

1 **Modeling harmful algal blooms in a changing climate**

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13 **Highlights:**

14 - Process-based models preferred to statistical for projecting climate change impacts

15 - Long-term observations are critical for model development and evaluation

16 - Evaluate model uncertainty with ensemble approaches and scenario planning

17 - Use robust downscaling of climate model projections

18

19 **Keywords:** harmful algal blooms, climate change, numerical modeling

20 **ABSTRACT**

21 This review assesses harmful algal bloom (HAB) modeling in the context of climate change, examining
22 modeling methodologies that are currently being used, approaches for representing climate processes, and
23 time scales of HAB model projections. Statistical models are most commonly used for near-term HAB
24 forecasting and resource management, but statistical models are not well suited for longer-term
25 projections as forcing conditions diverge from past observations. Process-based models are more
26 complex, difficult to parameterize, and require extensive calibration, but can mechanistically project HAB
27 response under changing forcing conditions. Nevertheless, process-based models remain prone to failure
28 if key processes emerge with climate change that were not identified in model development based on
29 historical observations. We review recent studies on modeling HABs and their response to climate
30 change, and the various statistical and process-based approaches used to link global climate model
31 projections and potential HAB response. We also make several recommendations for how the field can
32 move forward: 1) use process-based models to explicitly represent key physical and biological factors in
33 HAB development, including evaluating HAB response to climate change in the context of the broader
34 ecosystem; 2) quantify and convey model uncertainty using ensemble approaches and scenario planning;
35 3) use robust approaches to downscale global climate model results to the coastal regions that are most
36 impacted by HABs; and 4) evaluate HAB models with long-term observations, which are critical for
37 assessing long-term trends associated with climate change and far too limited in extent.

38 **1. Motivation and background**

39 Climate change is expected to affect the frequency, magnitude, biogeography, phenology, and toxicity of
40 harmful algal blooms (HABs) (Moore et al. 2008; Hallegraeff 2010; Anderson et al. 2015; Wells et al.
41 2015). Projecting likely responses of HABs to climate change is critical for informing the development of
42 societal response strategies to mitigate their impacts and requires development and application of various
43 types of models. Models used to project HAB response range from simple conceptual exercises to
44 complex, highly resolved dynamical systems (Anderson et al., 2015). Regardless of model complexity,
45 their efficacy depends on how well fundamental physical, biological, and biogeochemical processes are
46 represented, as well as the ability to prescribe accurate initial conditions (i.e., model starting conditions)
47 and model forcing at boundaries (i.e., time series of external variables essential to run the model). The
48 challenges associated with representing physical and biological processes important for HAB
49 development and prescribing accurate forcing vary greatly by region, HAB species, and time horizon, and
50 inevitably introduce some level of uncertainty in model output. HAB scientists have struggled with how
51 to address this uncertainty, as the complexity and multitude of processes that influence HAB response can
52 be overwhelming (e.g., Wells et al. 2015). This difficult conundrum of anticipating climate change effects

53 but struggling with how to evaluate potential HAB response has been described as a “formidable
54 predictive challenge” (Hallegraeff 2010), and has inhibited the development of actionable projections to
55 increase resilience to future HABs.

56 The term “harmful algal bloom” applies to a diverse subset of algae that cause a variety of negative
57 impacts when they bloom, including human illness from eating contaminated food, drinking contaminated
58 water, or breathing harmful aerosols, fish kills, and environmental degradation due to high biomass
59 (Erdner et al. 2008). Major types of HABs include toxin-producing pelagic diatoms (e.g., *Pseudo-*
60 *nitzchia*), dinoflagellates (e.g., *Alexandrium*, *Pyrodinium*, *Gymnodinium*, *Dinophysis*, *Karenia*), and
61 cyanobacteria (e.g., *Microcystis*, *Nodularia*); toxin-producing benthic dinoflagellates (e.g.,
62 *Gambierdiscus*); fish-killing raphidophytes (e.g., *Heterosigma*); and high-biomass events (e.g.,
63 *Phaeocystis*, *Ulva*). Consistent with this diversity in HAB organisms, the expected HAB response to
64 climate change is also diverse. The sensitivity and even the sign of the response of HABs to climate
65 change may vary depending on the organism and the setting. For example, increased temperature may
66 increase growth rates of organisms that are currently at the poleward limit of their thermal habitat at a
67 particular location, but may also result in some locations becoming too hot to support growth (e.g., Kibler
68 et al. 2015).

69 A number of in-depth reviews of climate change impacts on HABs identify a range of potential responses
70 to environmental factors including warming temperature, increased stratification, altered nutrient
71 availability and composition, light intensity, and ocean acidity (Moore et al. 2008; Hallegraeff 2010;
72 Anderson et al. 2015; Wells et al. 2015). HAB response may also depend on how climate change will
73 affect zooplankton grazers or microbial pathogens that limit their growth, which is particularly difficult to
74 characterize since grazer activity may also respond to the same changes in environmental factors that
75 determine HAB response and are also likely to be regionally specific (Wells et al. 2015). Many of the
76 projected responses of HABs to changing environmental factors rely primarily on theory or laboratory
77 studies that isolate particular organisms or processes. The derived rates and responses from these culture
78 studies do not always correspond with those observed in the field, potentially reflecting variation among
79 isolates, effects of competition, and/or interactions among factors that occur in the environment (Fu et al.
80 2012; Wells et al. 2015). Consequently, these interactions are typically not well parameterized in HAB
81 models, if they are included at all. This may lead to greater uncertainty in model projections if
82 interactions emerge or become more important to HAB formation in the future as a result of changing
83 climate conditions.

84 Directly linking changes in observed HAB distribution, frequency, or intensity to shifts in climatic
85 forcing remains difficult (Moore et al. 2008; Wells et al. 2015), but examples are emerging as time series

86 of observations accumulate. Identifying HAB responses (or lack thereof) to anomalous climate events or
87 natural climate cycles provide the best opportunities for formulating hypotheses as to how HABs might
88 respond to climate change (Trainer et al., 2019 this special issue). For example, anomalously warm water
89 associated with the 2014-16 northeast Pacific marine heatwave was associated with an intense,
90 widespread *Pseudo-nitzschia* bloom along the U.S. West Coast beginning in spring 2015 that may have
91 been fueled by the combination of higher growth rates at warmer temperatures and nutrients supplied by
92 upwelling (McCabe et al. 2016). Increased closures of shellfish harvesting due to domoic acid from
93 *Pseudo-nitzschia* and saxotoxin from *Alexandrium* were linked with anomalously warm sea surface
94 temperatures off the coast of Oregon during a positive phase of the Pacific Decadal Oscillation (PDO) and
95 strong El Niño event (McKibben et al. 2015). In the Rias Baixas along the Northwest Iberian Peninsula, a
96 decrease in upwelling intensity over the past 40 years was linked to increased time scales for flushing,
97 which corresponded with increased *Dinophysis* occurrence and shellfish harvest closures (Álvarez-
98 Salgado et al. 2008). The frequency and magnitude of *Pseudo-nitzschia* blooms off the coast of Southern
99 California was linked to the PDO and more directly with the North Pacific Gyre Oscillation (NPGO), but
100 the correlations were weak and exact mechanisms unclear (Sekula-Wood et al. 2011). Long time series
101 also reveal systems that are not responsive to climate regimes. For example, warm water anomalies in
102 Puget Sound (Washington State) generated during El Niño winters do not persist into the seasonal
103 window (summer and fall) when blooms of the dinoflagellate *Alexandrium* typically occur. Because of
104 this mismatch in timing, no robust relationship exists between levels of paralytic shellfish toxins in Puget
105 Sound shellfish and an index of the El Niño-Southern Oscillation (ENSO) (Moore et al. 2010). The use of
106 models prognostically to represent mechanistic links between climate and HABs enables some hypotheses
107 of HAB response to future climate change to be tested and remains a research priority.

108 Most models used to project HAB response at climate time scales (i.e., decades to a century) were
109 initially developed and applied over shorter time scales (i.e., several days to a season) to provide
110 hindcasts or forecasts of present conditions. Other reviews have richly detailed the current state of HAB
111 modeling over shorter time scales (Glibert et al. 2010; McGillicuddy 2010; Flynn and McGillicuddy
112 2018; Franks 2018), so modeling applications of present conditions will be addressed here only in the
113 context of how such models might be applied to understand future conditions. As a simplification, most
114 HAB models can be characterized as being primarily *statistical* or *process-based*. Statistical models are
115 developed from relationships between input and response variables in observations. While they have
116 proven effective for hindcasts and near-term forecasts, the statistical relationships become less predictable
117 as forcing conditions shift outside the range of past observations (Flynn and McGillicuddy 2018).
118 Process-based models may be more robust for projecting HAB response under novel environmental
119 conditions, but this assumes that the dominant processes remain unchanged under a different set of

120 forcing conditions. Additionally, models of response to climate change are dependent on the ability to
121 predict forcing conditions such as water temperature, wind strength, or river discharge at spatial and
122 temporal scales relevant to the processes represented in the HAB model. The uncertainty in the
123 environmental conditions increases greatly with the time scale of forecast, in part because of greater
124 uncertainty in the global circulation models (GCM) at longer time scales but also because the
125 unpredictability of human behavior becomes a greater factor. For example, representing the source of
126 nutrients that might fuel a bloom or affect toxicity could depend on resolving shifts in upwelling wind
127 intensity or hydrologic response to precipitation events from local watersheds, but changes in land use or
128 direct anthropogenic nutrient inputs may have even greater effects on regional nutrient concentrations
129 (Glibert et al. 2010). The paucity of successful HAB models at even interannual time scales and the
130 uncertainties in predicting future environmental conditions make extending meaningful projections to
131 climate time scales challenging.

132 This review examines the state of HAB modeling in the context of climate change. We assess the key
133 components of modeling HAB response to climate change, starting with an overview of the HAB
134 modeling methodologies currently in use, reviewing studies that have examined HAB response to climate
135 change, and offering recommendations on how to move forward by incorporating approaches used in the
136 broader climate and ecosystem modeling communities. Considerations include the spatial resolution, time
137 horizon, and forecast accuracy of HAB models developed in the present climate, representation of future
138 forcing conditions that govern bloom development and transport, and an assessment of whether the
139 models developed and calibrated under present forcing conditions can adequately represent future
140 response, or if additional factors might emerge to dominate bloom dynamics.

141 **2. Modeling HABs in the present climate**

142 Most HAB models currently in use for present climate conditions focus on either hindcasts in process
143 studies or near-term (a few days to seasonal) forecasts for operational and management uses. These
144 existing HAB models are the most likely bases for projecting future response to climate change. They use
145 a wide range of methodologies, in part reflecting the diversity of HAB species, the availability of data for
146 model forcing or calibration, and differences in motivation for model development. Here we broadly
147 classify HAB models as those that apply statistical (or empirical) techniques, process-based formulations,
148 or merge multiple approaches (i.e., hybrid models). The categorizations are not meant to be rigid. Other
149 key model attributes could instead be used to distinguish methodologies, such the level of complexity
150 from a single organism to full ecosystem, the degree of spatial and temporal resolution, the time scales of
151 simulation (event, seasonal, interannual, or longer), and whether models are diagnostic hindcasts or
152 prognostic forecasts. Nevertheless, we find our categorization of the current modeling approaches

153 facilitates thinking about how each of the methodologies might be adapted to assess HAB response to
154 climate change. A brief summary of the modeling studies reviewed here is given in Table 1, including
155 this categorization, HAB organism, geographic region, and model type and time scales.

156 2.1 Statistical models

157 Statistical models use observations to relate key forcing variables (e.g., a nutrient concentration,
158 temperature, upwelling wind index, or time of year) to relevant measures of HABs (e.g., the timing of
159 HAB events or the abundance, toxicity, and spatial distributions of HAB species). A wide range of
160 forcing variables are typically considered during model development, some of which may be interrelated
161 (e.g., temperature and time of year, salinity and river discharge). While the choice of forcing variables is
162 often guided by our understanding (theoretical or empirical) of the underlying physical and biological
163 processes, statistical models do not attempt to represent those processes directly, only the cumulative
164 effects of them. Statistical models require extensive observations to develop robust relationships between
165 forcing variables and HAB response. As such, some of the most compelling examples come from regions
166 with long records of HAB monitoring and investigation. Examples include *Pseudo-nitzschia* and
167 *Dinophysis* blooms off the Iberian Peninsula and Ireland (Raine et al. 2010; Cusack et al. 2015; Díaz et al.
168 2016), *Pseudo-nitzschia* off the U.S. West Coast (Anderson et al. 2009; Lane et al. 2009), *Alexandrium* in
169 Puget Sound and the U.S. Northeast (Moore et al. 2009; Ralston et al. 2014), *Karenia* in the Gulf of
170 Mexico (Stumpf et al. 2009), and multiple HABs on the Northwest European Shelf and in Chesapeake
171 Bay (Anderson et al. 2010; Brown et al. 2013). Statistical models are typically used in hindcasting, but
172 may provide nowcasts if real-time observations of forcing variables are available or limited forecasts if
173 lags are built in to the model. Alternatively, output from operational physical models can be used in place
174 of observations to provide input for statistical models, enabling near-term forecasts of HABs. A wide
175 variety of statistical approaches have been used to model HABs in the present climate, ranging from
176 simple linear regressions to more complex analyses using artificial neural networks, fuzzy logic, or
177 Bayesian inference. Here, we highlight a few approaches that have been used to predict the timing and
178 distribution of HABs.

179 Statistical analysis of observational data sets that record HAB response to changes in environmental
180 forcing at climate-relevant time scales can be informative for identifying forcing variables that are climate
181 sensitive. Past performance is no guarantee of future results, but multi-decadal observations provide
182 evidence at time scales relevant to climate change of HAB variation with forcing conditions. For
183 example, in Puget Sound (Washington State), optimal conditions for *Alexandrium catenella* blooms –
184 warm air and water temperatures in combination with low river discharge and wind speed – have become
185 more common over the past 30 years, as have the frequency and duration of toxic blooms (Moore et al.

186 2009). In many cases, identification of a “window of opportunity” with increased risk for bloom
187 development and toxin accumulation, and potential alterations to that window of opportunity with climate
188 change, is a primary goal of HAB modeling rather than representing specific events or the phytoplankton
189 community. Another example is a study of a 30-year record of *Dinophysis acuta* in the rias of northwest
190 Spain that used a general additive model (GAM) based on upwelling intensity, thermocline depth, tidal
191 range, and inoculum strength to predict cell abundances. The analysis did not find evidence for increasing
192 trends in bloom frequency or intensity, nor clear relationships to long-term climate indices like the North
193 Atlantic Oscillation (NAO) (Díaz et al. 2016). The study did, however, find that an exceptional bloom in
194 1989-1990 appeared to be associated with high positive anomalies in sea surface temperature (SST) and
195 the NAO index. That analysis did not extend their GAM to climate time scales. To do so effectively, a
196 GCM would need to represent the combination of upwelling and solar heating that are ideal for HAB
197 development. These ideal physical conditions occur relatively briefly and infrequently, and remain
198 challenging to reproduce in finer scale regional models that would be needed to adequately represent the
199 blooms (Ruiz-Villarreal et al. 2016).

200 Forcing variables that represent dominant physical and biogeochemical processes can serve as the basis
201 for forecasting the timing of HABs. For example, in southwestern Ireland, stratified, wind-driven
202 circulation during summer months can bring harmful *Dinophysis* spp. from the continental shelf into
203 coastal embayments where they can cause toxic events (Raine et al. 2010). A simple model based on the
204 5-day weather forecast for cross-shore wind and time of year was used to predict *Dinophysis* import
205 events and Diarrhetic Shellfish Poisoning (DSP) toxicity, and these model results were used to guide near-
206 term shellfish resource management. In Monterey Bay (California), a logistic regression model
207 incorporating multiple forcing factors including time of year, chlorophyll, silicic acid, water temperature,
208 upwelling index, river discharge, and nitrate was developed from 8 years of observations and used to
209 predict the probability of *Pseudo-nitzschia* blooms (Lane et al. 2009). Similarly, *Pseudo-nitzschia* blooms
210 off the coast of Ireland were linked to upwelling, and a statistical model using a wind index, water
211 temperature, and recent cell densities helped predict the timing, but not intensity, of bloom events
212 (Cusack et al. 2015).

213 Statistical models that spatially resolve forcing variables can provide information on HAB distribution
214 based on habitat suitability for the causative organism. For example, a regression model using satellite
215 ocean color and sea surface temperature (SST) detected 98% of toxic *Pseudo-nitzschia* blooms in Santa
216 Barbara Channel (California) with less than 30% false positive cases (Anderson et al. 2009). In Lake Erie,
217 satellite imagery of *Microcystis* spp. bloom extent was correlated with river discharge and nutrient
218 loading, and could be used to generate a seasonal forecast because of the several month lag between input

219 variables and bloom response (Stumpf et al. 2012). In northwest Spain, the presence or absence of
220 *Pseudo-nitzschia* blooms in several coastal embayments was linked to location, day of year, temperature,
221 salinity, upwelling index, and, most importantly, recent bloom occurrence using a support vector
222 machine, which is a common machine-learning algorithm (González Vilas et al. 2014). In Chesapeake
223 Bay, a Generalized Linear Model (regression-based approach allowing for both Gaussian and non-
224 Gaussian distributions) was developed with 22 years of cell abundance data and used to make hindcast
225 maps of *Pseudo-nitzschia* bloom probability based on factors including time of year, temperature, salinity,
226 nutrients (phosphate, nitrate, silicic acid), river discharge, dissolved organic carbon, and Secchi depth
227 (Anderson et al. 2010). Another approach in Chesapeake Bay used output from a physical model as input
228 for empirical habitat suitability models to make near-term forecasts of HAB occurrence (Brown et al.
229 2013). The methodologies (neural network or logistic regression) and input variables (time of year,
230 temperature, salinity, chlorophyll, nutrients, Secchi depth, total suspended solids, dissolved oxygen) for
231 the habitat models varied for the three HAB species (*Karlodinium veneticum*, *Prorocentrum minimum*,
232 and *Microcystis aeruginosa*) modeled. This approach relied on both physical model results and extensive
233 HAB observations for development of the empirical model.

234 2.2 Process-based models

235 Process-based (or mechanistic) models use mathematical equations to explicitly simulate key physical and
236 biological processes that govern HABs and HAB outcomes. Their development requires detailed
237 knowledge of critical life history characteristics and the factors that modulate them as well as transport
238 pathways. As such, they require large amounts data to represent the many processes in the system and can
239 be limited by their parameterizations of rates of growth, mortality, mobility, toxin production, and other
240 key processes that are typically derived from simplified laboratory studies of isolated strains. In situations
241 where observational or laboratory data are limited, process-based models instead may be informed by
242 data on similar organisms or may be limited to focusing on a subset of processes that are particularly
243 important to bloom dynamics. Because process-based models are more comprehensive than statistical
244 models, they take more time and effort to develop and are more computationally expensive to run.
245 Process-based models can be difficult to constrain given the nonlinearity and intermittency of HABs, but
246 they are usually more transferable across regions because of their explicit representation of physical and
247 biological processes.

248 In systems where transport processes are negligible, models based only on biological processes have
249 utility. For example, in Nauset Estuary on Cape Cod (Massachusetts), a small embayment with limited
250 exchange and long residence times, interannual variability in timing of *A. catenella* blooms was
251 reproduced with a simple model based temperature-dependent growth rates (Ralston et al. 2014). In

252 contrast, for many HABs physical transport provides the dominant control on bloom distribution. For
253 these cases a common approach is to use velocity fields from a circulation model to advect particles that
254 are representative of the HAB. For example, the accumulation of *Dinophysis acuminata* in the Bay of
255 Biscay at temperature and salinity gradients associated with river plumes, and subsequent dispersion of
256 the bloom by winds and tides, was well represented by passive particle tracking and circulation model
257 hindcasts (Velo-Suárez et al. 2010). A passive particle tracking approach was also used in a forecast
258 system for *Dinophysis* for the rias (drowned river valleys) of the northwestern Iberian coast (Ruiz-
259 Villarreal et al. 2016). Particle tracking similar to that used for oil spills was used for a *Microcystis*
260 *aeruginosa* bloom in western Lake Erie by linking satellite ocean color observations and a hydrodynamic
261 model, and importantly the study included quantitative skill assessment of the predictions relative to
262 persistence, or no influence of transport on the bloom (Wynne et al. 2011).

263 More commonly, both physical and biological processes play important roles in HAB development and
264 they cannot be treated independently. Individual-based models (IBMs), like passive particle tracking, can
265 be run within a circulation model or offline using model output to represent advection by currents, but
266 IBMs also can incorporate biological processes specific to the organism of interest. For example, an IBM
267 with growth dependent on temperature, mortality dependent on shear and population density, and
268 phototactic vertical migration was used to hindcast *Karenia mikimotoi* blooms along coastal Scotland
269 (Gillibrand et al. 2016). Results showed a strong dependence on bloom source region and uncertainty in
270 the biological rate parameters, making the model less practical for forecasts. In the Gulf of Mexico, an
271 IBM of *Karenia brevis* that included vertical migration based on internal nutrient ratios was used to
272 identify potential source regions by running simulations backwards in time (Henrichs et al. 2015).

273 Rather than IBMs, HAB growth, mortality, and redistribution can also be represented as cell
274 concentrations within circulation or biogeochemical models. For example, a model of *A. catenella* that
275 represents cyst germination, growth dependent on temperature, salinity, nutrients, and light, and mortality
276 has been used in diagnostic hindcasts and operational forecasts in the Gulf of Maine (Stock et al. 2005; Li
277 et al. 2009), and a related model that also imposed diel vertical migration was used to simulate *A.*
278 *catenella* in an estuary (Ralston et al. 2015). Those models treated the HAB as independent of the broader
279 plankton community by simulating only the species of interest and prescribing the nutrient field based on
280 observations rather than having it evolve dynamically. A more complete ecosystem, biogeochemical, and
281 circulation model of the northwest European shelf incorporated multiple phytoplankton, zooplankton, and
282 bacteria functional groups and benthic-pelagic coupling to simulate high biomass events, providing
283 predictions after calibration to satellite ocean color (Allen et al., 2008).

284 In general, the many biological processes that contribute to HAB development remain poorly defined and
285 present major sources of uncertainty in process-based models. Passive particle tracking models ignore this
286 and IBM or Eulerian-based hindcasts typically calibrate model parameters within acceptable ranges that
287 optimally correspond to observed blooms. However, models used to generate forecasts that have
288 operational utility cannot rely on retrospective calibration, and so many adopt hybrid approaches that use
289 physical models to predict transport processes along with empirical models to integrate biological
290 response. For example, near-term forecasts for *Pseudo-nitzschia* in Bantry Bay in southwest Ireland were
291 based on the combination of a passive particle tracking model to represent cross-shore advection by
292 upwelling, a circulation model, satellite observations, and in-situ sensors to characterize local water
293 properties, and recent toxicity reports (Cusack et al. 2016). Similarly, transport of *Pseudo-nitzschia* from
294 formation regions offshore to the coast depending on upwelling or relaxation along the Pacific Northwest
295 coast of the U.S. was simulated with particle tracking, and the rate of false positives for toxicity events
296 was reduced by incorporating thresholds for overall phytoplankton abundance from an ecosystem model
297 (Giddings et al. 2014). A hybrid approach using satellite SST and ocean color along with particle tracking
298 was used to explain accumulations of *Karenia* spp. in the eastern Gulf of Mexico (Stumpf et al. 2008),
299 although bloom forecasts are based primarily on satellite data (Stumpf et al. 2009). Satellite algorithms
300 for bloom identification are important components of many hybrid systems for early warning, using either
301 overall levels of chlorophyll-a (Stumpf et al. 2008; Cusack et al. 2016) or specific spectral response like
302 for *Microcystis* in Lake Erie (Stumpf et al. 2012). The utility of satellite data in hybrid models depends on
303 the HAB, as for example in Europe it was found to be useful for early warning of *Karenia mikimotoi* and
304 *Lepidodinium chlorophorum* but not *Dinophysis* (Maguire et al. 2016).

305 **3. Modeling HABs in a changing climate – what has been done?**

306 Projecting HAB response to climate change involves extending the simulation period of existing HAB
307 models to decades, centuries, or potentially paleo time scales for retrospective climate analyses. Data
308 describing future forcing conditions can be obtained from GCM simulations and used as input variables to
309 HAB models. GCMs forecast ocean circulation and water properties under future climate scenarios
310 informed by various greenhouse gas concentration trajectories. These scenarios describe a range of
311 possible futures based on greenhouse gas emissions, economic development, population growth, and
312 other factors. The output generated by GCMs quantify changes in physical and biogeochemical conditions
313 and can be combined with statistical relationships from past observations to project changes in HABs.
314 Additional model layers to represent climate change effects outside of the ocean, such as watershed
315 hydrology or land use, can also be integrated. This offers a relatively simple approach for examining
316 climate impacts on HABs, but statistical models become increasingly error-prone when projecting into

317 conditions different from the training data set (Flynn and McGillicuddy 2018). This is because the
318 statistical relationships may represent the cumulative effect of multiple processes or interactions that
319 cannot be extrapolated, and also because thresholds or tipping points that were not identified or
320 characterized by prior observations may be exceeded in the projections. Process-based models are less
321 prone to these potential issues, but they represent only a portion of the physical and biological complexity
322 due to computational constraints and data limitations, and so even process-based models validated under
323 present conditions may not simulate many of the hypothesized responses to climate change. Here we
324 discuss some of the approaches for using statistical and process-based HAB models to project HAB
325 response to climate change. The different approaches vary in complexity in terms of how many forcing
326 variables are considered and how they are derived.

327 3.1 Statistical models

328 A statistical modeling approach was used to link HAB observations in Puget Sound (Washington State)
329 with physical observations and climate model forecasts to evaluate long-term shifts in environmental
330 conditions favorable for blooms (Moore et al., 2011). Based on a 15-year record of paralytic shellfish
331 poisoning toxins in shellfish tissues, *A. catenella* blooms were associated with warm air and water
332 temperatures, low streamflow, weak winds, and small tidal height variability. The relationship was
333 extrapolated back in time using observations of the forcing variables, and the annual window of favorable
334 environmental conditions for *A. catenella* was found to have increased from 1967 to 2006, with two step-
335 like increases occurring in 1978 and 1992 when higher annual values were attained compared to previous
336 years. The 1978 step change may have been related to the reversal of the Pacific Decadal Oscillation
337 (PDO) from cool to warm phase in 1977. The 1992 shift did not directly correspond with regional climate
338 indices, and a lagged response to a regime shift to warmer summer SST off the Washington coast in 1989
339 could not be distinguished from natural variability. Projections of the statistical relationship using output
340 from a GCM indicated that by the end of the 21st century, the duration of favorable environmental
341 conditions for *A. catenella* would increase by about 2 weeks annually on average (Moore et al., 2011).

342 Another statistical approach to climate response defined habitat zones for the shelf sea of northwest
343 Europe based on temperature, salinity, depth, and stratification from regional climate projections, finding
344 a general northward shift in HAB species composition (Townhill et al. 2018). Species distribution
345 modeling based on current distributions was projected forward using a maximum entropy approach for
346 multiple HAB species. On the shelf, *Dinophysis acuta* and *Gymnodinium catenatum* had the greatest
347 northward shift of 200-500 km by 2055, while optimal habitat suitability for three species (*A. ostentfeldii*,
348 *A. minutum*, and *P. australis*) shifted southward. The southward shift was attributed to factors in addition
349 to temperature change, including how the regional bathymetry affects habitat suitability.

350 Models of HAB response have also been coupled to models of future changes in freshwater or nutrient
351 delivery from rivers, which are often not resolved in global models. For example, a Bayesian network
352 model was used to link GCM results with process-based models of watershed hydrology and a lake
353 ecosystem model to project climate impacts on cyanobacteria biomass in Lake Vansjø (Norway) (Moe et
354 al. 2016). The Bayesian approach allowed assessment of multiple land use scenarios and incorporation of
355 monitoring data and expert knowledge in the probabilistic links between nodes. Results suggest that the
356 benefits of better land-use management were partly counteracted by future warming.

357 3.2 Process-based models

358 Temperature is a keystone parameter of climate change, and warming of the sea surface is apparent in
359 many regions in observational records from satellites and in-situ measurements. Because temperature is a
360 strong determinant of growth, changes in temperature can be used to approximate changes in potential
361 growth rates of HAB organisms. Warmer waters may already be affecting bloom dynamics. For example,
362 sea surface temperature records from 1982 to 2016 were combined with laboratory-based growth rates for
363 *A. catenella (fundyense)* and *D. acuminata* (Gobler et al. 2017). In the North Atlantic, calculated mean
364 growth rates increased by about 0.01 d^{-1} over the study period and the duration of favorable growth
365 conditions increased by 2 to 3 weeks. In the North Pacific trends were less clear, but some regions (the
366 Salish Sea and coastal Alaska) were identified as having increasingly favorable growth conditions and
367 HAB prevalence.

368 Temperature is an important forcing variable in nearly every HAB model of climate response reviewed
369 here. A number of studies use projected changes in sea surface temperature at certain locations to
370 approximate changes in growth rates and identify expansions (or contractions) of optimal growth
371 windows for HAB organisms. The windows are defined as the number of days each year when
372 temperatures are projected to be within thresholds that support optimal growth (e.g., Moore et al. 2008).
373 For example, an ensemble of GCM projections were used to quantify changes in temperature-dependent
374 growth rates of *Gambierdiscus* and *Fukuyoa* species, dinoflagellates associated with ciguatera fish
375 poisoning (CFP), at six sites in the Gulf of Mexico through the end of the 21st century (Kibler et al. 2015).
376 The results suggest increased abundance and diversity of *Gambierdiscus* spp. and greater CFP risk in the
377 Gulf of Mexico, but a shift in the species composition at higher temperatures suggests lower overall risk
378 in the Caribbean. A similar ensemble approach was used to calculate shifts in the timing of temperature
379 growth windows for *A. catenella* and *Vibrio* spp. bacteria in Puget Sound and Chesapeake Bay, with the
380 *A. catenella* bloom period predicted to start 1 month earlier and end 1 month later (Jacobs et al. 2015). In
381 addition to changes in bloom timing, the study identified geographic shifts in optimal temperature zones
382 along coastal Alaska for *Vibrio*, which while not a HAB, presents a methodology that could be applied in

383 HAB studies to examine potential latitudinal shifts in species distribution without directly simulating
384 HAB dynamics.

385 Potential shifts in the timing of optimal growth windows as well as the spatial distributions of HABs can
386 be evaluated by utilizing spatially resolved information on future forcing conditions from GCMs or
387 regional models of climate change rather than projections at a single location. For example, in Puget
388 Sound, regional scale atmospheric, ocean, and hydrologic models were combined to represent multiple
389 potential influences on optimal temperature (and salinity) windows for growth of *A. catenella* (Moore et
390 al. 2015). Comparing model results for circa-1990 and circa-2050, atmospheric heating was projected to
391 increase the duration of favorable growth conditions by 30 days per year with the biggest increases in
392 HAB-favorable conditions occurring in the North Basin and Strait of Juan de Fuca. Changes in the timing
393 and magnitude of river discharge and upwelling on temperature and salinity were found to have less effect
394 on calculated growth rates. The study did not address potential changes in nutrient loading due to
395 upwelling or anthropogenic sources.

396 In addition to HAB growth rates, warming temperature may also be expected to increase growth rates of
397 some grazers that prey on HAB species, including zooplankton, benthic invertebrates, and fishes.
398 Moreover, predator-prey interactions and the response to changing environmental conditions are more
399 complex than species growth rates, as changes in the distribution, abundance, community composition,
400 toxicity, and nutritional quality of HAB species may all depend on temperature and can affect the relative
401 balance of growth rates and loss from predation, and thus bloom development (Wells et al. 2015).
402 Representing quantitatively the many factors contributing to effects of predation on HAB growth and
403 decline, including temperature, remains a major challenge for process-based models in both current and
404 climate change scenarios. To this point, most of the modeling of temperature impacts has focused on
405 HAB growth rates alone rather than assessing the potentially differential responses of grazers and prey.

406 The above examples directly link changes in temperature to temperature-dependent growth rates of HAB
407 organisms to examine changes in bloom timing and spatial distribution. Some other examples also
408 consider salinity, but the relatively small changes in salinity projected in the study regions meant that the
409 growth responses were primarily driven by changes in temperature. Nutrients are another forcing variable
410 that strongly determine growth rates and toxicity of HAB organisms and are projected to be altered by
411 climate change. For example, a model of the mixotrophic dinoflagellate *Karlodinium veneticum* and its
412 algal prey, *Rhodomonas salina*, was used to simulate growth under various temperature and nutrient
413 stoichiometry scenarios (Lin et al. 2018). While these scenarios were not directly linked to GCM output
414 of future climate change scenarios, they were informative of future HAB response and suggest that
415 warmer, wetter springs combined with increased nitrogen inputs to Chesapeake Bay may be more

416 favorable to HAB development. In contrast, GCM output was used as boundary conditions for a coupled
417 oceanographic and biogeochemical model with four classes of phytoplankton, three for zooplankton, one
418 for bacteria, nitrogen and phosphorous in different forms, and benthic mineralization on three regional
419 grids at 1/10-degree resolution to assess conditions for *Prorocentrum* and *Karenia* spp. around 2100
420 (Glibert et al. 2014). The study defined regions of suitable habitat or propensity for toxicity based on
421 temperature, salinity, and nutrients for two time slices: the period 1980-1990 for the present day and
422 2090-2100 for the future climate scenario. Model results showed expansion both spatially and temporally
423 of both species on the northwest European shelf and northeast Asia, and relatively little change in
424 southeast Asia.

425 **4. Modeling HABs in a changing climate – what should be done?**

426 The fact that relatively few modeling studies quantitatively project how climate change may affect the
427 distribution and abundance of HAB populations or toxicity is symptomatic of the challenges associated
428 with this important task. Challenges associated with understanding the biological response of HABs to
429 climate change, as well as suggestions for best practices that should be employed to address them, are
430 discussed in Wells et al. (2015); however, little attention was given to the modeling infrastructure needed
431 to project HAB response to climate change. Generating useful projections of HAB response to climate
432 change will require engagement with other communities that can help refine the representation of future
433 conditions in HAB models, including climate scientists, marine ecologists, watershed hydrologists,
434 invasive species biologists, and environmental managers and policy makers (Glibert et al. 2010). Here we
435 offer several suggestions to improve modeling of HABs in a changing climate, schematically summarized
436 in Figure 1.

437 *4.1 Use process-based models*

438 Even though there are challenges associated with uncertainty in model parameterizations, nonlinear
439 feedbacks, and computing power, process-based models have distinct advantages over statistical
440 approaches for projecting impacts of climate change on HABs. In many cases, data limitations initially
441 hinder development of process-based models for emergent HABs or regions without many observations,
442 and so statistical models can be extremely important in the diagnosis of bloom mechanisms and
443 development of process-based models. Statistical models are often well suited for shorter-term projections
444 and management applications, particularly when the models incorporate a dominant influence of periodic
445 forcing like from ENSO or PDO. Importantly for climate change response, process-based models
446 explicitly represent physical and biological mechanisms involved in HAB development, and so they are
447 less likely to lose validity when forcing variables are applied that extend outside of periods of historical

448 observation. Incorporating multiplicative effects of changes in temperature, nutrient availability, or
449 stratification (among other factors) into process-based HAB models requires focused, process-oriented
450 field or laboratory studies that record organism response beyond just abundance, ideally in the context of
451 the ecosystem response rather than just for individual strains (Flynn and McGillicuddy 2018). Changes in
452 HAB severity will depend on the cumulative effects of factors including differential responses of
453 predators and prey, changing nutrient availability, and shifts in transport patterns rather than a simple
454 parameter dependence from on lab studies. Circulation models can be directly coupled with ecosystem
455 models to simulate projected physical and biogeochemical changes at climate time scales. This approach
456 is intrinsic to many earth system models that have been used to examine changes in ecosystem and
457 nutrient dynamics globally and regionally using various downscaling methods. For HAB models, the
458 limited understanding of complex predator-prey interactions and competition among classes within the
459 ecosystem limit our ability to parameterize process-based models (Wells et al. 2015), and should be a
460 focus of future research.

461 Process-based models are typically more complex than statistical models. The introduction of additional
462 processes and parameters may improve model fit, but can also reduce predictive skill if not based on a
463 robust representation of the underlying processes (Bell and Schlaepfer 2016). Regime shifts, in which the
464 dominant processes or forcing variables controlling bloom development change in large, abrupt, and
465 persistent ways, are particularly challenging to model, and additional complexity may increase variability
466 in the results without incorporating the relevant combination of stressors leading to the regime shift,
467 particularly if the model is not validated with data independent from the training region and forcing
468 conditions. HAB models used to assess climate impacts should be rigorously evaluated to identify model
469 parameters that most sensitively determine model outcomes, and this should guide efforts to simplify
470 complex models and to focus laboratory and field studies to refine the uncertainty in those key parameters
471 (Flynn and McGillicuddy 2018). The development of process-based models requires parallel efforts of
472 laboratory and observational studies to refine key rate parameters and process dependencies, including the
473 effects of changes to multiple forcing factors changing simultaneously. The applicability of process-based
474 models is predicated on validation across a broad set of forcing conditions, and so data collection is
475 particularly critical for in developing models for HABs in regions that have a sparse history of monitoring
476 and research. Statistical approaches should continue to play an important role in HAB modeling,
477 particularly for resource management and public health protection over event to seasonal time scales, but
478 extending statistical models to predict climate change response has limited merit.

479 *4.2 Use an ensemble approach*

480 An ensemble approach can be used to address the uncertainty that is introduced to long-term projections
481 of HAB response from a wide range of sources, including HAB or ecosystem model parameterizations,
482 variability in the climate model forcing (GCM selection, emissions scenario, downscaling approach), and
483 the stochastic response of non-linear physical-biological interactions within the model system. An
484 ensemble approach considers multiple model scenarios to quantify how different choices of key input
485 factors, and potentially within the model formulation as well, affects the uncertainty in model projections.
486 The selection of scenarios to use in an ensemble approach depends on the particular application and
487 available resources, but sensitivity testing based on a subset of potential cases can be used to identify
488 components of the model system that are particularly important sources of uncertainty in the long-term
489 response. The central tendency (or “most likely” scenario) of the ensemble might be the focus of analysis
490 and reporting on the modeling, but it may also be informative to select scenarios that encompass the full
491 range of possible future outcomes. The process used to develop the scenarios and the sensitivity to
492 various model aspects within the ensemble provide critical context for interpreting the results and for
493 guiding future research efforts to minimize or mitigate model uncertainty.

494 HAB models constitute a small subset of the broader array of ocean biogeochemical models, so models
495 representing similar processes can provide context for assessing climate change response. A common
496 approach is to couple global or regional circulation models with biogeochemistry models of varying
497 complexity to project ecosystem response under future climate forcing. The ecosystem response depends
498 both on the circulation model and the biogeochemical formulation, so generally an ensemble approach
499 evaluating multiple, independent models with the same set of forcing conditions provides critical context
500 for evaluating model results. For example, a study using six climate model simulations along with an
501 empirical model for predicting chlorophyll from physical model fields projected a global increase in
502 primary productivity of 0.7-8% in response to warming over the 21st century (Sarmiento et al. 2004). In
503 contrast, analysis of four coupled climate-carbon cycle models projected a global decrease in primary
504 productivity of 2-20% (Steinacher et al. 2010). The differences between the results were attributed to
505 differences in the biological model formulations, in that nutrient availability was incorporated in the
506 coupled model but not directly in the empirical approach. Both studies found large regional variability in
507 the response to climate change, as well as regional differences in the agreement among the ensemble
508 members. Model skill varied regionally depending on the model, so appropriately weighting the ensemble
509 members based on their skill regionally can provide a better solution than a simple average of ensemble
510 members, and quantifying the inter-model variation provides a valuable measure of the uncertainty in the
511 region of interest (Steinacher et al. 2010; Stock et al. 2011). Evaluation of model skill for ecosystem
512 response requires long-term observations, as discussed in greater detail below. For chlorophyll,
513 identifying observational declines at both regional and global scales required using Secchi depth

514 measurements spanning more than 100 years because fluctuations in chlorophyll at the interannual to
515 decadal time scales were sufficiently large that long-term trends were not robust over the ~30 years of
516 satellite data (Boyce et al. 2010).

517 Modeling studies of climate impacts on HABs have typically examined responses at time scales of 50 to
518 100 years (e.g., Moore et al. 2008; Glibert et al. 2014; Townhill et al. 2018), as this is when greenhouse
519 gas concentration trajectories associated with the different potential futures diverge and high emission
520 scenarios become distinguishable from natural variability. Yet for management and public policy
521 decisions, characterizing changes in HAB risks at shorter time scales (i.e., decadal) may be more critical.
522 For physical models, projection of climate response at decadal time scales remains a major challenge
523 (Zhang and Kirtman 2019). At decadal time scales, both external forcing and internal ocean response can
524 be dominated by noise, making model response unpredictable. Internal climate variations like ENSO,
525 AMO, or PDO may dominate responses of key climate variables like upwelling strength or river
526 discharge, particularly at decadal time scales, swamping trends at century time scales that are more
527 robustly represented across the suite of climate models. Climate predictability at decadal time scales
528 varies regionally with the local modes of internal variability, such that some regions have greater
529 predictability (North Pacific, North Atlantic, Southern Ocean) than others (tropical Pacific) (Zhang and
530 Kirtman 2019). An understanding of the regional predictability of climate model, including variation
531 among models, is particularly important for HAB models that are typically only simulating regional
532 scales at decadal time scales.

533 Using validation and sensitivity testing to understand uncertainty in HAB models, in addition to the
534 uncertainty in projections of the physical and biogeochemical conditions, is a critical step prior to
535 projecting HAB response to climate change. HAB models of present conditions need to include more
536 thorough assessments of model uncertainty, with ensemble sensitivity studies or more formal means like
537 Bayesian models that incorporate uncertainty estimates in the results (Anderson et al. 2015), as the
538 uncertainty compounds when run in climate forecast scenarios. HAB model failures also are instructive
539 particularly in the context of potential regime shifts with climate change when major shifts in forcing
540 conditions are not adequately represented in the model setup, as with anomalous conditions that affected
541 *Alexandrium* in the Gulf of Maine (McGillicuddy et al. 2011).

542 Scenario planning is becoming a popular approach for decision-makers to address uncertainty in future
543 projections and help prepare for conditions that may be substantially different from current conditions
544 (Star et al. 2016). Scenario planning involves crafting stories about how the world *might* turn out in the
545 future, it is not about predicting what *will* happen. Scenarios are developed around major uncertainties, or
546 *what ifs*, in how key parameters might change in the future. Scenario planning can combine both

547 quantitative and qualitative components, and involve input from researchers as well as stakeholders.
548 Working through scenarios not only informs the development of societal response strategies to deal with
549 future HABs, but also helps to understand how socioecological systems work and respond to HABs under
550 current climate conditions. Benefits from scenario planning include increased flexibility to react quickly
551 to a changing world, more thoughtful strategic planning and decisions, innovative ideas, early and broad
552 risk assessment, and increased ability to achieve a common vision (Star et al. 2016). The use of scenario
553 planning for evaluating HAB response to climate change offers a path forward for addressing some of the
554 major uncertainties in biological responses identified in Wells et al. (2015) while still providing
555 actionable projections.

556 *4.3 Use downscaled climate models*

557 Global earth system models typically have spatial resolution too coarse (nominally 1° for CMIP5
558 generation of climate models) to represent regional variability like tides, river inflows, coastal
559 topography, or water column structure in detail. Even high resolution global models at $1/12^\circ$ can't resolve
560 features at the scale of the baroclinic Rossby radius (c_i/f , where c_i is the internal wave speed and f the
561 Coriolis parameter), which is relevant to coastal upwelling, frontal jets, and buoyant plumes, in more than
562 90% of the coastal ocean. To get to 70% coverage, 6 times higher resolution would be required (Holt et
563 al. 2017). Higher resolution regional circulation models provide better model skill for resolving
564 stratification and variability at seasonal time scales, but linking regional scale models to forcing from
565 GCMs requires accounting for the coarse resolution and regional biases through downscaling, bias
566 corrections, and multi-model ensembles (Stock et al. 2011). Resolving physical and biogeochemical
567 processes at coastal scales is critical for HAB modeling, as the HABs that have the greatest impacts on
568 fisheries, aquaculture, or through direct exposure typically occur near the coast.

569 Downscaling from global models can be statistical or dynamical. Dynamical downscaling provides
570 physically consistent representations of the dynamical system at higher resolution, but it is comparatively
571 expensive to setup and run the models and remains subject to regional biases in the global models (Stock
572 et al. 2011). For example, dynamical downscaling was used to model the North Sea at 3 km resolution to
573 project changes in bottom temperature and salinity, and these physical model fields were used to project
574 changes in distributions of 75 benthic species (Weinert et al. 2016). The results indicated northward shifts
575 for about 2/3 of species and southward shifts for the rest, and the downscaled model illustrated the strong
576 influence of bottom topography on habitat gains and losses. An ensemble of dynamically downscaled
577 regional models of the Baltic Sea with different nutrient loading scenarios was used to assess hypoxic and
578 anoxic extent and potential influences of changes in river discharge, air-sea fluxes, and intensified
579 nutrient cycling (Meier et al. 2011). The variance in biogeochemical response with forcing from three

580 physical models with different structures but similar forcing provided a metric of the robustness of the
581 results relative to model variability.

582 Statistical downscaling can take various forms, including linear regression, general additive models, and
583 neural networks, and can link global climate model output variables to variables of interest in a particular
584 region. Approaches for selecting appropriate downscaling approaches are reviewed elsewhere (e.g.,
585 Wilby et al. 2004; Haylock et al. 2006). The robustness of the downscaling depends in part on the data
586 available to develop statistical relationships between predictor and response variables, and it requires
587 keeping a subset of the observations separate from the training data for validation. Statistical downscaling
588 also faces limitations when extrapolating into climate conditions that are outside the bounds of the
589 observational record, as model failures may not be apparent even when using independent validation data
590 from the same parameter space as the training data (Bell and Schlaepfer 2016).

591 Various statistical downscaling approaches have been used to link climate model outputs to
592 biogeochemical models at regional, coastal, or estuarine scales. A constructed analogues approach that
593 represents sharp geographical gradients and daily variability through linear regressions of model output to
594 observations (Hidalgo et al. 2008) was used to relate air temperatures from GCMs to water temperature in
595 the San Francisco Estuary, and thus project climate impacts on an endangered fish species (Brown et al.
596 2016). Four different downscaling methods were trained on 20 years of observations to downscale air
597 temperature and precipitation fields from four GCMs to the Susquehanna River watershed to generate
598 inputs to a water balance model and predict changes in surface salinity and temperature in Chesapeake
599 Bay (Muhling et al. 2018). Those downscaled salinity and temperature projections were combined with
600 habitat models for three *Vibrio* species to predict future increases in the seasonal duration and spatial
601 extent of the pathogens (Muhling et al. 2017). Several examples using statistical downscaling, bias
602 correction, and ensemble approaches to model climate change impacts on regional fisheries are examined
603 in Stock et al. (2011), which details many of the considerations in using downscaled climate models to
604 drive ecosystem forecasts that are relevant to HAB models.

605 *4.4 Evaluate models with long-term observations*

606 Global climate models are known to have biases and skill that vary regionally, and these can be assessed
607 by comparison with observation records during GCM model hindcast periods. Observations to evaluate
608 physical parameters like air temperature or wind speed, and to lesser extent water temperature and
609 salinity, are far more prevalent than long-term observations of biogeochemical parameters like nutrient or
610 chlorophyll concentrations. Extended time series of HAB abundance or toxicity that are needed to
611 evaluate HAB model hindcasts at climate time scales are even rarer. Long-term observations of

612 biologically relevant data are critical to identify trends in what are often sparse, patchy distributions
613 (Ducklow et al. 2009), and they also need to be incorporated into assessments of climate forecasts.
614 Fisheries surveys are an example of a rich data type that has been used to identify decadal scale variability
615 associated with the PDO or NAO as well as seasonal to interannual variability with ENSO (Lehodey et al.
616 2006). Models of climate impacts on fisheries incorporate these long-term records into statistical
617 relationships between physical fields and the response of the variable of interest, and those relationships
618 can be continually updated as additional data are collected (Hollowed et al. 2009; Hare et al. 2010). The
619 Continuous Plankton Recorder (CPR) survey is another observational record that goes back more than
620 half a century, and it has been used to document shifts in community composition with decreased
621 abundance of dinoflagellates and increases of some diatoms, including *Pseudo-nitzschia*, which were
622 attributed to increased sea surface temperatures and stronger stratification (Hinder et al. 2012). CPR data
623 were used to identify increases in warm-water phytoplankton and zooplankton species and decreases in
624 cold-water species that were correlated with sea surface temperature in the northeastern Atlantic, air
625 temperature in the Northern Hemisphere, and the NAO (Beaugrand and Reid 2003). Northward shifts in
626 community composition in a coupled physical and biogeochemical model that were consistent with CPR
627 observations were used to diagnose the processes leading to the changes, and showed that in addition to
628 warmer temperatures that changes in circulation and stratification contributed to the patterns in the model
629 (Barton et al. 2016).

630 To be useful for assessing climate impacts on biological systems, models must be able to distinguish the
631 response to climate variability from internal biological dynamics (Lehodey et al. 2006), and ideally HAB
632 models of climate response should help in identifying similar responses among different regions.
633 Successful modeling approaches can be transferred to new regions, but requires accounting for
634 similarities and differences in the physical environment, ecosystem characteristics, and HAB population,
635 all of which are multi-dimensional and difficult to quantify without observations. Identifying climate
636 effects in observations requires at least several decades of consistent HAB monitoring, and yet few
637 regions have such high-quality time series data, nor is there monitoring in regions where future outbreaks
638 may occur (Anderson et al. 2015; Wells et al. 2015). In addition to climate change, anthropogenic
639 stressors such as fishing pressure, nutrient inputs, and invasive species introduction increase the
640 challenges of identifying trends in observations of HAB abundance and distribution. Nutrient inputs have
641 increased more than ten-fold in some coastal regions over the past few decades with usage of synthetic
642 nitrogen fertilizer usage and urbanization, but the impacts vary widely (Howarth 2008). Projecting future
643 nutrient conditions may require accounting for regional increases or decreases in nutrient loading with
644 watershed land-use changes (Bouwman et al. 2009; Glibert et al. 2010) in addition to physical changes in
645 the nutrient delivery by river discharge or coastal upwelling that are incorporated in models of HAB

646 dynamics presently. Shifts in nutrient inputs by eutrophication or climate change may also affect nutrient
647 limitation and require incorporating currencies in addition to nitrogen into HAB models (Flynn and
648 McGillicuddy 2018).

649 While it is generally accepted that HABs are globally increasing in severity and extent, the role of climate
650 change in the observed trends has been challenging to isolate mechanistically among the many other
651 contributing factors (Moore et al. 2008). HAB models applied retrospectively at climate time scales may
652 provide a useful means of hypothesis testing as opposed to focusing on predictions of future impacts. As
653 has been done with observations (Moore et al. 2011), weather events, anomalous seasonal conditions, or
654 sharp changes in forcing can be simulated retrospectively with HAB models as analogues for climate
655 change impacts. Such scenarios can more realistically incorporate multiple stressors, and allow for
656 quantitative assessment of model performance and uncertainty using observations that are independent
657 from the model calibration. For example, laboratory studies have found that growth rates for *Alexandrium*
658 spp. increase up to 20-24 °C (Watras et al. 1982; Etheridge and Roesler 2005; Bill et al. 2016), suggesting
659 that warmer water will lead to faster growth and greater bloom intensity. Observations of *A. catenella* in
660 an estuary in the northeastern U.S. found that the blooms in warmer years occurred earlier but did not
661 have longer duration or greater maximum cell abundance, and instead the blooms terminated before water
662 temperatures reached the values corresponding with maximum growth rates from the laboratory (Ralston
663 et al. 2014). A process-based, single-species model that used the laboratory growth rates could effectively
664 reproduce the growth phase across multiple years with widely varying temperature conditions, but an
665 empirical formulation for mortality that was not strictly temperature-dependent was needed to represent
666 bloom termination across the years, and could only be calibrated based on comparison with the multi-year
667 observations (Ralston et al. 2015). Bloom dynamics in that system remained similar enough over several
668 years that the empirical formulation for mortality had predictive skill, but climate change can potentially
669 induce more fundamental shifts in ecosystem dynamics, for example changing from bottom-up (nutrient
670 availability regulating growth) to top-down (grazing control) control (Wells et al. 2015). Developing
671 robust models of the interactions between HAB growth rates and grazer response under changing forcing
672 conditions, particularly when the relationships may be strongly non-linear, remains a central challenge for
673 HAB modeling across all simulation time scales (Flynn and McGillicuddy 2018).

674 **5. Conclusions**

675 Modeling HAB response to future climate change is still an emerging field, as evidenced by the limited
676 number of studies (fewer than 10) and diversity of approaches reviewed here. Extending HAB models to
677 decadal time scales or longer, extrapolating into forcing regimes that are outside historical observations,
678 representing potential regime shifts in the dominant processes controlling HAB development, and

679 incorporating uncertainty and variability in physical climate model projections are challenging but
680 feasible tasks. Based on this review, we offer several recommendations for how to best move forward
681 with modeling HAB response to climate change. Statistical models have predominantly been used for
682 near-term and operational HAB forecasts, but the uncertainty in model output increases as forcing
683 conditions diverge from the historical observations that were used to develop them. Process-based models
684 more directly represent key physical and biological factors in bloom development, and thus are better
685 suited to extrapolation into future climate forcing conditions. HAB models should be developed in the
686 context of the ecosystem response to climate change, recognizing that the response of many key processes
687 and the potential for regime shifts are common to the broader ecosystem. Uncertainty in HAB model
688 projections associated with process formulations or climate model forcing should be quantified and
689 conveyed using ensemble approaches and scenario planning. Downscaling of global (and potentially
690 regional) climate models to coastal scales should be done robustly in collaboration with physical climate
691 modelers to preserve features of the forcing that are key to HAB development. Finally, long-term
692 observations of HABs and forcing conditions are essential to identify trends associated with climate
693 change and for rigorously assessing HAB model results. Long-term observations are critically lacking in
694 many HAB impacted regions, and this may represent the biggest impediment to the development of
695 models that can effectively assess HAB response to climate change. Multiple decades of HAB monitoring
696 are often necessary to distinguish long-term trends from the response to cyclic climate forcing, so any
697 model-based assessment of HAB response to climate change needs to be closely coupled to high quality
698 observations. Modeling studies of HAB response to climate change will likely expand as resource
699 managers and policy makers increasingly demand projections of HAB impacts at both near-term and
700 longer time scales. As such, HAB models will be crucial for informing the development of strategies to
701 reduce socioeconomic and public health impacts as well as to increase resilience of socioecological
702 systems to future HABs.

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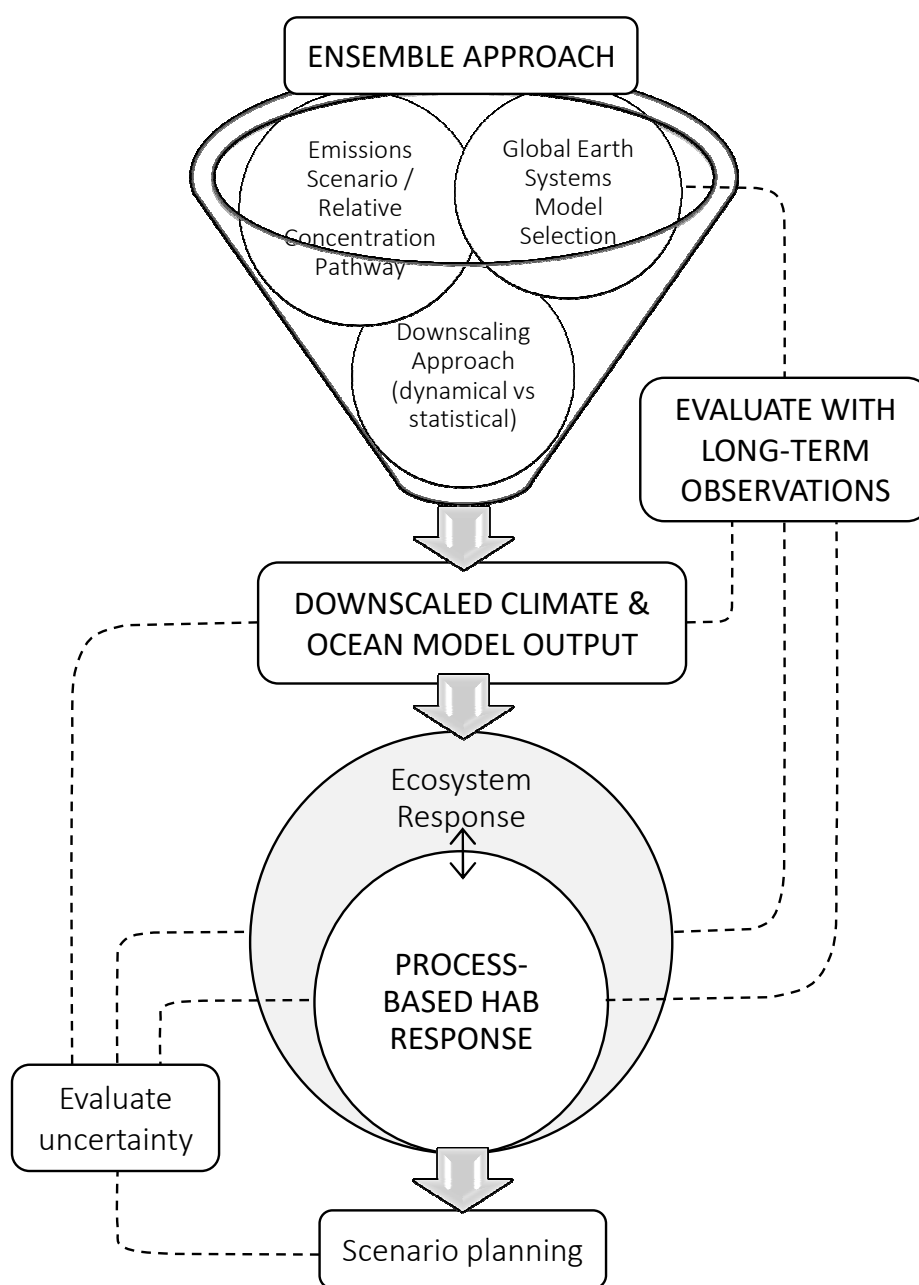
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978 **Figure**

979

980 **Figure 1.** Schematic diagram summarizing considerations for improving modeling of HAB response to
 981 climate change. Multiple global earth systems models, emissions scenarios/relative concentration
 982 pathways, and downscaling approaches should be considered in an *ensemble approach* to generate
 983 *downscaled climate and ocean model output*. Downscaling is necessary to resolve critical physical and
 984 biogeochemical processes for HAB development at coastal scales. These downscaled data should be used
 985 to force *process-based models of HAB response* with the results considered in an ecosystem context.
 986 Models should be *evaluated with long-term observations*. This step can be informative for selecting
 987 global models, identifying biases in downscaled model projections, and validating models of HAB and

988 ecosystem response. An important final step is to identify components of the model system that are key
989 sources of uncertainty in the long-term HAB response (i.e., *evaluate uncertainty*) and to develop
990 scenarios (i.e., *scenario planning*) around those sources of uncertainty in the development of societal
991 response strategies.

992

993 **Table**

994 **Table 1.** Table summarizing the HAB modeling studies reviewed here. Models are categorized based on whether they focus on present-day
 995 (hindcasts, event-based, near-term forecasts) or future climate conditions (using climate model projections) and the modeling approach (statistical,
 996 process-based, or a hybrid). Information on the HAB organism being modeled, geographic region, and a brief description of the model formulation
 997 and timescale are listed.

	Present vs future climate	Model type	HAB organism	Region	Brief description
Allen et al., 2008	Present	Process-based	High biomass species	NW European shelf	Ecosystem + circulation; seasonal
Anderson et al., 2009	Present	Statistical	<i>Pseudo-nitzschia</i>	California	Regression; spatial + temporal; seasonal
Anderson et al., 2010	Present	Statistical	<i>Pseudo-nitzschia</i>	Chesapeake Bay	Generalized linear regression; spatial + temporal; interannual
Brown et al., 2013	Present	Statistical	<i>Karlodinium</i> , <i>Prorocentrum</i> , <i>Microcystis</i>	Chesapeake Bay	Neural network and logistic regression; spatial + temporal; interannual
Cusack et al., 2015	Present	Statistical	<i>Pseudo-nitzschia</i>	SW Ireland	Zero-inflated negative binomial regression; interannual
Cusack et al., 2016	Present	Hybrid	<i>Pseudo-nitzschia</i>	SW Ireland	Observations + particle tracking; near-term
Diaz et al., 2016	Present	Statistical	<i>Dinophysis</i>	Portugal	General additive model; interannual
Giddings et al., 2014	Present	Hybrid	<i>Pseudo-nitzschia</i>	Pacific NW	Particle tracking + ecosystem; seasonal to interannual
Gillibrand et al., 2016	Present	Process-based	<i>Karenia mikimotoi</i>	Scotland	IBM with growth; event
González Vilas et al., 2014	Present	Statistical	<i>Pseudo-nitzschia</i>	NW Spain	Machine learning; spatial + temporal; interannual
Henrichs et al., 2015	Present	Process-based	<i>Karenia brevis</i>	Gulf of Mexico	IBM with behavior; interannual
Lane et al., 2009	Present	Statistical	<i>Pseudo-nitzschia</i>	California	Logistic regression; interannual
Stock et al., 2005; Li et al., 2009	Present	Process-based	<i>Alexandrium</i>	Gulf of Maine	Ecosystem + circulation; seasonal to interannual
Moore et al., 2009	Present	Statistical	<i>Alexandrium</i>	Puget Sound	Regression + trend analysis; interannual
Raine et al., 2010	Present	Statistical	<i>Dinophysis</i>	SW Ireland	Based on wind index, near-term forecast
Ralston et al., 2014	Present	Process-based	<i>Alexandrium</i>	Cape Cod	Local growth; seasonal to interannual
Ralston et al., 2015	Present	Process-based	<i>Alexandrium</i>	Cape Cod	Ecosystem + circulation; seasonal to interannual
Ruiz-Villarreal et al., 2016	Present	Process-based	<i>Dinophysis</i>	NW Spain	Particle tracking; seasonal to interannual
Stumpf et al., 2008;	Present	Hybrid	<i>Karenia</i>	Gulf of Mexico	Observations + particle tracking; near-

Stumpf et al., 2009					term forecast
Stumpf et al., 2012	Present	Statistical	<i>Cyanobacteria</i>	Lake Erie	Regression; spatial + temporal; seasonal
Velo-Suarez et al., 2010	Present	Process-based	<i>Dinophysis</i>	NW Spain	Particle tracking; event
Wynne et al., 2011	Present	Process-based	<i>Microcystis</i>	Lake Erie	Particle tracking; event
Gobler et al., 2017	Future	Process-based	<i>Alexandrium</i> , <i>Dinophysis</i>	NE and NW Atlantic, NE Pacific, Alaska	Growth rates (temperature)
Jacobs et al., 2015	Future	Process-based	<i>Alexandrium</i> , <i>Vibrio</i>	Chesapeake, Puget Sound, Alaska	Growth rates/windows (temperature)
Kibler et al., 2015	Future	Process-based	<i>Gambierdiscus</i>	Caribbean	Growth rates (temperature)
Lin et al., 2018	Future	Process-based	<i>Karlodinium</i>	Chesapeake Bay	Growth rates (temperature, nutrients)
Moe et al., 2016	Future	Statistical	<i>Cyanobacteria</i>	Norway lake	Bayesian network linking ecosystem and watershed models
Moore et al., 2011	Future	Statistical	<i>Alexandrium</i>	Puget Sound	Regression + trend analysis; growth window
Moore et al., 2015	Future	Process-based	<i>Alexandrium</i>	Puget Sound	Regional physical models; growth windows (temperature, salinity)
Glibert et al., 2014	Future	Process-based	<i>Prorocentrum</i> , <i>Karenia</i>	NW European shelf, NE Asia, SE Asia	Regional physical + ecosystem models; habitat suitability (temperature, salinity, nutrients)
Townhill et al., 2018	Future	Statistical	<i>Pseudo-nitzschia</i> , <i>Alexandrium</i> , <i>Dinophysis</i>	NW European shelf	Habitat suitability (temperature, salinity, bathymetry); maximum entropy approach