from fluorometer readings tended to be greater than the
262 cell counts by about a factor of 2, perhaps due to the presence of other phytoplankton, although no whole

263 phytoplankton community counts were conducted to assess this. Cell counts from bottle samples were
264 used for model evaluation, but the fluorometer data were used to characterize the spatial distribution of *A.*
265 *fundyense*.

266 2.3.2 Moored instruments

267 Moored, internally recording instruments were deployed during the blooms to provide continuous
268 records of water properties. The configuration of moored sensors varied among years, but typically water
269 level and near-surface and near-bottom temperature and salinity were measured in each pond (Mill Pond,
270 Salt Pond and Town Cove) and in the central marsh (Hemenway) (Fig. 1). In 2009, water level and
271 temperature sensors (Onset HOBO) were deployed at these four locations. In 2010 and 2011, surface and
272 bottom CTDs (Richard Brancker Research) were deployed in the deep parts of Salt Pond and Mill Pond,
273 while Town Cove and Hemenway had shallower water level and temperature sensors. In 2012, surface
274 and bottom CTDs were deployed in the centers of Town Cove, Salt Pond, and Mill Pond, and a water
275 level and temperature sensor was at Hemenway. Sampling intervals for all the moored sensors were 10
276 minutes or less. The moored time-series were compared with the profiling CTD data from the weekly
277 surveys to identify periods when fouling compromised moored data quality. Near-surface conductivity
278 measurements were affected by fouling at several locations toward the end of the deployments, and these
279 data were removed from the analysis.

280 2.3.3 Cyst mapping surveys

281 To map cyst distributions, sediment samples were collected in the falls of 2008, 2009, and 2011
282 at 73 stations around the estuary. Details on sample collection and cyst enumeration are given in Crespo
283 et al. (2011). Cyst counts from the top (0-1 cm) sediment layer were mapped to the model grid to provide
284 the bottom boundary condition for the *A.fundyense* model.

285 3. RESULTS

286 3.1 Hydrodynamics and physical conditions

287 Tidal forcing offshore of Nauset is predominantly semidiurnal with a tidal amplitude of 1 to 2 m.
288 Tidal nonlinearities through the shallow central marsh make tidal water levels in the estuary highly
289 asymmetric, with a brief flood period of elevated velocities (~3-4 h) and a longer, slower ebb (~8-9 h)
290 (Aubrey and Speer, 1985). The hydrodynamic model reproduced the observed tides well, with skill scores
291 typically greater than 0.95 (Fig. 3, Table 2). The nonlinearity of the tide was sensitive to the bottom
292 roughness (z_0) and to relatively modest changes in the bathymetry. Water level observations were used to
293 calibrate the bottom roughness in the model, resulting in $z_0 = 0.024$ m. In the absence of a spatially
294 resolved map of bed composition, bottom roughness was assumed to be spatially uniform.

295 Seasonal warming of water temperatures depended on several factors including the surface heat
296 flux, tidal exchange, and bathymetry. Surface layers of the three ponds warmed faster than the central
297 marsh due to the more limited influx of cooler water from the coastal ocean and the more limited
298 exposure to wind forcing (Ralston et al., 2014). The deeper layers of the ponds remained cooler than the
299 surface, as stratification limited the influence of surface heating at depth. Early in the spring, the salinity
300 anomaly due to groundwater influx was the primary source of stratification, but as the surface layer
301 warmed, temperature became an equal or greater contributor to stratification. The spatial and temporal
302 distribution of seasonal warming in the model (Fig. 4) compared well with observations (Fig. 3 in Ralston
303 et al., 2014). The ponds warmed faster than the central marsh, with temperature increases in Mill Pond
304 and Town Cove leading Salt Pond.

305 Variation in tidal energy affected stratification in the ponds at spring-neap time scales (Fig. 3).
306 During neap tides, tidal velocities and exchange with the coastal ocean decreased, so the surface layers of
307 the ponds warmed and stratification increased (e.g., Apr 24-29). During spring tides, stratification
308 decreased. Wind events also affected stratification in the ponds, both through mixing of the surface layer
309 and by driving coastal set-up that increased influx of cooler coastal ocean water. Diurnal solar heating of
310 the surface layer and convective cooling at night altered water temperature at daily time scales. The
311 model reproduced much of the daily to fortnightly variations in stratification. Stratification in Salt Pond
312 (Fig. 3b) was well represented, including the warming of the surface layer during neap tides and the
313 warming of the lower layer during spring tides. In Mill Pond the temperature variation in the surface layer
314 was reasonably well represented, but the lower layer in the model became too warm, indicative of
315 excessive mixing down from the surface. The extra vertical mixing was insensitive to the turbulence
316 closure, and was apparently due to high rates of numerical mixing associated with steep topography,
317 sigma coordinate systems, and lower order advection schemes (Burchard and Rennau, 2008). As shown
318 later, numerical mixing also smoothed vertical profiles of *A. fundyense*. The skill metrics showed
319 reasonable overall agreement with observed temperatures. For surface waters, most correlations (r^2) were
320 0.8 or greater and skill scores were between 0.4 and 0.9 (Table 2).

321 Large differences in water properties were observed between the ponds and central marsh, as seen
322 in transects through a tidal cycle in Salt Pond (Fig. 5). During the ebb (transects 1 and 2), the pond was
323 strongly stratified and warm water ebbing out into the marsh formed a sharp temperature gradient with
324 cooler water that entered from the coastal ocean during the previous flood (Fig. 5a,b). During the flood
325 (transects 3 and 4), ocean water moved back into the marsh and into Salt Pond (Fig. 5c,d). The ocean
326 water was cooler and saltier, and thus denser than the surface layer of the pond, leading to convective
327 mixing downward near the pond inlet. The model captured the critical elements of this tidal pattern,

328 including the maximum in stratification during the ebb, the front between pond and ocean water, and the
329 downward mixing at the inlet during flood tides. More generally, both the survey and time series data
330 indicate that temperatures in the model corresponded with observations at seasonal and tidal time scales,
331 an important component for *A. fundyense* growth.

332 **3.2 *A. fundyense* population**

333 The *A. fundyense* blooms in Nauset were highly localized within the ponds, with cell
334 concentrations that were substantially greater than in the central marsh (Fig. 6), indicating little exchange
335 of cells between the salt ponds (Crespo et al. 2011). The modeled spatial distribution and seasonal
336 evolution of the bloom were consistent with observations in 2011 (Fig. 2 in Ralston et al., 2014) and other
337 years (e.g., 2009 bloom in Fig. 7 of Crespo et al. 2011). As with temperature, the cell concentration maps
338 were selected to correspond with observations that occurred near high-tide, and thus coastal ocean water
339 in the central marsh had low cell concentrations.

340 A comparison of the model results with mean cell concentrations measured in the weekly surveys
341 finds that the model captured the seasonal trends at multiple stations, especially when variation with depth
342 was considered (Fig. 7). However, the model did not reproduce the bloom phasing among the three ponds,
343 a commonly observed pattern whereby cells accumulate first in Mill Pond, then Town Cove, and lastly
344 Salt Pond. This may be due to discrepancies in water temperature, as the surface waters of Mill Pond and
345 Upper Mill Pond were slightly cooler than observed, and thus growth rates were reduced. The daily
346 variations in cell concentration in the central marsh were greater than at stations in the ponds, as tidal
347 advection brought low concentrations from the coastal ocean during floods and higher concentrations
348 from the ponds during ebbs. The weekly survey data occurred around high tide and therefore
349 corresponded with the lower bound of the concentration envelope for the central marsh. Skill metrics for
350 the cell time series varied by location and year (Table 2). Correlations (r^2) were often greater than 0.5,
351 and while the skill scores were lower, the *A. fundyense* model had positive skill scores in many cases,
352 particularly in the ponds.

353 Tidal cycle transects in Salt Pond provide greater detail on the spatial and temporal variability in
354 *A. fundyense* cell distributions around the peak of the bloom (Fig. 8). During the ebb, cells were
355 concentrated in a relatively thin layer near the pycnocline, with much lower concentrations ebbing out
356 near the surface (Fig. 8a). Late in the ebb as the water level dropped and surface layer thinned, export of
357 cells from the pond increased, but concentrations in the marsh remained lower than in the pond (Fig. 8b).
358 During the following flood, the incoming ocean water was cooler, saltier, and had lower concentrations
359 (Fig. 8c,d). As it entered the pond and mixed down, the layer of cells near the pycnocline was mixed and
360 displaced, reducing cell concentrations near the inlet. Late in the flood, maximum cell concentrations

361 were deeper in the water column and nearer the periphery of the pond (Fig. 8d). The model reproduced
362 the key elements of the observed *A. fundyense* distributions, including the local maxima at the pycnocline,
363 the low concentrations exported late ebb, and the mixing and displacement of cells away from the inlet
364 during the flood. The model had some discrepancies in phasing, for example, the flooding ocean water
365 arrived slightly earlier in the observations than in the model, but overall the comparison with the high-
366 resolution survey data suggests that the model is plausibly representing the hydrodynamics and *A.*
367 *fundyense* in the pond. Subsequent sections use the model to analyze factors controlling bloom
368 development, including the role of vertical migration for cell retention in the ponds, the dependence of the
369 bloom on cyst distribution and germination rate, and the parameterization of bloom termination.

370 **3.3 Vertical migration and residence time**

371 Previous observational studies indicated that the vertical migration pattern of *A. fundyense* in Salt
372 Pond was essential to the high rates of retention in the ponds and facilitated the intense blooms there
373 (Anderson and Stolzenbach, 1985). Most of the observations in this study occurred during daylight hours,
374 making it difficult to diagnose the diel variability in the cell population. Our tidal cycle survey in Salt
375 Pond (Figs. 5 and 8) was also during the day, but additional profiles were collected in the center of the
376 pond at midnight and 8 am the following morning (Fig. 9). The fluorometer profiles were consistent with
377 the conceptual model that during the day cells are concentrated near the pycnocline, about 3 m below the
378 surface and roughly corresponding with the $1/k_w$ level of irradiance, and at night the center of mass is
379 deeper, about 5 m below the surface. The following morning the cells appeared to be moving up toward
380 the surface again. The movement of cells downward at 17:21 was likely due to a combination of vertical
381 migration late in the day and convective mixing due to the jet of denser water flooding from the central
382 marsh (Fig. 5d). The observed profile at 8:04 the following morning was shallower than in the model,
383 which could be due to the phasing of the vertical migration leading the irradiance. Overall however, the
384 observations were consistent with previous studies and with the simple parameterization of vertical
385 migration in the model.

386 To quantify the role of vertical migration in retention of cells in the pond, we ran a series of
387 model experiments. Cell growth and mortality were removed from the model to assess directly the
388 dependence of advective losses on swimming behavior, tidal forcing, and stratification. Representative
389 spring and neap tide cases from Salt Pond (April 17 and April 24, 2011, respectively) were selected as
390 starting points for full model simulations, with growth and mortality turned off. The subsequent evolution
391 of the bloom was due strictly to hydrodynamic processes and various swimming behaviors for *A.*
392 *fundyense*, and cell concentrations decreased through cell export from the pond to the central marsh (Fig.
393 10a). Residence times were calculated by fitting an exponential decay curve to the total cell population in

394 the pond, resulting in an e -folding time scale; the fitted curves are shown with the concentration time
395 series for the spring tide cases (Fig. 10a).

396 Several swimming behaviors were examined. In addition to the base case where cells migrate
397 between $1/k_w$ and $2/k_w$ (“swim”), cases were tested with no vertical migration (“don’t swim”) and with
398 vertical migration to the surface rather than to $1/k_w$ (“swim to surface”) (Fig. 10b). All cases started with
399 the same initial distribution of cells. In addition to the behavior of *A. fundyense*, stratification in the pond
400 alters vertical mixing and thus cell retention, so a case was run with the default vertical migration strategy
401 but barotropic hydrodynamics. The barotropic case assumes uniform water density, removing effects of
402 stratification on turbulent mixing and increasing the vertical mixing of cells by wind and tidal forcing.

403 The numerical experiments showed that residence times for *A. fundyense* depended substantially
404 on the tidal forcing, the swimming behavior, and the model hydrodynamics (Fig. 10b). For reference, the
405 volumetric residence time, equal to the volume of the pond divided by the tidal volume exchange, is
406 shown with dashed lines for spring and neap tides. The *A. fundyense* residence times were all greater than
407 the volumetric exchange rate because cells were not completely, continuously mixed in the pond, as that
408 analytical model assumes. The cases with the default swimming behavior still had longer residence times
409 than the alternatives of not swimming or swimming to the surface. Residence times were longer during
410 neap tides than during spring tides, particularly with vertical migration. During spring tides, not only did
411 the volumetric exchange increase, but vertical mixing of cells into the surface layer also increased,
412 accelerating export of *A. fundyense* from the pond.

413 Decreased residence times for the barotropic cases versus the “swim” and “don’t swim” cases
414 illustrated the importance of vertical mixing for cell retention. Stratification reduced vertical mixing at the
415 pycnocline, which was typically near the upper limit of vertical migration. Turbulent mixing, particularly
416 due to wind stress, was greater in the barotropic case, transporting cells into the surface layer for
417 subsequent export. Wind mixing was the major source of the vertical flux, as a barotropic case without
418 wind forcing had longer residence times than the full physics case (Fig. 10). The barotropic cases also did
419 not include the energetic vertical mixing of cells downward by the dense jet of oceanic water entering the
420 pond during spring flood tides (Fig. 8d), further reducing the tidal exchange of cells. Effective growth
421 rates for these temperature and light conditions were $0.2-0.3 \text{ d}^{-1}$ (Watras et al., 1982), equal to doubling
422 times of 2.3 to 3.5 d. The doubling times were similar to or greater than the volumetric residence times, so
423 cell accumulation is enhanced by retention due to active avoidance of the surface layer and the reduction
424 in mixing by stratification.

425 **3.4 Bloom initiation: Sensitivity to cyst distribution and germination rate**

426 In the Gulf of Maine, the cyst bed distribution has leading order effects on the *A. fundyense*
427 bloom (Anderson et al., 2014). In Nauset, cyst distributions varied from year-to-year, although cyst
428 abundance was greater in the ponds than in the central marsh (Fig. 11, Table 3). Mean cyst concentrations
429 in and near the ponds were a factor of 10 to 30 greater than mean concentrations in the central marsh, and
430 mean values in the ponds varied by a factor of about 5 over the 3 years of sampling (Table 3).

431 Ideally, the model would be forced with cyst data from surveys conducted the fall prior to each
432 spring bloom, but surveys were only conducted in 2008, 2009, and 2011. The model was run with prior
433 fall observations when available (2009 and 2012 blooms) and the 2011 bloom was initialized with the
434 cyst distribution from the prior survey closest in time, from fall 2009. Additionally, simulated cyst fields
435 were used to initialize the 2011 case to assess the sensitivity of the bloom to the cyst distribution, as
436 described below. A formulation for temperature-dependent germination rates from the Gulf of Maine
437 (Stock et al., 2005) was applied although the transferability of those rates to Nauset remains uncertain.
438 The Nauset simulations did not apply the endogenous clock germination rhythm from the Gulf of Maine
439 (Anderson and Keafer, 1987), and all cysts in the surface layer (0-1 cm) were assumed to be viable.

440 To test the sensitivity of the model to bloom inoculation by cysts, we altered both the germination
441 rate and the spatial distribution. Observed cyst abundance near the sediment-water interface (0-1 cm
442 depth in bed) had substantial heterogeneity around the estuary. To test sensitivity to this distribution, a
443 case was run with a uniform cyst distribution equal to the mean of the mapped observations (Fig. 12). The
444 uniform cyst case resulted in slightly higher cell concentrations early in the bloom for parts of the estuary
445 (e.g. Town Cove and Salt Pond) and slightly lower in others (e.g., Mill Pond), but the differences were
446 small compared with the concentrations at the peak of the bloom, and model skills were not significantly
447 different from the base case. The result confirmed that the bloom is relatively insensitive to the cyst
448 distribution and that vegetative cell division is the primary mechanism underlying bloom development,
449 provided there is sufficient germination to initiate the bloom.

450 The sensitivity of the bloom to the number of cysts was examined with simulations using lower
451 cyst abundance, reduced by factors of 10 and 100 from the observed distributions (Fig. 12). A factor of 10
452 reduction is similar to the observed range of spatial variability, while a factor of 100 reduction represents
453 a significant decrease in cyst abundance, perhaps as might be associated with remedial action to reduce
454 cyst concentrations. Blooms from the depleted cyst beds followed similar temporal development as the
455 base case, but cell concentrations were reduced by factors similar to the 10 or 100 times reductions in cyst
456 abundance. Cases were also run assessing the connectivity among the ponds by removing all cysts in the
457 northern or southern part of the estuary. The ponds are isolated from each other by the hydrodynamics of
458 the marsh, so cases with cysts only in the southern half had essentially no bloom in Salt Pond and cases

459 with cysts only in the northern half did not have blooms in Mill Pond or Town Cove. Together, the cyst
460 sensitivity results suggest that modifications to the cyst distribution in and near the ponds might alter the
461 size or local geography of the blooms.

462 Along with the cyst distribution, bloom initiation depended on the rate at which cysts germinate
463 into vegetative cells. In the base case, germination rates varied with temperature from about 1.5 % d⁻¹ at
464 less than 5°C to about 9 % d⁻¹ at greater than 11°C (Anderson, Stock, et al., 2005). In 2012, January and
465 February were mild and water temperatures were a few degrees warmer than in 2009 or 2011 (Ralston et
466 al., 2014). Also in 2012, the bloom occurred about 1 month earlier than in the other years. To test whether
467 higher temperatures and increased germination rates may have accelerated bloom development, a case
468 was run with the germination rate always equal to its maximum value, independent of temperature (Fig.
469 13). Faster germination early in the year produced greater cell concentrations in the first month of the
470 bloom, but the discrepancy with the base case was only at relatively low concentrations (< 300 cells L⁻¹)
471 and was largely eliminated by late March. Early in the bloom, the total number of germinated cysts was
472 large compared with the number of vegetative cells, but as the water warmed and growth rates increased,
473 cell concentrations were several orders of magnitude greater than the number of germinated cysts.

474 **3.5 Bloom termination: Interannual variability in loss rates**

475 Modeling the termination of *A. fundyense* blooms in Gulf of Maine has been challenging. A
476 constant mortality rate does not account for variability associated with increased temperature and
477 development of a thermocline toward the end of blooms, and it was difficult to separate increased
478 mortality from decreased nutrient availability as causes of bloom decline (Stock et al., 2005).
479 Subsequently, a temperature-dependent loss term (Q_{10}) was introduced that better simulated bloom
480 termination (He et al., 2008). This function represented a variety of mechanisms including predation,
481 parasitism, mortality and encystment.

482 A similar Q_{10} formulation was initially adopted for the Nauset model. The approach gave
483 reasonable results for both the 2009 and 2011 blooms using a single set of parameters (Fig. 14). However,
484 as discussed above, the winter of 2012 was anomalously warm and the Nauset bloom occurred about 1
485 month earlier than in the previous years (Ralston et al., 2014). January and February were several degrees
486 warmer in 2012 than usual, spurring rapid growth earlier in the year, but temperatures in March and April
487 were similar to 2009 and 2011. The bloom duration and maximum concentrations were similar in the
488 three years, but the 2012 bloom was shifted about 1 month earlier. As a result, water temperatures during
489 the termination phase of the bloom were several degrees lower in 2012 than in the other years, and the Q_{10}
490 formulation significantly underpredicted loss rates (Fig. 14c).

491 Alternatively, a simple degree-day model for cumulative, temperature-dependent growth can
492 collapse temporal variability among the 3 years (Ralston et al., 2014). When loss rates were made a
493 function of degree day, the termination phase of the bloom was reasonably represented by the same
494 formulation in all 3 years (Fig. 14). Due to the model architecture, it was necessary to calculate degree
495 days locally within each grid cell, an approach that was not optimal given the diel ambit of individual *A.*
496 *fundyense* cells through temperature stratification. The degree day formulation is therefore entirely
497 empirical and specific to the Nauset observations and model, but it does provide greater skill than a single
498 Q_{10} approach over multiple years (Table 2).

499 **4. DISCUSSION**

500 **4.1 Factors contributing to bloom development and structure**

501 The coupled hydrodynamic-biological model compared well with the observed physical
502 conditions and *A. fundyense* concentrations over multiple years, and the model can be used to assess the
503 factors contributing to the development of the recurrent HAB in Nauset estuary. As noted from
504 observational data, the effect of temperature on growth rate was a key factor controlling bloom
505 development (Watras et al., 1982; Crespo et al., 2011; Ralston et al., 2014). Temperature in the ponds
506 depended both on the seasonal increase in surface heat flux and on spring-neap variability in tidal
507 exchange, with warming of the surface layer during neap tides and cooling from coastal ocean water
508 during spring tides. The spring-neap variability in exchange affected the residence time of cells in the
509 ponds, but for cell retention to be substantially longer than the cell doubling time required both active
510 vertical migration and stratification that inhibits vertical mixing of cells into the surface layer. The model
511 results were consistent with a previous observational study in Salt Pond using a dye tracer (Anderson and
512 Stolzenbach, 1985), but emphasized that stratification is important in addition to migration. Similarly, a
513 HAB in Cork Harbor (Ireland) has been found to develop when spring tides are relatively weak around
514 the summer solstice, reducing the loss of cells to tidal mixing and advection (Raine, 2014). In Thau
515 Lagoon (France), wind is the dominant energy source and control on retention, and *Alexandrium* blooms
516 are restricted to periods of weak wind mixing (Laanaia et al., 2013).

517 Unlike *A. fundyense* blooms in the Gulf of Maine, interannual variability in cyst distribution does
518 not appear to be the dominant control on the intensity or geography of the Nauset blooms. Instead the
519 Nauset system appears to be more similar to Cork Harbor, a coastal embayment the intensities of
520 *Alexandrium* blooms have been shown to be independent of pre-bloom cyst abundance (Cosgrove et al.,
521 2014). In Nauset, comparisons between cyst abundance and peak toxicities or maximum cell
522 concentrations were inconclusive due to the limited number of realizations (3 years). Maximum toxicity
523 recorded at shellfish monitoring stations in Salt Pond and near Mill Pond were correlated with cyst

524 abundances in the ponds the previous fall ($n = 6$, $r^2 = 0.80$, $p=0.02$), but the correlation was dominated the
525 elevated toxicity and cyst abundance recorded in Mill Pond for the 2012 bloom; without that data point
526 the relationship fell apart ($n=5$, $r^2 = 0.01$, $p=0.86$). The relationship between cyst abundance and bloom
527 intensity was much stronger in the model results. Although cell concentrations varied little between cases
528 with a realistic or a spatially uniform cyst distribution (Fig. 12), peak cell concentrations decreased nearly
529 proportionately to 10- or 100-fold decreases in cyst abundance. An important caveat to the model is that
530 bloom termination depends heavily on the degree-day heuristic. This relationship between heat
531 accumulation and increasing cell loss is derived from observations, without an understanding of the
532 underlying mechanism. Other mortality formulations such as a concentration-based approach could allow
533 the bloom to continue to develop to similar maximum concentrations. .

534 Modifications to the biological model suggest differences in the *A. fundyense* population from the
535 Gulf of Maine. An endogenous germination rhythm for cysts in Nauset, if it is present, is shifted earlier in
536 the year. Population losses at the end of the bloom are highly nonlinear, but do not appear to be strictly a
537 function of temperature. Instead, given that inferred losses are extremely low during early phases of the
538 bloom and increase rapidly at similar cell concentrations across multiple years, termination may be
539 concentration-dependent. The apparent skill of the degree day approach then relies on a linear relationship
540 between temperature and growth rate until exceedance of a cell concentration threshold that triggers rapid
541 losses to parasitism and/or sexual encystment. More observations are needed to isolate mechanisms of
542 termination to provide the basis for a more mechanistic model.

543 **4.2 Model attributes and limitations**

544 The highly resolved 3-d hydrodynamic and *A. fundyense* model represents strong spatial gradients
545 in water properties and cell concentrations, both spatially among the ponds and central marsh and
546 vertically due to stratification. A coarser or more idealized model, such as depth-averaged or box model
547 approach, would be unlikely to capture the dominant role of bathymetric features in determining the
548 structure of the bloom. The model demonstrated robust skill for hydrodynamics and water properties, and
549 provided order-of-magnitude predictive capability for cell concentrations across multiple years.

550 While the comparisons with observations were favorable, key uncertainties remain in the model
551 formulation. The high loss rates at bloom termination may be due to multiple processes including
552 encystment, parasitism, and grazing. The controlling factors are not obvious, but are likely to depend on
553 the life history of the organism (sexual induction and encystment), infection by the parasite *Amoebophrya*
554 (Velo-Suárez et al., 2013), grazing pressure, and physical properties of the environment. A Lagrangian
555 modeling approach might better represent the declining phase of the bloom by tracking individual
556 particles. Similarly, the approach in the current model to vertical migration would benefit from a

557 mechanistic approach based on external cues (light, nutrients, density, velocity shear) and organism state
558 (life stage, nutrient status; Ralston et al., 2007) for a more robust examination of how vertical migration
559 influences residence time and bloom development.

560 The dependence of the Nauset bloom on nutrients remains unresolved. Observationally, growth
561 rates based on cell concentrations from weekly surveys were not correlated with measured nutrient
562 concentrations (Ralston et al., 2014). To force the model, samples from Niskin bottles at discrete stations
563 and depths did not resolve well the strong spatial gradients in nutrient concentrations. High resolution
564 surveys of nitrate concentration along the shoreline of Salt Pond detected spatial gradients in nitrate
565 corresponding with groundwater seeps (J. Colman, pers. comm.). Late in the blooms, ammonium
566 concentrations below the pycnocline in Mill and Salt Ponds were high enough to be toxic to organisms
567 through inhibition of nitrate uptake (Dugdale et al., 2007). However, the swimming ability of *A.*
568 *fundyense* may allow it to actively avoid inhibitory concentrations in the lower water column. Similarly,
569 we could not assess whether limitations of other nutrients or altered nutrient stoichiometry associated with
570 anthropogenic loading (Glibert et al., 2013) may affect bloom development.

571 The model presented here is consistent with the available observations from Nauset, but that does
572 not exclude alternative model formulations. For example, similar skills can be obtained removing
573 nutrients as a growth factor by setting $k_N = 0$. Similarly, the mortality function assumes loss processes
574 occur in the water column (grazing, encystment, parasitism), but benthic grazing may also be important.
575 As in many ecosystem models, the justification for adding complexity is limited by the availability of
576 field or lab observations to constrain the model. The results here are perhaps the most resolved and
577 validated simulation of an HAB to date, but observations should continue to inform both its conceptual
578 and numerical development.

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734

735

736 TABLES

Table 1. *A. fundysense* model parameters
Model formulae and parameters not listed here are as in Stock et al. (2005).

| Parameter | Units | Range of values | Description |
|------------|---------------------|-----------------|---------------------------------------|
| G_{max} | d^{-1} | 1.0-1.6 | Maximum instantaneous growth rate |
| K_N | μM | 0-0.5 | Half saturation constant for nitrate |
| m | d^{-1} | 0.2-0.5 | Mortality |
| w_s | $m d^{-1}$ | 10 | Maximum vertical swimming speed |
| α_g | $d^{-1} W^{-1} m^2$ | 0.055 | Growth efficiency |
| k_w | m^{-1} | 0.2-0.5 | Diffuse attenuation of light in water |

737

Table 2. Model skill: correlations (r^2) and skill scores (SS)

| Parameter and location | 2009 | | 2011 | | 2012 | |
|--|-------|-------|-----------|------------|-----------|-----------|
| | r^2 | SS | r^2 | SS | r^2 | SS |
| Water level | | | | | | |
| Town Cove | 0.98 | 0.97 | 0.96 | 0.94 | 0.97 | 0.96 |
| Mill Pond | 0.97 | 0.96 | 0.94 | 0.93 | 0.97 | 0.90 |
| Salt Pond | 0.95 | 0.94 | 0.97 | 0.97 | 0.97 | 0.95 |
| Hemmenway | 0.96 | 0.95 | 0.97 | 0.97 | 0.97 | 0.95 |
| Water temperature (surface/bottom, where available) | | | | | | |
| Town Cove | 0.86 | 0.79 | 0.78 | 0.72 | 0.95/0.91 | 0.92/0.90 |
| Mill Pond | 0.85 | 0.62 | 0.00/0.25 | 0.00/-6.8 | 0.95/0.60 | 0.77/-2.8 |
| Salt Pond | 0.83 | 0.35 | 0.01/0.80 | -0.01/0.59 | 0.85/0.81 | 0.71/0.08 |
| Hemmenway | 0.48 | 0.46 | 0.75 | 0.55 | 0.62 | 0.52 |
| <i>A. fundysense</i> concentration (log transformed): degree-day mortality | | | | | | |
| Town Cove | 0.60 | -0.76 | 0.87 | 0.62 | 0.46 | -0.51 |
| Mill Pond | 0.71 | 0.54 | 0.62 | 0.38 | 0.68 | 0.60 |
| Salt Pond | 0.40 | 0.35 | 0.05 | -0.13 | 0.55 | 0.40 |
| Hemmenway | 0.29 | -4.9 | 0.48 | 0.40 | 0.68 | -1.2 |
| <i>A. fundysense</i> concentration (log transformed): Q_{10} mortality | | | | | | |
| Town Cove | 0.35 | 0.28 | 0.52 | 0.39 | 0.20 | -0.07 |
| Mill Pond | 0.56 | 0.31 | 0.33 | -0.20 | 0.08 | -0.71 |
| Salt Pond | 0.47 | 0.41 | 0.86 | 0.60 | 0.10 | -0.42 |
| Hemmenway | 0.15 | -0.97 | 0.18 | -0.83 | 0.79 | 0.57 |

738

Table 3. Observed *A. fundysense* cyst abundance in fall surveys (0-1 cm sediment depth)

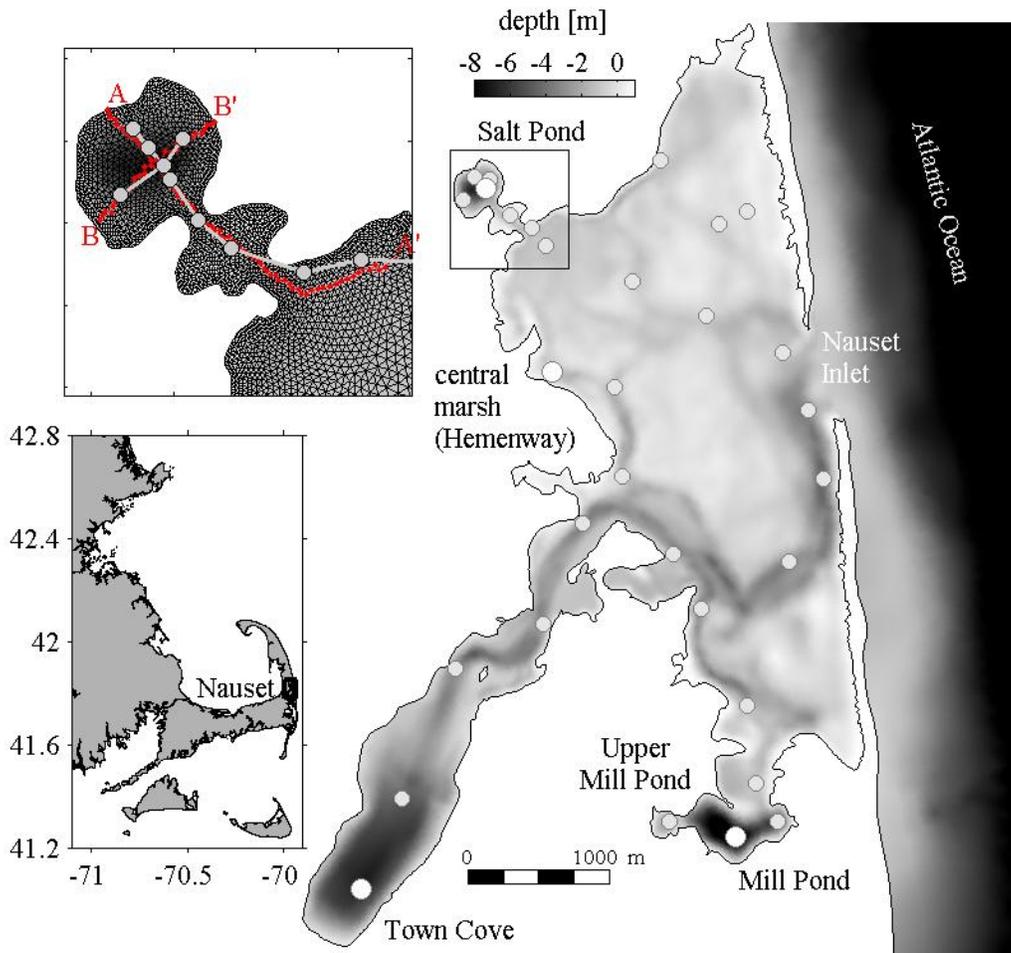
| Year | Max (cysts cm^{-3}) | In and near ponds | | In central marsh | |
|------|------------------------|-------------------|-------------------------|------------------|-------------------------|
| | | Samples | Mean (cysts cm^{-3}) | Samples | Mean (cysts cm^{-3}) |
| 2008 | 2,909 | 34 | 480 | 40 | 42 |
| 2009 | 4,965 | 34 | 762 | 38 | 47 |
| 2011 | 18,150 | 34 | 2,786 | 31 | 76 |

739

740

741 **FIGURES**

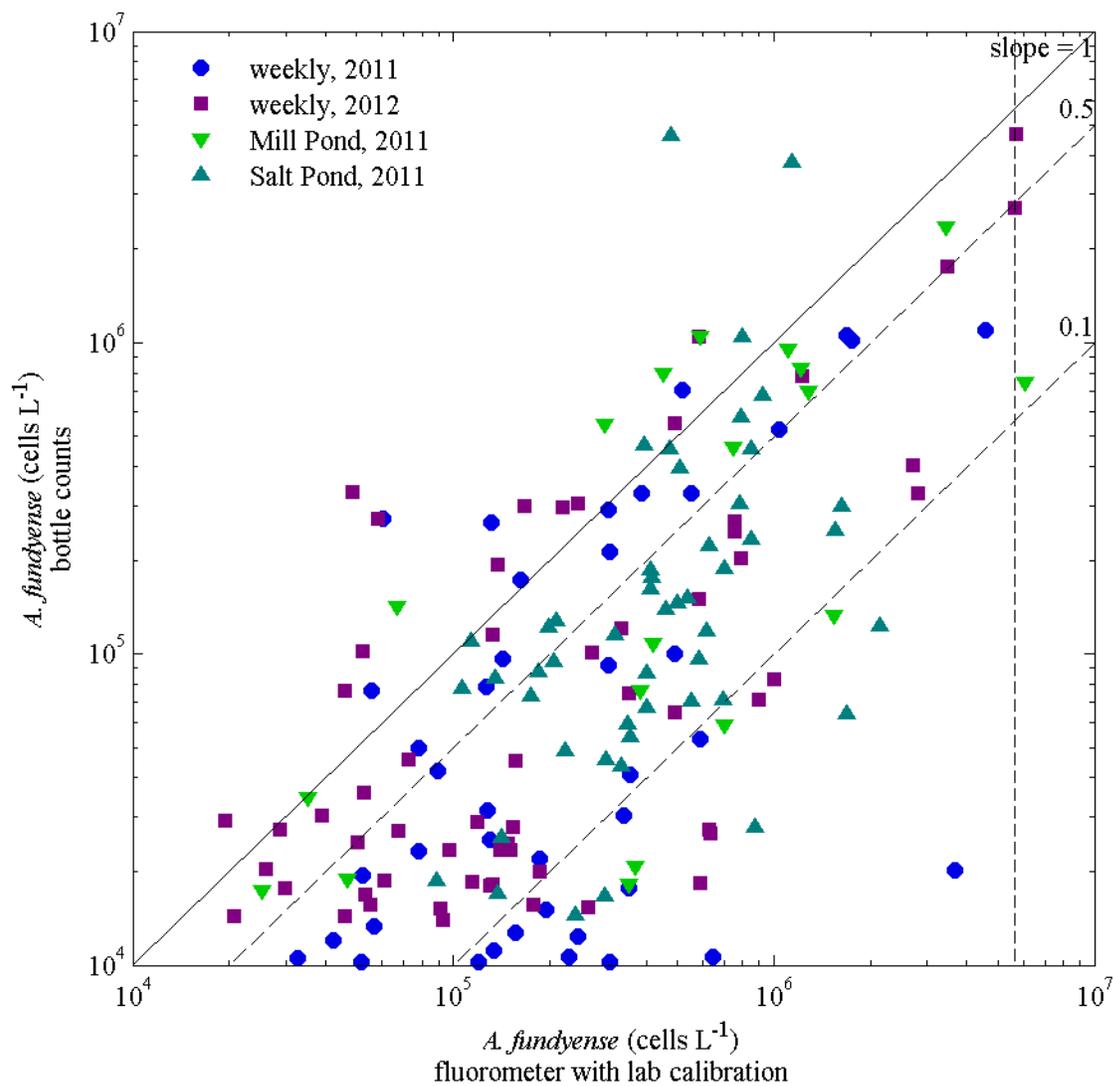
Figure 1



742

743 **Figure 1.** Nauset estuary location, bathymetry, and model grid detail. Sampling stations from the marsh-
 744 wide surveys are shown on the main map (gray circles), with the larger dots showing the locations of the
 745 time series in Fig. 7. A detail of Salt Pond illustrates the model grid resolution, and also shows the
 746 locations of transects A-A' and B-B' for field observations (casts at gray circles) and model results (red
 747 line) shown in Figs. 5 and 8. Note that the model bathymetry extends above mean higher high water to
 748 allow wetting and drying of the marsh, while plots of interpolated observations (Fig. 11) are shown with
 749 the coastline as the mean sea level contour to demark the navigable channels.

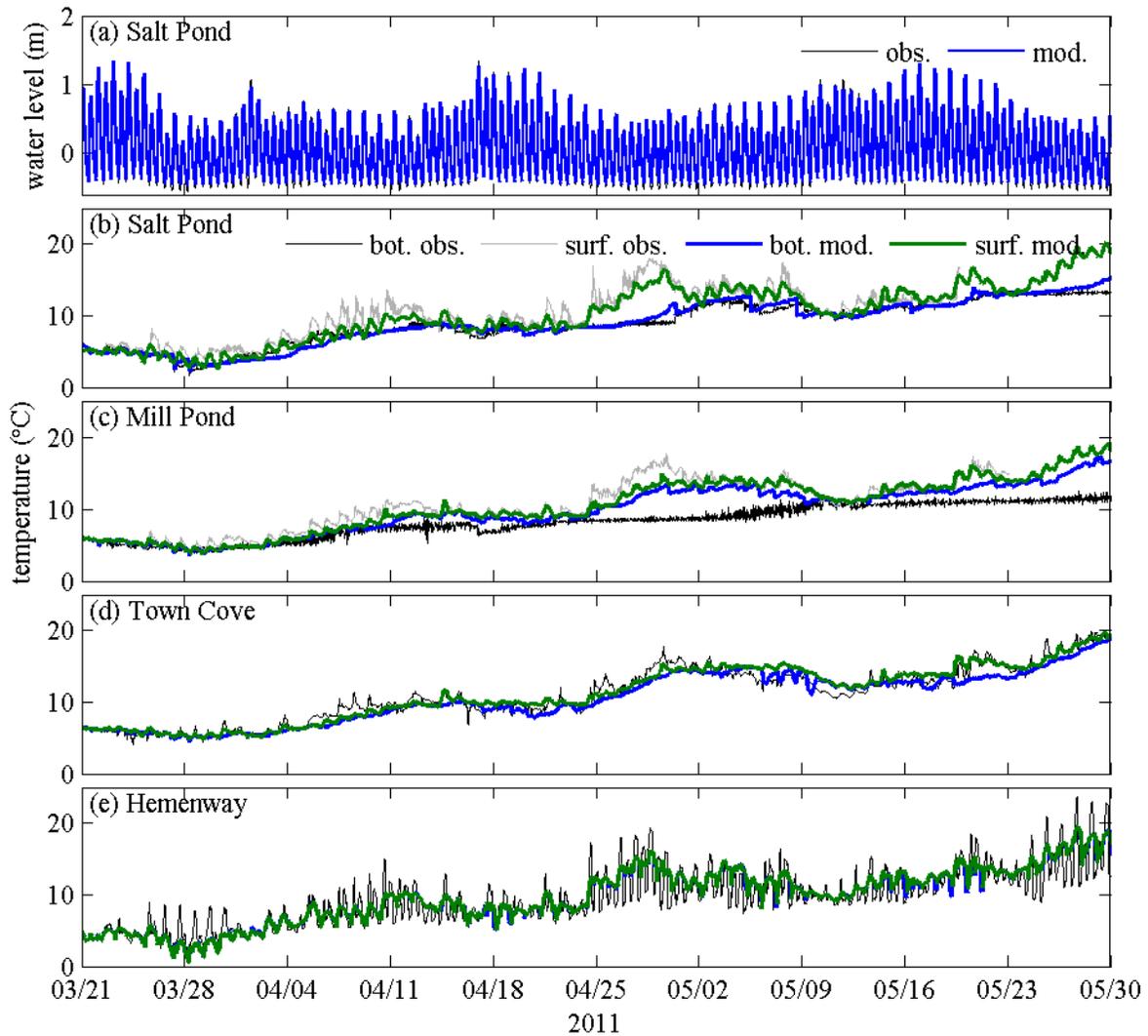
Figure 2



750

751 **Figure 2.** Comparison of *A. fundyense* concentrations derived from bottle samples and from chlorophyll
752 fluorescence. Data are from large-scale, weekly surveys in 2011 and 2012 and from high-resolution, tidal
753 cycle surveys in Mill Pond and Salt Pond in 2011. In-situ fluorometer profiles were converted to cell
754 concentrations using a laboratory calibration to cultured *A. fundyense*, and extracted at depths
755 corresponding with the sample bottles. The vertical dashed line is the concentration at which the
756 fluorometer saturated on the CTD used for the weekly surveys, and lines with slopes of 1, 0.5, and 0.1 are
757 shown for reference.

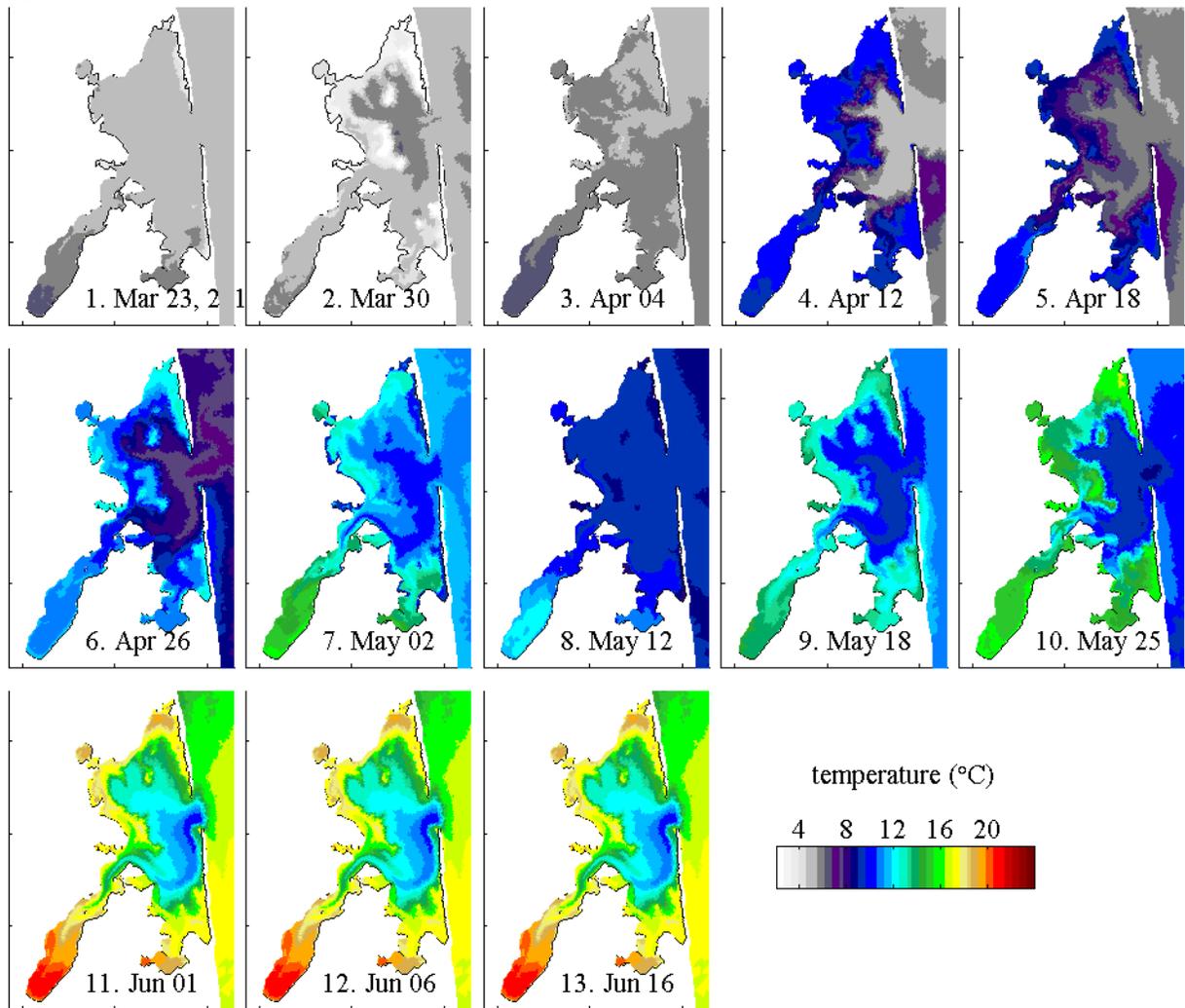
Figure 3



758

759 **Figure 3.** Observations and model results from spring 2011. (a) Water level in Salt Pond. (b) Near surface
760 and near bottom temperature in Salt Pond and (c) Mill Pond, (d) Town Cove, and (e) near-bottom
761 temperature at Hemenway in the central marsh.

Figure 4

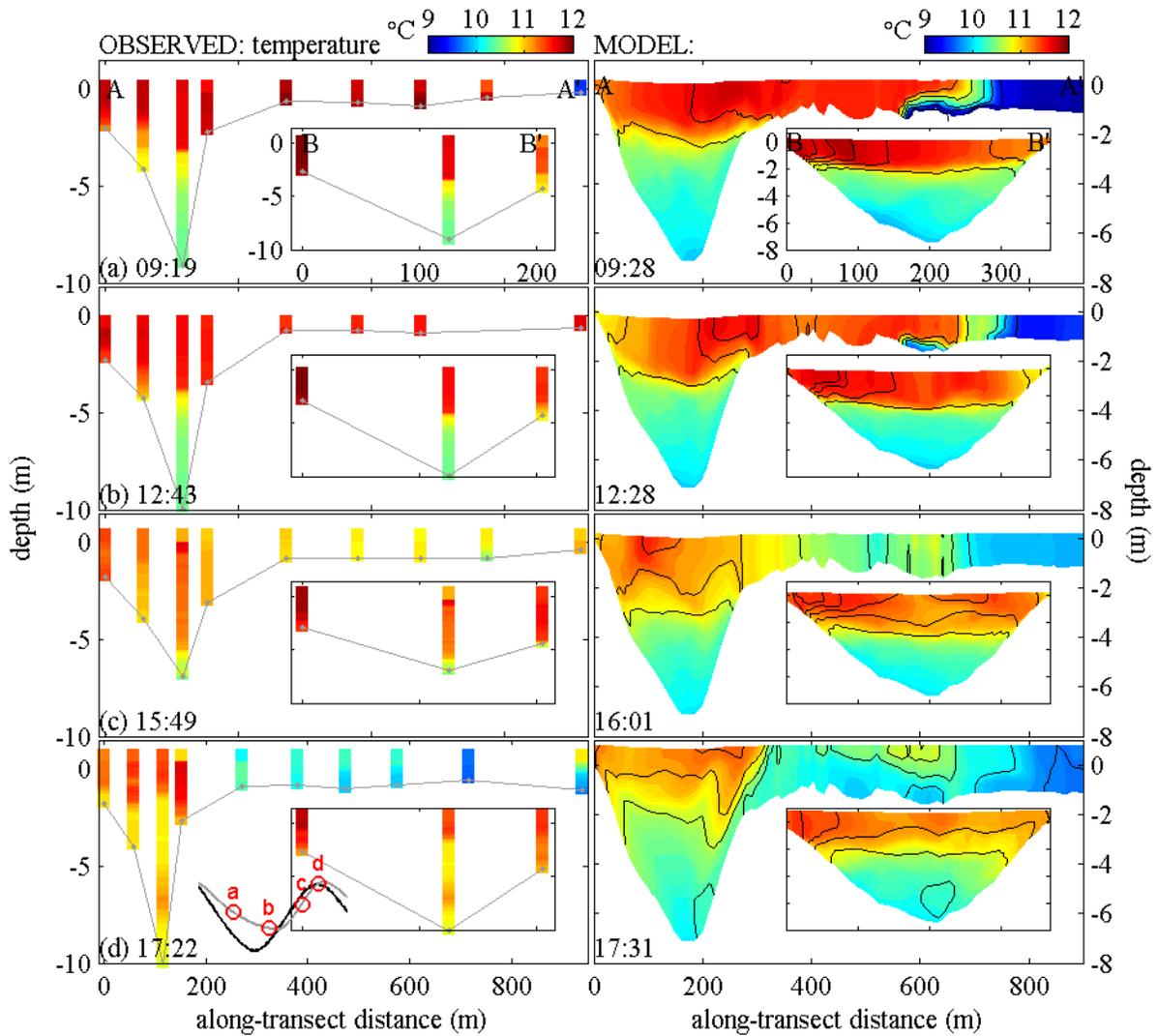


762

763 **Figure 4.** Maps of surface temperature from model results for spring 2011. Times shown are extracted to
764 correspond with marsh-wide CTD surveys that occurred around high water, as in Fig. 3 of Ralston et al.
765 (2014).

766

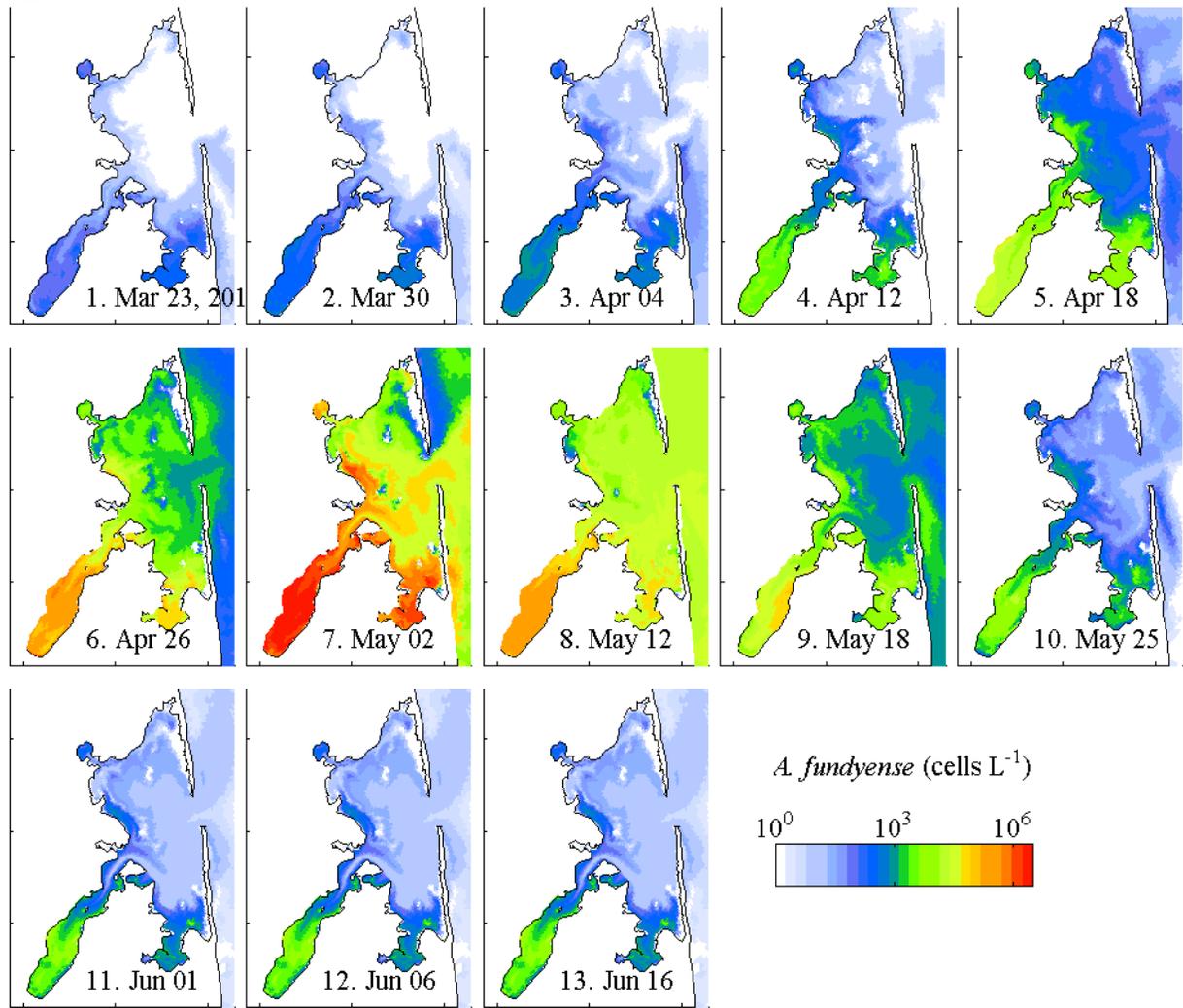
Figure 5



767

768 **Figure 5.** Temperature sections from Salt Pond observations (left column) and model results (right) for 9
 769 May 2011. Sections are from the pond through the channel into the central marsh (A-A', larger panels),
 770 and across the pond (B-B', inset panels); section locations are shown on the Salt Pond inset of Fig. 1.
 771 Time of day is shown in the lower left of each panel, and tidal phases for the 4 sections are shown in the
 772 lower left panel with the water levels in Salt Pond (gray) and at Nauset Inlet (black). Salinity contours
 773 (0.2 psu interval) are overlaid on the model results.

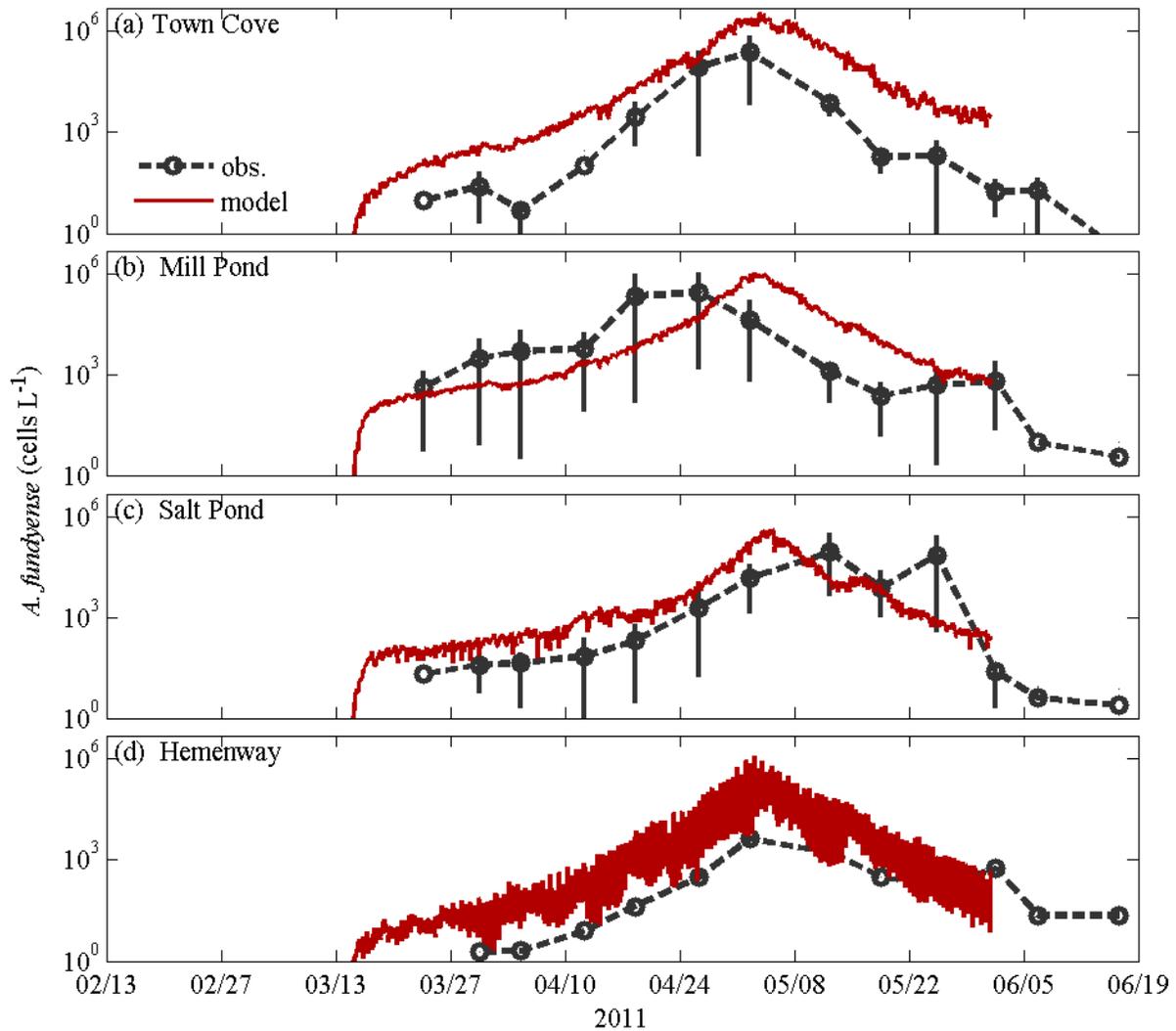
Figure 6



774

775 **Figure 6.** Maps of mean *A. fundyense* concentration from model results for spring 2011. Times shown are
776 extracted to correspond with marsh-wide CTD surveys that occurred around high water, as in Fig. 2 of
777 Ralston et al. (2014).

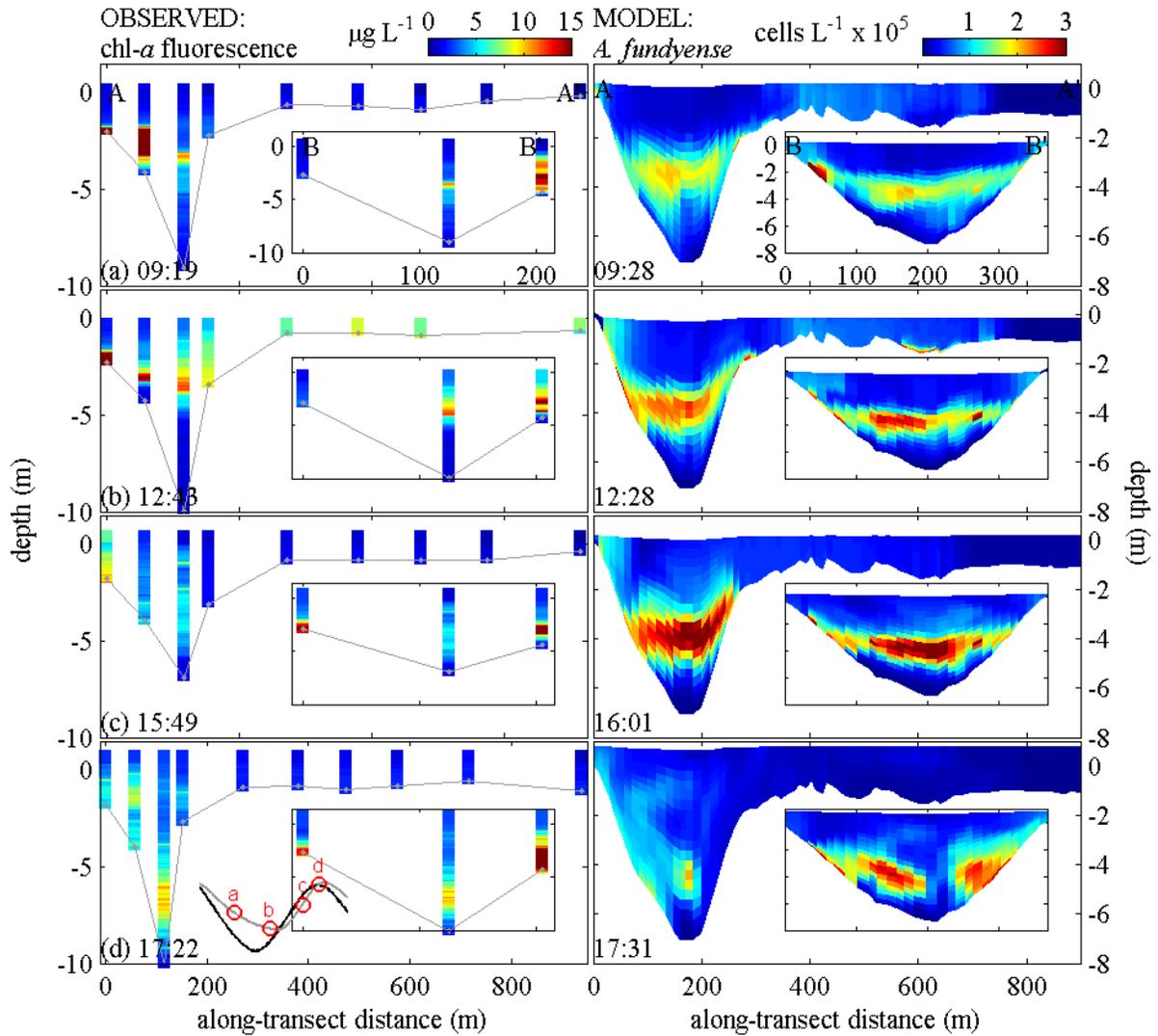
Figure 7



778

779 **Figure 7.** Depth-averaged *A. fundyense* cell concentrations stations from weekly surveys and model
780 results in spring 2011: (a) Town Cove, (b) Mill Pond, (c) Salt Pond, and (d) Hemenway. Station
781 locations are shown in Fig. 1. Vertical lines indicate the concentration range observed in samples
782 collected at multiple depths

Figure 8

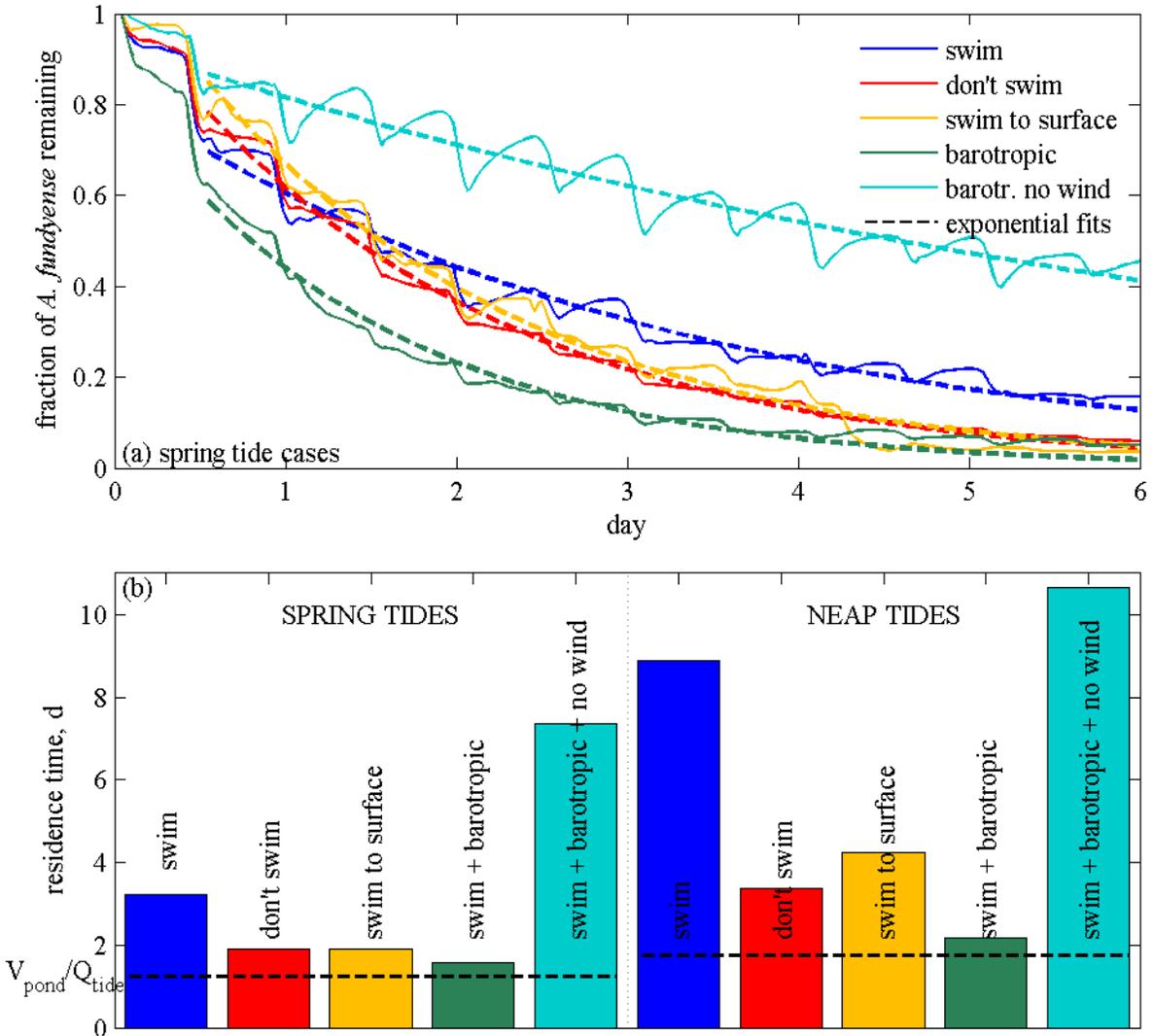


783

784 **Figure 8.** Observed chlorophyll-*a* fluorescence (left column) and modeled *A. fundyense* concentration
785 (right) from Salt Pond for May 9, 2011. Sections are the same as in Fig. 5. Time of day is shown in the
786 lower left of each panel, and tidal phases for the 4 sections are shown in the lower left panel with the
787 water levels in Salt Pond (gray) and at Nauset Inlet (black).

788

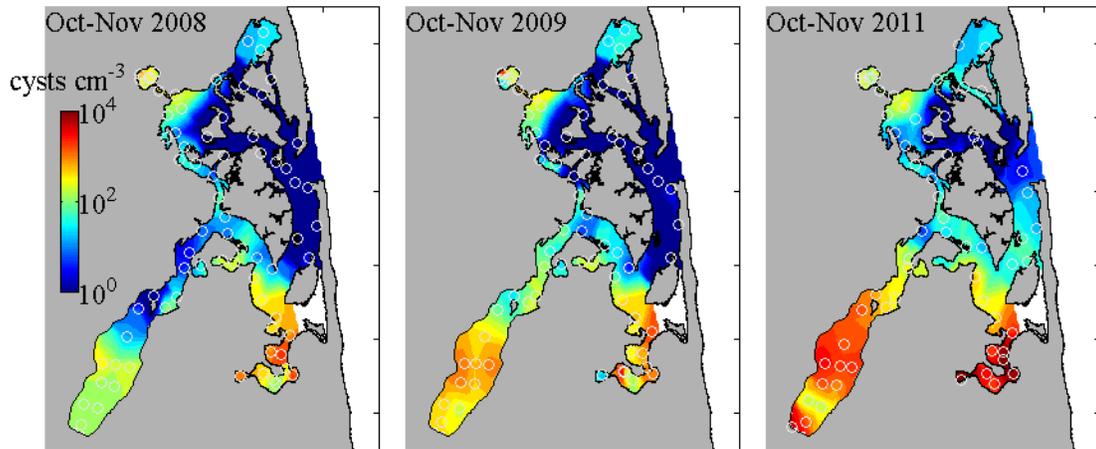
Figure 10



794

795 **Figure 10.** Residence time calculations from model results for different swimming and forcing cases. (a)
 796 Concentration of *A. fundyense* remaining in Salt Pond for spring tide cases: diel vertical migration up to
 797 $1/k_w$ depth (swim), no vertical migration (don't swim), diel migration to the surface (swim to surface), and
 798 diel vertical migration to $1/k_w$ with barotropic physics and barotropic physics and no wind forcing.
 799 Exponential fits are shown for each case. (b) Residence time calculated from exponential fits for spring
 800 tide (shown in (a)) and neap tide cases. For reference, the residence time for tidal exchange with a well-
 801 mixed pond (V_{pond}/Q_{tide}) is shown for spring and neap tide cases.

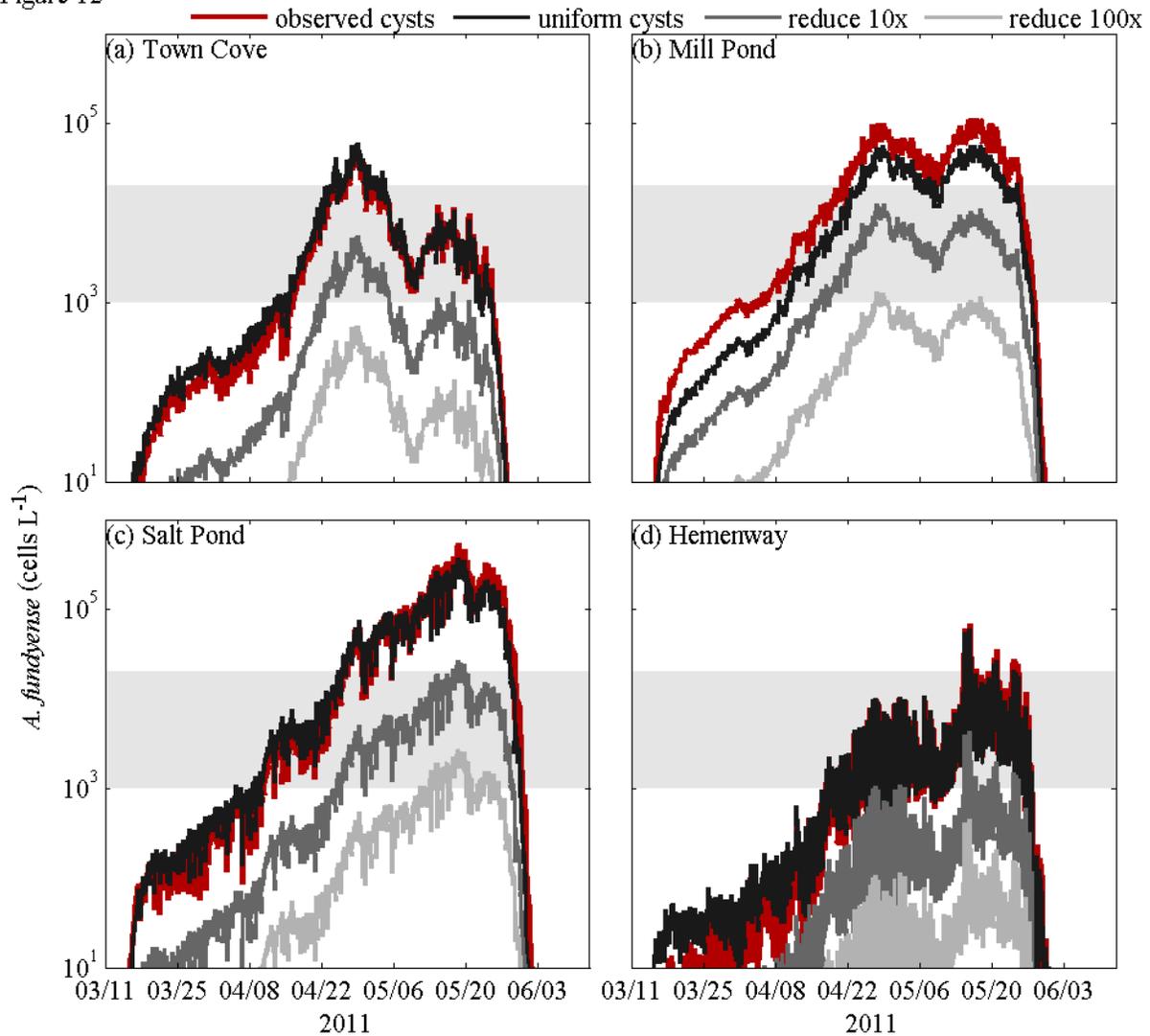
Figure 11



802

803 **Figure 11.** Maps of observed cyst distributions (0-1 cm sediment depth) in the falls of 2008, 2009, and
804 2011. Sample locations are shown with circles, and interpolated maps were used as bottom boundary
805 conditions for the *Alexandrium* model. The coastline shown here is the mean sea level contour.

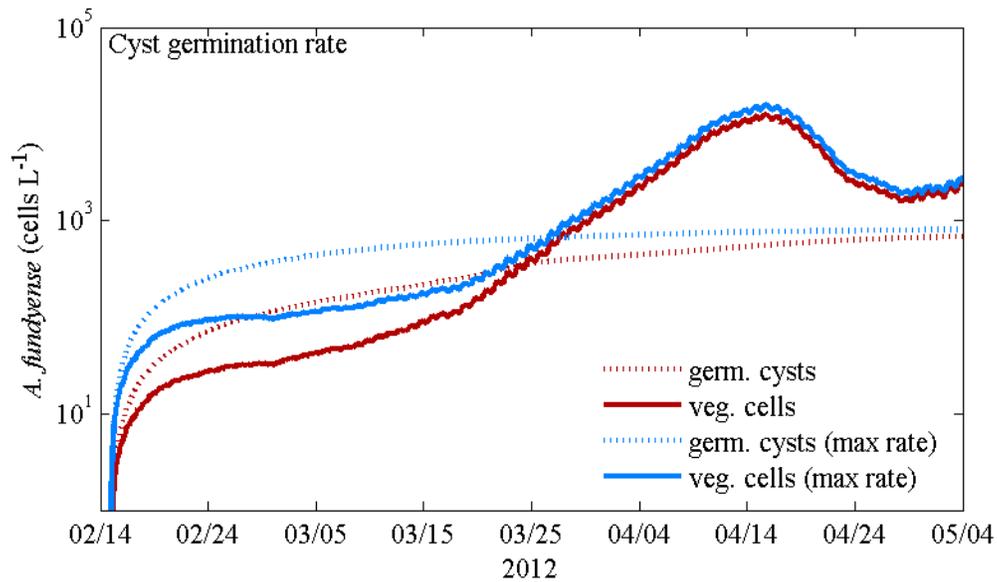
Figure 12



806

807 **Figure 12.** Sensitivity to cyst distribution, comparing model results using the observed cyst distribution
 808 with a spatially uniform cyst distribution equal to the average cyst concentration and with cyst densities
 809 reduced by factors of 10 and 100. Cell concentrations from spring 2011 are shown for (a) Town Cove, (b)
 810 Mill Pond, (c), Salt Pond, and (d) Hemenway. Horizontal gray bar represents approximate range of
 811 concentrations in the ponds at the times that weekly toxicity sampling exceeded the regulatory threshold
 812 of 80 µg toxin per 100 g mussel tissue (MA Division of Marine Fisheries).

Figure 13

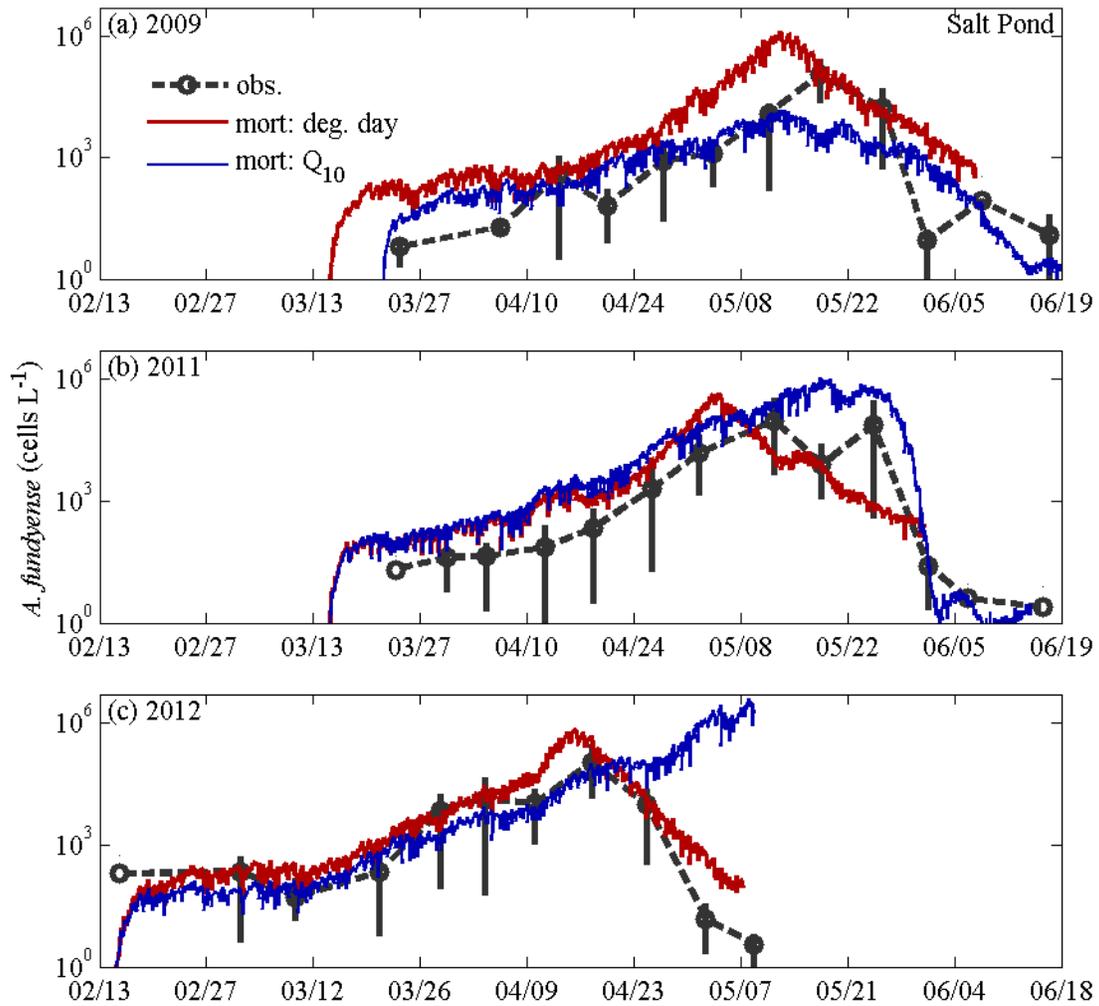


813

814 **Figure 13.** Sensitivity of model results to cyst emergence rate, comparing the base case of temperature-
815 dependent cyst emergence with a case with cyst emergence at the maximum rate from lab data,
816 independent of temperature. Cell concentrations in the water column and the total number of germinated
817 cysts are shown for each case; both are averaged over the entire Nauset marsh to remove effects of spatial
818 variability in cyst concentration.

819

Figure 14



820
821 **Figure 14.** *A. fundyense* concentration from observations and model results from Salt Pond for (a) 2009,
822 (b) 2011, and (c) 2012. Observations are from weekly surveys each year, and vertical bars represent the
823 range of concentrations from samples at multiple depths. Model results are shown using two different
824 mortality formulations: based on temperature (Q_{10}) and on growing degree days.
825