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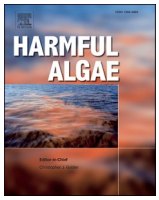

Thermal traits of marine harmful algal species discerned from bloom events

Stephanie I. Anderson [a,*], Niall McGinty [b], Alexa R. Sterling [c], James D. Hagy III [a]

[a] Office of Water, U.S. EPA, 27 Tarzwell Dr., Narragansett, RI, 02882, USA
[b] Marine and Freshwater Research Institute, Fornubúðum 5, 220 Hafnarfjörður, Iceland
[c] Region 1, U.S. EPA, 5 Post Office Square – Suite 100, Boston, MA, 02109, USA

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ABSTRACT

Marine harmful algal blooms (HABs) pose a significant economic burden and public health concern for coastal regions. To aid management with HAB monitoring and mitigation, HAB forecasting models are often utilized to predict bloom occurrence, and they typically incorporate HAB species traits. However, HAB species are diverse, each characterized by unique physiologies, and discerning their traits can be labor intensive. To better constrain the traits of North American HAB species (n= 29), we performed an analysis of 595 historical HAB events from coastal North America, totaling >4000 weeks, and correlated each event with sea surface temperature at time of occurrence. We then constructed species distribution models to discern species thermal traits, with unimodal temperature probability curves characterized for 18 HAB species (6 previously uncharacterized). We found HAB events to be correlated with species' laboratory-determined thermal optima (Topt), the temperature that produces maximal growth. However, HAB events often occurred below the Topt and over a narrower range of temperatures, suggesting analyses of HAB events could better constrain realized temperature thresholds and improve HAB forecasting models. In an analysis of species traits, HAB species also clustered into distinct groups based primarily on their physiological traits as opposed to morphological or behavioral traits, with toxin and temperature traits explaining much of the variation between species. With these data, we documented the fundamental and realized thermal traits of HAB species, increasing our collective ability to predict and monitor future HAB events.

1. Introduction

Marine harmful algal blooms (HABs) cause ecological and public health impacts on United States coastal regions, imposing economic costs conservatively estimated in 2021 at $10 to $100 million annually (Suddleson and Hoagland, 2021), with some singular HAB events exceeding that annual range (Adams et al., 2018). HABs are characterized by high cell densities that can negatively impact tourism and recreation or by toxins that can bioaccumulate in marine organisms, decreasing seafood safety, and harming human health. These blooms often result in fisheries losses and closures, as well as lost tourism revenue (D. M. Anderson et al., 2021b; Hoagland et al., 2002). This social and economic burden is anticipated to worsen as HABs become more prevalent due to increasing ocean temperatures (D. M. Anderson et al., 2021b, 2021a; Hallegraeff et al., 2021; Lefebvre et al., 2025). To mitigate losses and protect human health, many states have developed monitoring plans to survey HABs along their coastlines. To maximize the benefits obtained from these monitoring efforts, HAB forecasting models are increasingly employed to help management better target their sampling and mitigation efforts.

Mechanistic HAB forecasting models are typically constructed for single HAB species using an ecosystem or regional physical model and each HAB species' respective environmental response traits (Ralston and Moore, 2020). Parameterizing these traits accurately is necessary to ensure the efficacy of forecasting models (Ralston and Moore, 2020) and their economic value to stakeholders (Jin et al., 2024). However, HAB species are diverse, comprising roughly 200 taxa (Hallegraeff et al., 2021), each characterized by unique life cycles and physiologies. Quantifying species' respective traits in a lab requires labor-intensive, single-strain experiments to characterize growth in response to an environmental variable. This limits forecasting models, which often utilize growth as a response variable, to well-studied and culturable species (Ralston and Moore, 2020). In addition, while growth can predict algal abundance, it does not always predict bloom toxicity. Growth

* Corresponding author.
E-mail addresses: anderson.stephanie@epa.gov, sianderson@uri.edu (S.I. Anderson), niall.mcginty@hafogvatn.is (N. McGinty), sterling.alexa@epa.gov (A.R. Sterling), hagy.jim@epa.gov (J.D. Hagy).

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and toxicity can have opposing relationships to environmental variables like temperature (Navarro et al., 2006). Constraining the values of environmental factors that lead to HAB events (both abundance and toxicity) by quantifying relationships observed in the field could improve forecasting models.

Discerning the relationship between HABs and in situ environmental conditions can be challenging. Environmental information is not always collected during routine HAB surveys and, as a result, the majority of HAB records lack the data needed to assess the environmental drivers of HAB events (Wells et al., 2020). Relating HAB monitoring datasets to oceanographic data could better resolve the environmental conditions that contribute to HAB occurrence, or HAB "windows of opportunity" (Moore et al., 2008; Wells et al., 2021, 2020).

To address this need, we combined observational data from varied sources to quantitatively discern the thermal conditions that enable HAB formation and to constrain the HAB-temperature relationship, a critical need in species forecasting (Kearney and Porter, 2009; Wells et al., 2015). We selected temperature because temperature is a principal factor influencing marine algal community structure (Sunagawa et al., 2015) and ocean warming is anticipated to impact HAB frequency, magnitude, toxicity, and phenology in the future (Fu et al., 2012; Moore et al., 2008; Wells et al., 2015). Temperature is also the most commonly incorporated forcing variable in nearly every HAB forecasting model (Ralston and Moore, 2020). We used a high-resolution sea surface temperature (SST) product to reconstruct approximate thermal conditions at the time and location of historical HAB events. We then built correlative species distribution models (SDMs) for several problematic U.S. HAB species (D. M. Anderson et al., 2021b), modeling individual HAB species distributions as a function of SST. While SDMs have previously been used to examine HAB species presence (e.g., Townhill et al., 2018), to our knowledge, this is the first use of SDMs to evaluate HAB events.

These SDMs allowed us to define thermal traits for HAB species, such as the HAB realized thermal niche, the thermal conditions that enable a species to bloom in the environment (Hutchinson, 1957), and the HAB mean niche, the temperature at which the probability of HAB occurrence is highest. The modeled HAB traits were then compared in a meta-analysis to those derived from laboratory experiments. With these data, we documented the fundamental and realized thermal niches for several HAB species. These analyses will better constrain the HAB-temperature relationship and improve our ability to monitor and forecast HAB events.

2. Materials and methods

2.1. Field data compilation

We assessed HAB events characterized within the Harmful Algal Event Database (HAEDAT), accessed via the Ocean Biodiversity Information System (OBIS; https://www.obis.org) node 'HAB OBIS' (downloaded: 06/2023). HAEDAT contains data on HAB events that led to management decisions, or negative economic or ecological impacts. These may include events that resulted in i) water discoloration or foam/mucilage formation, ii) biotoxin accumulation in seafood exceeding levels that are considered safe for human consumption, iii) cell concentrations above management thresholds, or iv) mass mortalities of marine organisms. HAEDAT is a presence-only database and does not contain records of monitoring efforts outside of HAB events. In total, 10,240 HAB events occurring between 1770 and 2023 were downloaded from the database.

HAB events were then constrained to only those that occurred within the Intergovernmental Oceanographic Commission United Nations Educational, Scientific and Cultural Organization (IOC-UNESCO) HAB regions covering North America: Regions 1) Atlantic coast U.S.A., Canada, and Greenland, 2) Florida, Caribbean, Central America, and Venezuela, and 4) Pacific coast U.S.A., Canada, and Alaska. This process was carried out by intersecting the locations of HAB events with polygons defined by shapefiles (https://github.com/iobis/hab-regions; (Hallegraeff et al., 2021)). Events were then filtered to include only those in which the causative species was identified and of known concern in U.S. coastal waters (D. M. Anderson et al., 2021b). Events were also filtered to include those with a valid date and a duration less than one year. This eliminated events with date listings that were likely inaccurate (e.g., events spanning January 1st to December 31st) and focused on HAB events that were more likely to have a temperature signal. Only species with at least two events totaling 10 or more weeks were assessed in downstream analyses, following Irwin et al. (2012) (**Tables S1 & S2**). We also aggregated *Pseudo-nitzschia* species at the genus level because *Pseudo-nitzschia* spp. pose significant harm to both the U.S. Atlantic and Pacific coasts (D. M. Anderson et al., 2021b) and are cryptic under light microscopy (Lundholm et al., 2006; Orsini et al., 2004).

The approximate surface water temperature at the time of each HAB event was reconstructed using the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation (OI) Sea Surface Temperature (SST) V2 data. We focused on temperature because i) temperature is a principal factor shaping phytoplankton physiology (Eppley, 1972), ii) SST is better resolved in coastal regions than other environmental variables like salinity or nutrients, and iii) temperature responses are often incorporated into HAB forecasting models (Ralston and Moore, 2020). NOAA's OISST is a high-resolution SST product that has been available since late 1981, and is constructed from satellite, ship, buoy, and Argo float observations (Huang et al., 2021; Reynolds et al., 2002). For our analyses, we selected a $1^\circ \times 1^\circ$ weekly mean OISST product to match the likely frequency of HAB in situ monitoring efforts (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.html). This further constrained our HAB event database to 1982 or later (**Table S1**).

2.2. Species distribution modeling

Our species distribution model (SDM) procedure was modified from McGinty et al. (2021). SDMs were developed for each HAB species (or genus for *Pseudo-nitzschia*) using BIOMOD from the 'biomod2' package in R (Thuiller et al., 2024). BIOMOD can utilize presence-only datasets to create SDMs and implement several varied algorithms, which can be combined to create ensemble models. For our SDMs, we selected one machine learning algorithm (artificial neural network – ANN) and three regression models: generalized linear models (GLM), generalized additive models (GAM), and multivariate adaptive regression splines (MARS). These algorithms work with univariate data and are readily utilized with presence-only datasets (Hao et al., 2019).

For each species, data were randomly divided into training and testing datasets, with 25% of the data reserved for testing. Because we were working with a presence-only dataset, in which absences were not recorded, we generated 'pseudo-absences' from background environmental data. Pseudo-absences were randomly selected using the 'disk' method, in which pseudo-absences were drawn from an area surrounding HAB events (presences). After conducting tests with several background thresholds, we selected $\pm 5^\circ$ latitude from the maximum and minimum latitudinal extent of HAB events for each species along each coast (Pacific and Atlantic coast of North America). This range resulted in sufficient pseudo-absence data to produce correct presence assignments, but was narrow enough to avoid inflating SDMs (VanDerWal et al., 2009). This distance also approximates the distance that phytoplankton populations are likely to travel within a year (Doblin and Van Sebille, 2016). Models were trained on radially-selected pseudo-absences equal to three times the number of presences for each HAB species following BIOMOD recommendations (Barbet-Massin et al., 2012). Models were constructed using each pseudo-absence dataset with each of the four algorithms. This process was cross-validated 10 times for a total of 400 model runs per species (10 pseudo-absence datasets $\times$ 4 algorithms $\times$ 10 cross-validations). Modelling parameters

were kept the same across species to maintain consistency. A weighted mean of SDMs was calculated using BIOMOD with the area under the curve (AUC) and true skill statistic (TSS), where weighting was increased for models that had higher AUC and TSS to create an ensemble probability curve. We only included models with TSS $\geq$ 0.3 and AUC $\geq$ 0.7 in the ensemble models, and only included ensemble models with AUC $\geq$ 0.6 in downstream analyses (McGinty et al., 2018).

2.3. SDMs with abundance data, or by coast or toxin

For one species, *Karenia brevis*, HAB events often occurred year-round, which made it difficult to construct a presence-only model. To address this, we also tried SDMs using either presence-absence data or severity thresholds. We obtained abundance data from the HAB Monitoring Database of the Florida Fish and Wildlife Conservation Commission (**Figure S1a**), part of the Fish and Wildlife Research Institute (FWC-FWRI). FWC-FWRI routinely surveys *K. brevis* cell concentrations along the Florida coastline (Florida Fish and Wildlife Conservation Commission, 2025). From this dataset, we restricted our analyses to surface samples ($\leq$1 m) collected from 1982 to 2023 (n= 161,925) and utilized associated contemporaneous in situ temperature data when available (n= 71,630). When SST was not available, we used the NOAA OISST weekly mean to estimate surface water temperature as previously described (n= 90,295; **Figure S1b**). We then constructed SDMs using threshold values to recode the abundance data as a binary variable, wherein abundance exceeding a threshold was classified as present and below a threshold was considered absent. We tested several different bloom severity thresholds, each established by the State of Florida and implemented in previous studies (e.g., Stumpf et al., 2022a), which included >5000, >50,000, >100,000, or >1000,000 cells/L. We also tested a SDM using abundance data without thresholds. These SDMs followed the same methods as previously described, with the exclusion of pseudo-absences, as these were abundance or presence-absence datasets rather than presence-only datasets.

In addition to analyzing HAB events by species, we also examined HAB events between coasts (Pacific and Atlantic coasts of North America) for bicoastal species, or based on the type of toxin produced using presence-only data. For coastal analyses, we filtered species to include only those that met the minimum data requirements: at least two events totaling 10 or more weeks along each coast (**Table S3, Figure S2**). For analyses by toxin, HAB events were grouped by the toxin that each species produces and analyzed separately. We focused on species that produce four of the most common types of toxins: amnesiac shellfish toxins (AST), diarrheic shellfish toxins (DST), neurotoxic shellfish toxins (NST), and paralytic shellfish toxins (PST) (**Table S4**). In each case, we developed SDMs for each group of HAB events as previously described. The presence of differences in HAB probability distributions between coasts or toxins was then assessed with a weighted Kolmogorov-Smirnov (K-S) test, with the logistic probability response curve as the weight function.

2.4. Laboratory data compilation

HAB forecasting models often include temperature response traits, which are typically derived from single strain growth responses measured in controlled environments (Ralston and Moore, 2020). To compare our temperature niche derived from HAB events (i.e., realized niche) with the laboratory-measured niche (i.e., fundamental niche), we aggregated temperature-growth data from the literature for each of our HAB species. We began with existing compilations (S. I. Anderson et al., 2021; Thomas et al., 2012), and added HAB species that had not been included previously (number of strains = 21, number of species = 12, **Table S5**), following S.I. Anderson et al. (2021). When growth data were not accessible, PlotDigitizer (https://plotdigitizer.com/) was used to extract rate measurements from published figures. For *Pseudo-nitzschia*, only toxic species were considered (Bates et al., 2018).

Thermal performance curves were then fit to thermal growth data following S.I. Anderson et al. (2021), using a modified Norberg curve (Norberg, 2004). For strains compiled previously (S. I. Anderson et al., 2021), the computed thermal performance curve parameters were retained. For additional strains, we estimated parameters using growth data and the 'growthTools' package in R (Kremer, 2025). Constructed thermal performance curves for each strain were then used to estimate thermal traits for each HAB species. These included the minimum and maximum viable temperatures (thermal minimum (Tmin) and thermal maximum (Tmax), respectively), and the thermal optimum (Topt), which is the temperature that results in the highest growth rate. For Tmin and Tmax, viability was characterized as the range of temperatures where HAB species growth was at least 20% of each species' growth maxima (S. I. Anderson et al., 2021).

We also characterized HAB species in terms of several morphological (e.g., coloniality, structure), behavioral (e.g., motility, mixotrophy), life history (e.g., resting stages) and physiological traits (e.g., toxin production) (Litchman and Klausmeier, 2008), which were compiled from published sources (Table 1). For morphology, we classified species by their ability to form chains and the composition of their outer structure, with diatoms designated by silica and dinoflagellates differentiated based on whether or not they possess theca (Klais et al., 2017). For behavioral traits, species were distinguished by their ability to consume prey (i.e., mixotrophy (Mitra et al., 2023)) and their use of flagella for movement (Klais et al., 2017). HAB species were also categorized regarding life cycle based on whether they can form cysts or resting cells (**Table S6**). Lastly, HAB species were grouped based on the types of toxins they produce (D. M. Anderson et al., 2021b), including: AST, PST, NST, and DST. All other toxins or chemicals (e.g., allelochemicals) were grouped into "other."

2.5. Trait analyses

For each species, we compared traits derived from the literature with thermal trait values discerned from HAB events. For HAB events, the thermal HAB niche was defined using BIOMOD following McGinty et al. (2021). Briefly, we considered a temperature part of a species' niche when the logistic probability of that species producing a HAB event at that temperature exceeded a threshold defined by the TSS for each ensemble model. For species with unimodal probability curves, we also characterized the temperature where a HAB event was most likely to occur using a weighted mean, with the logistic probability response curve as the weight function (McGinty et al., 2018). In short, the HAB niche characterizes the temperatures at which HAB events were likely to occur, extending from the HAB Tmin to HAB Tmax, while the HAB mean niche describes the temperature that was associated with the highest probability of a HAB occurrence. We then compared the HAB mean niche to the literature Topt using a linear model.

We also analyzed trait variation among HAB species using a principal coordinate analysis (PCoA) conducted with the 'FD' package in R (Laliberté et al., 2014). PCoA is an ordination method that evaluates a dissimilarity matrix to reduce dimensionality and enable multi-dimensional analyses and hierarchal clustering. We used the Gower dissimilarity matrix (computed via 'gowdis' (Gower, 1971) because it can handle diverse trait types (e.g., continuous, categorical). For this analysis, we used the traits assembled in Table 1, with the exception of the HAB mean niche, which was highly correlated with both the Tmin and the Tmax (Pearson's $r > 0.9$). However, both Tmin and Tmax were retained (Pearson's $r = 0.774$). The Ward method (Ward, 1963) was used to cluster HAB species, and species were grouped at a dendrogram height of 0.8 (**Figure S3**). The significance of each trait in determining placement of HAB species within the first two axes of the PCoA ordination was evaluated with a permutation test (999 permutations) followed by a Bonferroni correction using the 'vegan' package in R (Oksanen et al., 2024).

Table 1
Thermal traits discerned from HAB events or literature review. Traits were grouped into categories following Litchman & Klausmeier (2008): Morphological, behavioral, life history, or physiological traits. Thermal traits (Tmin, Tmax and HAB mean niche) were discerned from HAB events and represent the minimum (Tmin), maximum (Tmax), and highest probability (mean niche) temperatures at which HAB events are likely to occur.

	Morphological			Behavioral		Life History	Physiological			
	Chain	Thecate	Silica	Mixotroph	Flagellated	Resting Stage	Toxin	Tmin (°C)	Tmax (°C)	Mean niche (°C)
Akashiwo sanguinea	no	no	no	yes	yes	yes	none	27.4	28.3	27.8
Alexandrium catenella	yes	yes	no	yes	yes	yes	PST	8.1	15.6	11.8
Alexandrium monilatum	yes	yes	no	no	yes	yes	PST	25.0	31.3	28.1
Alexandrium ostenfeldii	yes	yes	no	yes	yes	yes	PST	11.5	15.8	13.6
Aureococcus anophagefferens	no	na	no	no	yes	yes	other	13.9	25.8	20.3
Aureoumbra lagunensis	no	na	no	no	yes	yes	other	25.2	28.6	27.0
Chaetoceros convolutus	yes	na	yes	no	no	no	none	9.8	12.2	11.0
Dinophysis acuminata	no	yes	no	yes	yes	unknown	DST	11.0	17.4	14.2
Dinophysis norvegica	no	yes	no	yes	yes	no	DST	5.9	22.0	13.8
Gymnodinium catenatum	yes	no	no	yes	yes	yes	PST	16.3	28.6	22.4
Heterosigma akashiwo	no	na	no	yes	yes	yes	other	13.7	15.7	14.7
Karenia brevis	no	no	no	yes	yes	unknown	NST	20.9	31.0	25.5
Karenia papilionacea	no	no	no	yes	yes	unknown	NST	17.2	30.9	24.2
Margalefidinium polykrikoides	yes	no	no	yes	yes	yes	other	22.1	31.9	27.1
Olisthodiscus luteus	no	na	no	no	yes	yes	other	10.8	21.6	16.2
Pseudo-nitzschia australis	yes	na	yes	no	no	no	AST	14.4	15.8	15.1
Pyrodinium bahamense	yes	yes	no	no	yes	yes	PST	28.2	30.8	29.5
Prorocentrum cordatum	no	yes	no	yes	yes	yes	other	10.0	19.2	15.0

2.6. Multivariate SDM comparison

For three HAB species with the greatest number of HAB events (*Alexandrium catenella, Karenia brevis*, and *Margalefidinium polykrikoides*), we also constructed multivariate SDMs to assess the importance of SST on HAB events in the context of other environmental variables. For these analyses, we included sea surface salinity (SSS), wind speed, and downward shortwave radiation (DSR) flux (total light). Each of these variables contribute to the phytoplankton environmental niche (Wells et al., 2015) and are available as reanalysis products. Sea surface salinity was estimated for each HAB event using the National Aeronautics and Space Administration (NASA) Multi-Mission Optimally Interpolated Sea Surface Salinity (OISSS) Global Dataset V2, which is available from 2011 and has a 0.25° spatial resolution on a 4-day temporal grid (https://podaac.jpl.nasa.gov/dataset/OISSS_L4_multimission_7day_v2). Downward shortwave radiation (DSR) flux (W m^{-2}), zonal wind (uwnd, m s^{-1}), and meridional wind (vwnd, m s^{-1}) were obtained from the NOAA North American Regional Reanalysis (NARR) product (https://psl.noaa.gov/data/gridded/data.narr.html), which has a resolution of approximately 0.3 degrees (32 km) at a 3-hour interval. Data were downsampled to reduce grid resolution to 1° and time-series were averaged into weekly bins to match the weekly resolution of the NOAA OISST dataset. Wind speed (m s^{-1}) was then computed from the wind vectors as $\sqrt{u^2+v^2}$. Analyses were restricted to HAB events occurring after 2011, when NASA OISSS became available.

Multivariate SDMs were constructed following the same methods as those described previously. For comparison, univariate SDM's using temperature as the only environmental variable were also constructed using this abbreviated dataset (beginning in 2011 rather than 1982). Variable importance was calculated using the 'biomod2' package in R (Thuiller et al., 2024). Potential differences in temperature response curves between univariate and multivariate models were assessed with a weighted K-S test. All graphs and analyses were done in R version 4.2 (R Core Team, 2024), the SSS reanalysis products were downsampled in Python version 3.12.4 (www.python.org), and code to repeat analyses has been archived on Zenodo (Anderson and Hagy, 2026). HAB species icons were drawn with Procreate (https://procreate.com/).

3. Results

3.1. HAB event probabilities

From HAEDAT, 595 HAB events with a collective duration of 4353 weeks met the criteria for analysis. These events spanned the Atlantic, Gulf, and Pacific coasts of North America, and almost 60° of latitude, with several observations in the Caribbean Sea and one in the Arctic (Fig. 1). They included events caused by 29 HAB species prevalent in U. S. coastal waters, with the most events attributed to *Alexandrium catenella, Pseudo-nitzschia* spp., and *Karenia brevis,* each with over a decade of collective recorded disturbances (**Table S2**). For all species, HAB events occurred over a range of temperatures, but for some species, HAB events were restricted to certain seasons, particularly summer (Fig. 2), or climates (temperate or tropical; **Figure S2**). Of the species examined, ensemble SDMs that met our minimum criteria (AUC $\geq$ 0.6) could be constructed for 18 species and one genus (Fig. 3). AUC scores ranged from 0.629 to 0.912, indicating that temperature alone was a moderate to strong predictor of HAB events for these species. Predictive power (AUC) was not correlated with the amount of HAB data available (linear model, p= 0.42). For example, the ensemble model for *Akashiwo sanguinea,* with only 16 weeks of data, had more predictive power than the model for *Karenia brevis,* despite *K. brevis* having almost 700 weeks of data, but year-round occurrence (Fig. 2).

For single species models, probability curves were predominately unimodal (Fig. 3). An exception was individual *Pseudo-nitzschia* species which often had multimodal probability curves (**Figure S4**). Apart from *Pseudo-nitzschia australis*, which displayed a unimodal constrained probability distribution, *Pseudo-nitzschia* species were excluded from trait analyses because they had multimodal distributions. For all other species, a unimodal probability curve allowed for the characterization of both a HAB niche and a HAB mean niche.

The HAB Tmax varied by almost 20 °C between species, with the dinoflagellate *Margalefidinium polykrikoides* exhibiting the highest Tmax at 31.9 °C and the diatom *Chaetoceros convolutus* having the lowest Tmax at 12.2 °C (Table 1). Similarly, Tmin for HAB species varied widely, from 5.9 °C for *Dinophysis norvegica* to 28.2 °C for *Pyrodinium bahamense,* with both species being dinoflagellates. Niche widths for HABs varied from 0.9 °C for *Akashiwo sanguinea* to 16.1 °C for *Dinophysis norvegica* (Fig. 4C). Additionally, HAB species exhibited a wide range of HAB mean niches, with the highest probabilities of a HAB event extending from 11 °C for *Chaetoceros convolutus,* to 29.5 °C for *Pyrodinium*

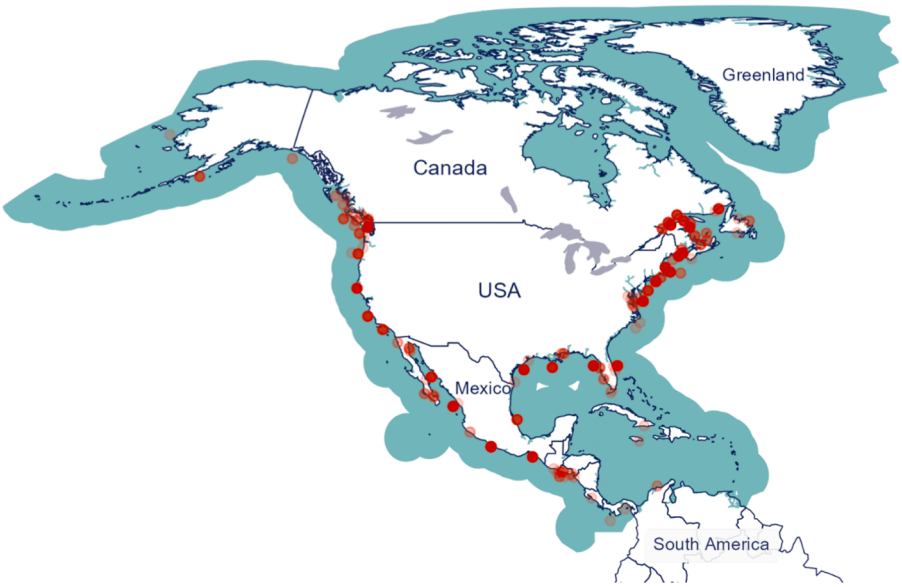

Fig. 1. Locations of HAB events from 1982 to 2023 assessed in this study (n= 595). Only HAEDAT events occurring within the IOC-UNESCO HAB regions covering North America (blue) were included. Points are transparent to better discern overlapping events.

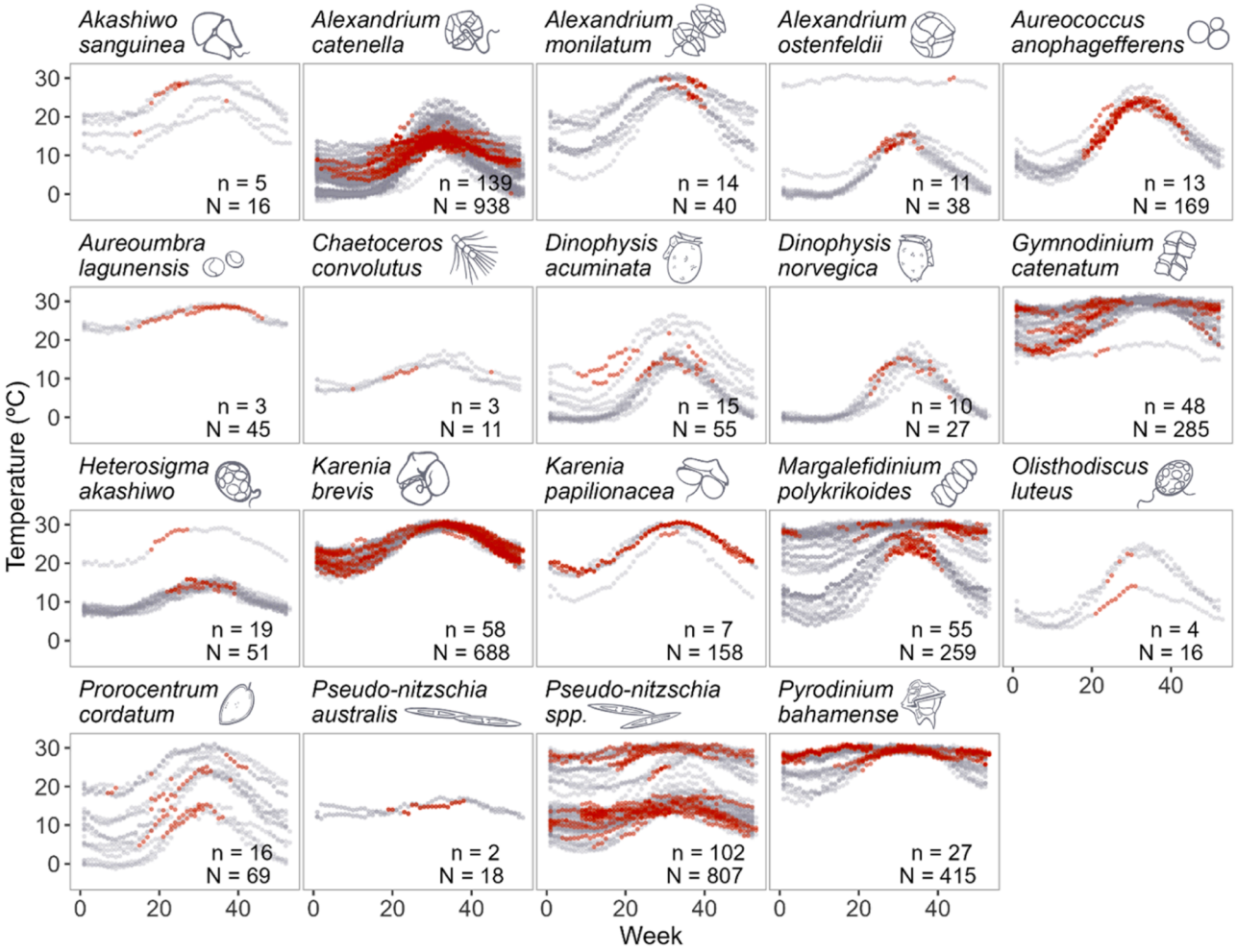

Fig. 2. Weekly NOAA OISST during HAB events (red) and throughout the year at the same localities (grey). For each species, the number of discrete HAB events (n) and the total duration of HAB events in weeks (N) are listed.

bahamense (**Table 1**; Fig. 4D).

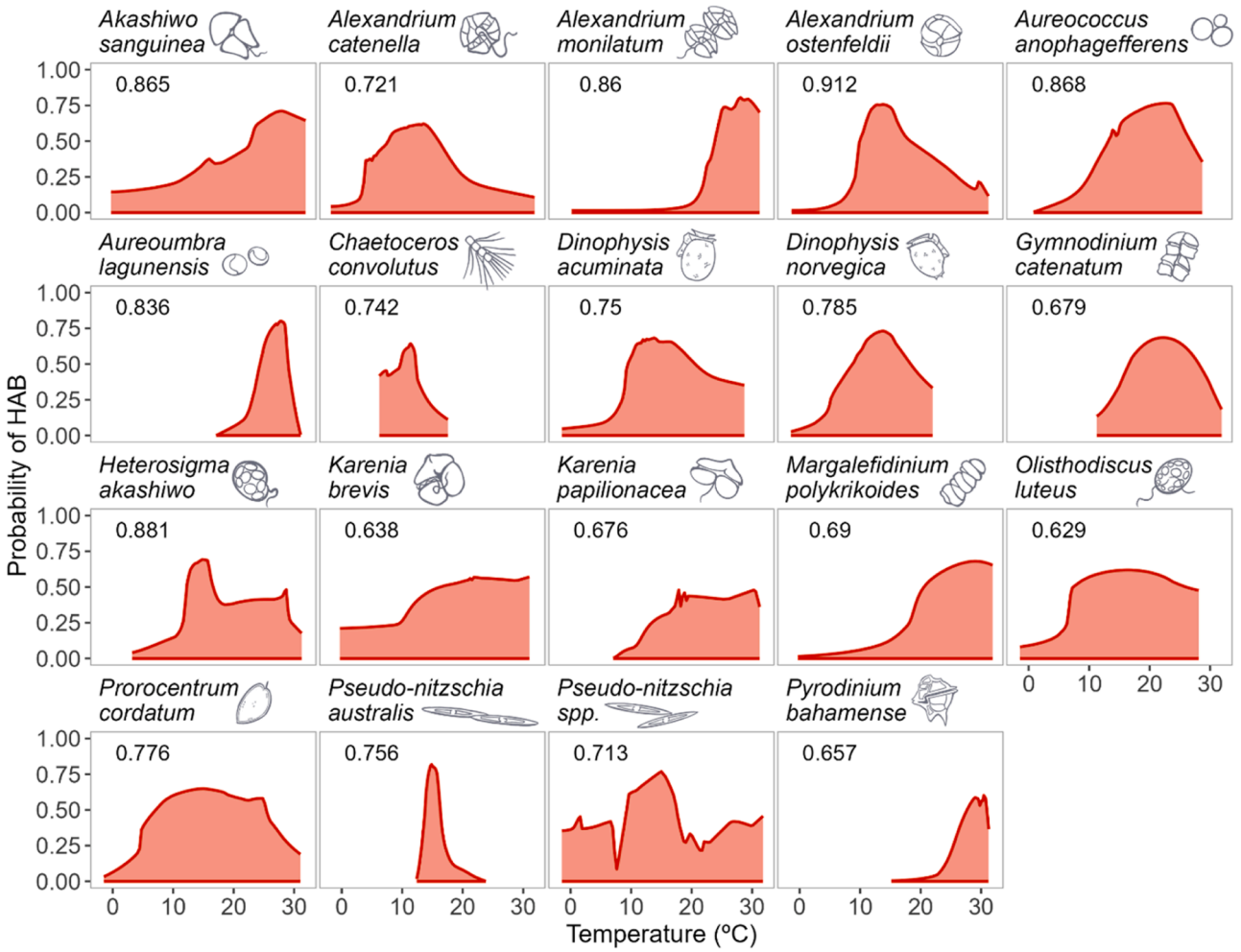

Fig. 3. Univariate response curves showing the probability of a HAB event as a function of temperature. For each ensemble model, the AUC, a performance metric, was calculated (upper left in each panel). AUC values closer to 1 suggest the model will correctly predict the occurrence of a HAB based on SST alone, while values closer to 0.5 indicate that the predictive capacity of the model is not better than chance. Only ensemble models with an AUC $\geq$ 0.6 were included.

3.2. Coast, toxin, and abundance SDMs

We also assessed temperature traits based on ocean coast, toxin, or abundance. First, we examined the thermal traits of bicoastal species to discern whether there might be intraspecific variability between oceans (Pacific vs. Atlantic). Of the species assessed, a distinct SDM for each coast could be constructed for only one species, *Margalefidinium polykrikoides*. From our analyses of this single species, we found *M. polykrikoides* had significantly different HAB probability distributions between coasts (weighted K-S test, p= 0.004), with HAB events more likely to occur at warmer temperatures in the Pacific than in the Atlantic (**Figure S5**). Second, we were able to construct SDMs for species grouped by the toxins they produce. Each toxin SDM had high predictive power (AUC $>$ 0.65), but produced multimodal probability curves (**Figure S6**). Last, for our analyses with *Karenia brevis,* we found both abundance data and management threshold levels resulted in individual models that did not meet the minimum required threshold to construct an ensemble model (TSS $\geq$ 0.3, AUC $\geq$ 0.7). Therefore, these SDMs were not included in further analyses.

3.3. Comparison with literature values

HAB species traits were compared to thermal trait values derived from experimental studies in the laboratory. Traits derived from laboratory studies differed from traits we derived from field data in that they were based on growth rates, rather than occurrence. A niche derived in the lab represents the temperatures at which species could grow, and the Topt represents the temperature that resulted in maximal growth (Fig. 4B). Though these metrics differ, they can roughly be compared as the temperatures at which HABs could occur (fundamental niche) versus when they were likely to occur (realized HAB niche), as well as the temperature in which species were likely to be abundant (Topt, maximal growth) versus the temperatures at which they were likely to cause a HAB (HAB mean niche). From our literature compilation of thermal growth data, we discerned thermal traits for 25 HAB species comprising 57 individual strains. These included 12 of the HAB species from our study as well as additional species of concern in the coastal U.S. (D. M. Anderson et al., 2021b). For the remaining six species that we examined, temperature-growth data were not available and thus, their niche had not been previously characterized.

For HAB species that had been characterized in the literature, the HAB niche was narrower than the fundamental niche (Fig. 4C), occupying only 3 to 57% (average = 30%) of the fundamental niche. This percent niche coverage was loosely correlated with the number of HAB events (Spearman's $\rho = 0.62$, p= 0.037) and the duration of HAB events (Spearman's $\rho = 0.59$, p= 0.043). However, the variance in percent niche coverage increased with the number of HAB events (**Figure S7**). Additionally, we found the HAB mean niche was correlated with the literature Topt (linear model, $y = 13.01 + 0.47x$, $R^2 = 0.68$, $p< 0.001$; Fig. 4D), but averaged 2.6 °C less than the Topt. The difference between

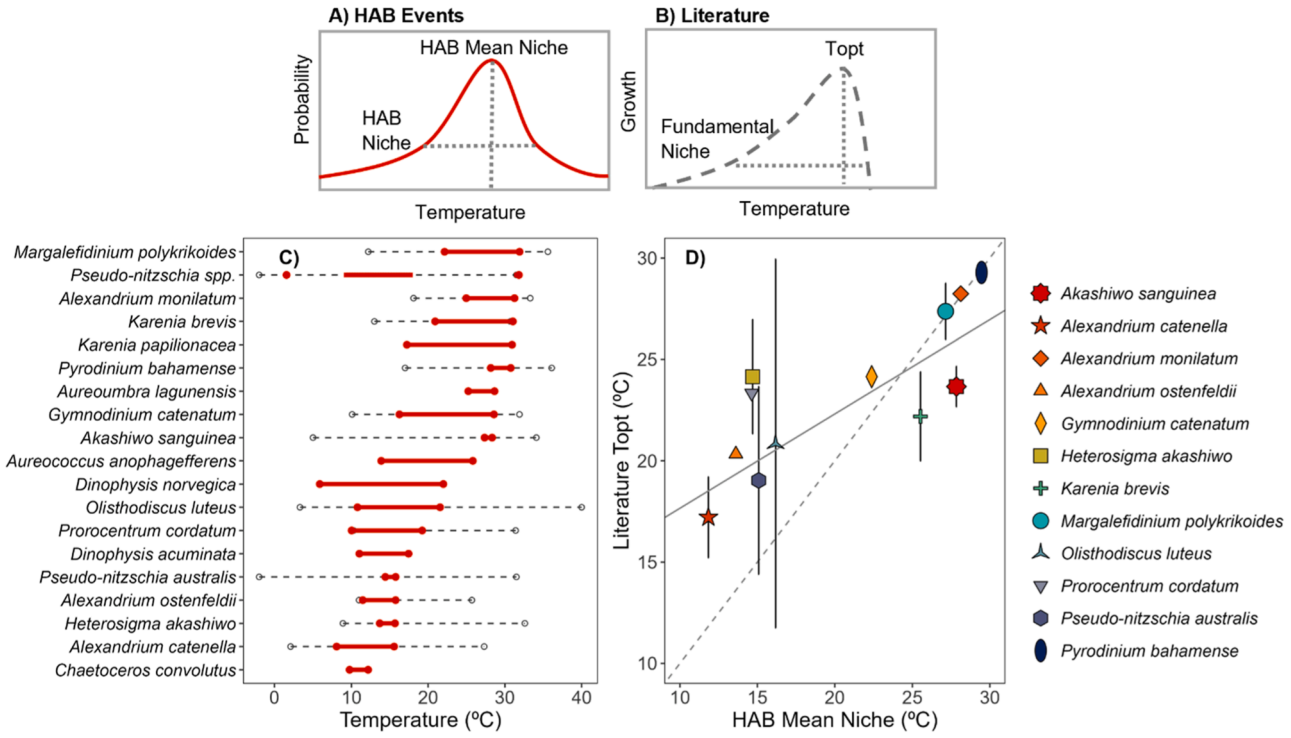

Fig. 4. Diagrams illustrating how traits were derived from HAB events (A) or in the literature (B). The HAB niche (C, red) depicts the range in which the probability of a HAB exceeded a threshold defined by each model. For empirically characterized species, the fundamental niche is shown (grey). The HAB mean niche (D) was calculated for species with unimodal probabilities using a weighted mean, with the probability as the weight function. Of the 18 species characterized, only those that had a unimodal probability curve and whose thermal optima (Topt) had been established (n= 12) are shown. The relationship between the literature Topt and HAB mean niche is characterized with a linear regression (solid, y = 13.01 + 0.47x, R^2 = 0.68, p< 0.001), and a 1:1 line is shown for comparison (dashed).

the HAB mean niche and Topt was larger at lower water temperatures, but converged at high temperatures.

3.4. HAB species patterns

Principal coordinate axes (PCoA) combining HAB thermal traits with morphological, behavioral, physiological, and life history traits illustrated trait-based similarities and differences among HAB species (Table 1). The first two axes of the PCoA explained 45.3% of the total variance in species traits (Fig. 5). Permutation tests showed that all traits except the presence of a theca in dinoflagellates contributed significantly to the positioning of species along the first two axes (Table 2). For example, thermal traits (Tmin and Tmax) contributed strongly to species positions within the PCoA (permutation tests, $R^2 > 0.5$, $p \leq 0.006$). Additionally, hierarchical clustering based on the PCoA showed that diatoms differentiated from other HAB species at the first node (**Figure S3**). Of the non-diatoms, HAB species separated primarily based on the type of toxin they produce and then by their respective thermal traits (Fig. 5B, **S3**).

3.5. Comparison with multivariate SDMs

We constructed multivariate SDMs for the most prevalent HAB species in our dataset to assess whether additional variables might impact estimates of the thermal niche and to examine the relative importance of different environmental variables in predicting HAB events. The temperature-response curves for each species were not significantly different between univariate and multivariate models (weighted K-S tests, $p > 0.7$; **Figure S8**), indicating that our univariate SDMs produced estimates of the species' realized thermal niche that were similar to estimates produced by multivariate models. For *A. catenella* and *M. polykrikoides*, temperature was the dominant predictor of HAB events of the variables tested, but for *K. brevis*, salinity emerged as a slightly more important factor, though none of the variables tested had a strong influence on the model for *K. brevis* (**Figure S8**). Across all species, additional variables increased model predictive power (AUC) by an average of 14.6% (t-test, p= 0.002; **Table S7**).

4. Discussion

Ocean warming is anticipated to expand the HAB "window of increased opportunity" (Moore et al., 2008), potentially altering the spatial distribution and bloom season of HAB species (Gobler et al., 2017). An example of this may already be seen with marine heat waves, which often prolong the occurrence of HABs (McCabe et al., 2016; Trainer et al., 2020). Predicting changes to the HAB season will require a greater understanding of the HAB-temperature relationship (Wells et al., 2020) and will need to combine observational data with mechanistic-based laboratory studies (Kearney and Porter, 2009; Wells et al., 2015). Using historical records of HAB events and SST observations, we assessed the HAB-temperature relationship in the field and compared our findings to laboratory-based studies. While single-isolate laboratory studies capture the species' fundamental thermal niche and the temperature-growth response, they may not be representative of genetically diverse natural populations (Fu et al., 2012) and measured response traits may be influenced by the isolation location of each strain (Boyd et al., 2013). Our approach complements laboratory-based methods, by evaluating the realized thermal niche of diverse populations across a wide geographical range. Together, these approaches illuminated the role of temperature as a driver of HABs and allowed us to document the fundamental and realized thermal traits for several HAB species. This will improve our ability to forecast HAB events by better defining the HAB-temperature relationship and may improve HAB monitoring by allowing monitoring resources to be focused on conditions where HABs are most likely to occur.

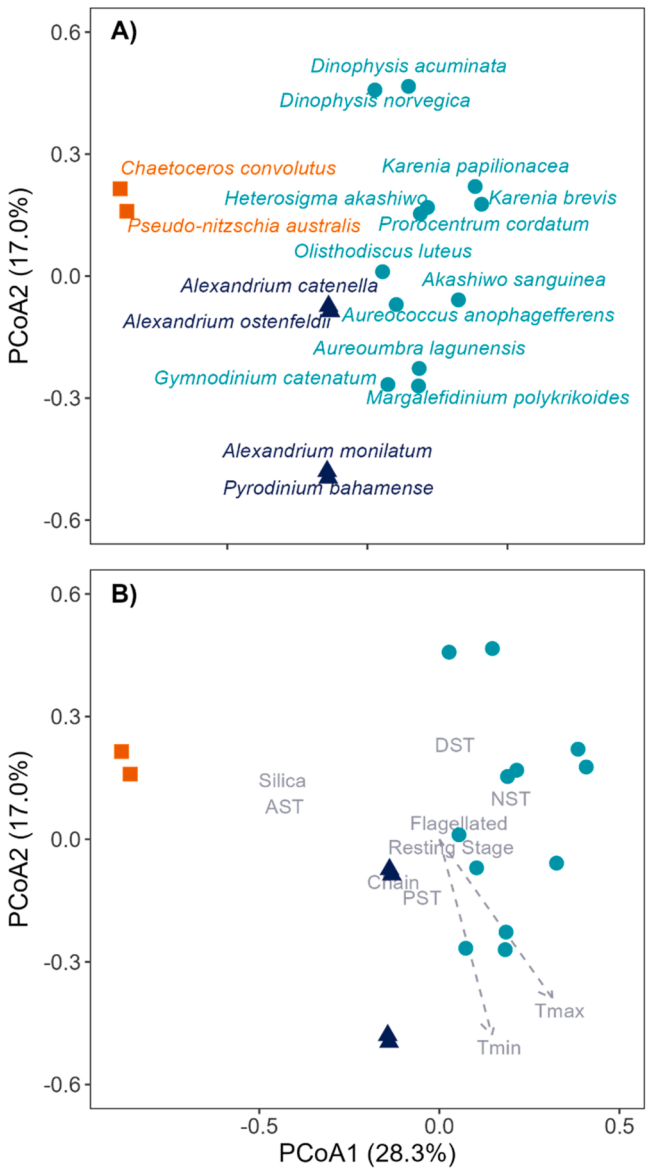

Fig. 5. Principal coordinate analysis (PCoA) of HAB species using trait values. Panels show species positions in relation to one another (A), with colors denoting groups discerned via hierarchal clustering. Traits which significantly drove species positions along PCoA axes 1 and 2 are shown (B), with quantitative traits represented by vectors and qualitative traits indicated at their positive centroid (where trait values are true).

Table 2
Traits incorporated into multi-dimensional analysis. Traits which significantly contributed to the placement of HAB species within the first two axes of the PCoA ordination (permutation test, 999 permutations, $p < 0.05$) are noted with an asterisk.

Factor	R^2	p-value
Toxin	0.6685	0.005 *
Tmax	0.6016	0.002 *
Resting Stage	0.5790	0.001 *
Tmin	0.5324	0.006 *
Silica	0.5057	0.008 *
Flagellated	0.5057	0.008 *
Chain	0.3727	0.001 *
Mixotroph	0.2396	0.010 *
Thecate	0.0026	0.958

4.1. Species thermal traits

With temperature alone, we were able to construct SDMs with high predictive power for 18 HAB species. For six of those species, our results provide the first quantitative characterizations of their species-specific HAB-temperature relationships. Though multivariate models often have higher predictive power (Barton et al., 2016; McGinty et al., 2021), and temperature may not be the dominant environmental driver for many species, our univariate models demonstrate that temperature is still a strong predictor of HAB events for several species, a critical need in HAB ecology (Wells et al., 2020). Our estimates of the HAB mean niche, the temperature that is associated with the highest probability of HAB occurrence, also reflected findings from laboratory studies. For example, *Karenia brevis* has been noted to have a Topt in the range of 22 - 28 °C (Vargo, 2009). Using our methods, we were able to characterize a HAB mean niche of 25.5 °C for *K. brevis*. Similarly, maximum domoic acid production by *Psuedo-nitzschia australis* is thought to occur at cool temperatures (10–15 °C; Kudela et al., 2020), and we estimated a HAB mean niche of 15.1 °C. However, the literature Topt for growth was generally higher than our HAB mean niche, especially for temperate species.

On a global scale, phytoplankton Topts often exceed their respective habitat temperatures by several degrees (Thomas et al., 2012). This may occur because phytoplankton are ectotherms that exhibit left-skewed performance curves (ex. Fig. 4B) and exceeding the Topt can result in severe reductions in fitness (Martin and Huey, 2008). Thus, species generally inhabit temperatures below their Topt, and this mismatch may increase with habitat variability (Angilletta Jr., 2009; Martin and Huey, 2008). This parallels our results in which temperate species like *Alexandrium catenella*, which are exposed to a greater temperature range during the annual cycle, had a greater difference between their Topt and their HAB mean niche than more tropical species, such as *Pyrodinium bahamense*. Some differences between the Topt and the HAB mean niche may also be due to other abiotic and biotic factors which were not accounted for in our models, such as nutrient availability, light, competition, and predation, which are likely to impact the realized niche (Wells et al., 2015) and Topt (Heinrichs et al., 2025). However, the HAB mean niche provides a valuable complement to the literature Topt, by capturing the temperatures at which HAB events are likely to occur in the environment. This HAB mean niche could be incorporated into mechanistic forecasting models to assess shifts in both HAB phenology and spatial distribution with ocean warming (Ralston and Moore, 2020).

In addition to the HAB mean niche, our models enabled us to define a HAB realized niche. While many studies have documented the general ranges in which HAB species occur (e.g. Vargo, 2009), this approach provided a quantitative assessment of the probability that a HAB would occur across a temperature gradient, condensing disparate observations into one niche estimate. We found the proportion of the fundamental niche that the realized HAB niche occupied (percent niche coverage) was correlated with the number of HAB events observed, signifying more observations could broaden the HAB niche. However, the variance in niche coverage increased with the number of HAB events observed, suggesting more observations may not always lead to a wider realized HAB niche. Instead, the percent niche coverage may also depend on whether the HAB species is a temperature specialist or generalist, excelling in a narrow or broad range of temperatures, respectively (Angilletta Jr., 2009), the species functional group (Brun et al., 2015), or the position of the niche center, with niches at temperature extremes tending to be narrower (Brun et al., 2015). As more data are collected, a tool such as a rarefaction curve could be used to discern if the HAB niche for each species has been sufficiently characterized. As we noted earlier, these characterizations of the HAB niche may allow managers to better target monitoring efforts by constraining the range of temperatures that are likely to contribute to bloom formation, potentially reducing costs, decreasing uncertainty, or both.

4.2. Patterns in HAB species traits

In our study, we assessed a diverse array of HAB species that spanned several functional types, each with unique morphological, behavioral, life history, and physiological traits. We asked whether HAB species might form distinct groups, and if so, what traits might drive group clusters. Our trait relationships suggest diatoms may group separately due to morphological and behavioral traits that differentiate that group (e.g., silica frustules, non-flagellated). However, the factors that explained the largest proportion of trait variation were the type of toxin each species produces, species' thermal traits (Tmin, Tmax) and the presence of a resting stage in the species' life cycle. This suggests non-diatom HAB species may be more connected by their physiology than their morphology or behavioral strategy. We also found dinoflagellates and other non-diatom HABs exhibited a wide range of thermal traits, even though most HAB species, including dinoflagellates, are generally thought to perform best at warmer temperatures (Glibert, 2020). This suggests that HAB species assemblages are associated with thermal regimes in the ocean. As the ocean warms, we may see regional changes in the composition of HAB species, similar to global projections for all phytoplankton, which predict shifts in species range and diversity (S. I. Anderson et al., 2021).

The type of toxin produced was also a significant driver of species groupings. We explored this relationship between temperature and toxin further by constructing SDMs that aggregated species based on the type of toxins they produce. However, we found results were largely uninformative, with SDMs leading to wide and multimodal probability curves (**Figure S6**). This suggests HABs may be driven more by species-specific thermal preferences than by their toxin production pathways. Species traits may also be interactive (Anderson et al., 2022), influencing each other in ways that could not be discerned with our methodology, and exploring trait relationships further could aid with the characterization of the HAB niche.

4.3. Model limitations and future studies

Though presence-only SDMs are not able to capture nuances in species' relationships to temperature, such as cumulative temperatures needed for germination in *Alexandrium catenella* cysts (Fischer and Brosnahan, 2022), they do provide estimates of thermal traits comparable to those derived from laboratory studies (Lv et al., 2026). For species that could not be assessed with SDMs, results may have been limited due to one or more of the following: 1) insufficient HAB event data, 2) a cosmopolitan distribution of HAB events, or 3) a mixed community of causative HAB species. First, correlative SDMs require several observations to model the observed distribution of a species as a function of environmental conditions (Kearney and Porter, 2009). This limited model development to species that had been better sampled in the environment. However, for some species, such as *Pseudo-nitzschia australis*, as few as two HAB events were sufficient for SDM development.

Second, SDMs have higher predictive power for seasonal or endemic rather than cosmopolitan species (Elith and Leathwick, 2009). This is clearly visualized with *Karenia brevis*, which had substantial HAB data, but year-round occurrences that limited model development. We explored several methods to better resolve *K. brevis*, including using higher resolution temperature data taken in situ, using abundance data rather than presence-only data, and implementing bloom severity thresholds as has been done previously (Stumpf et al., 2022). In each case, model performance declined, suggesting higher resolution data may not alleviate the challenges posed by a cosmopolitan species and may even add more variability which is difficult to account for in an SDM. It is also likely that for some species, temperature may not be the primary driver of HABs. Future analyses incorporating other environmental variables known to contribute to HAB dynamics (e.g., salinity, irradiance, wind/mixing, nutrients) in a multivariate SDM could allow one to assess the relative importance of several environmental variables in predicting HAB events.

In our multivariate SDM example, which included SST, SSS, DSR flux, and wind speed, salinity emerged as a slightly more important predictor of *K. brevis* HABs than temperature. This result does not negate the value of univariate SDMs in predicting the thermal niche, which was comparable between models, but it does illustrate the additional insight that could be gained from multivariate studies, especially for species like *K. brevis*, which are difficult to model using a single environmental variable. In cases where two species exhibit the same thermal range, additional variables may also highlight niche differences between HAB species. For example, *M. polykrikoides* and *K. brevis* were characterized by similar thermal niches, but greatly differed in their salinity ranges (**Figure S8B**). Future analyses incorporating multiple variables could better decipher these interspecific differences, increasing our ability to forecast HAB events. These models would be supported by improved monitoring of environmental conditions, especially around HAB events.

Lastly, we found some species, particularly those from the genus *Pseudo-nitzschia*, displayed multimodal probability curves. This may have resulted from *Pseudo-nitzschia* HAB events being caused by multi-species assemblages, as is commonly observed in the environment (Hubbard et al., 2023; Sterling et al., 2022), but being attributed to only one *Pseudo-nitzschia* species. In many cases, field efforts investigating *Pseudo-nitzschia* spp. either quantify domoic acid concentrations (the toxin produced by some *Pseudo-nitzschia* species) or evaluate species composition via molecular techniques, but not both. However, deciphering which *Pseudo-nitzschia* species are causing which HABs would improve the accuracy of SDMs and quantification of the HAB-temperature relationship.

There may have been additional physiological differences that were not captured by our species-specific analyses. For example, phytoplankton species, including HAB species, often exhibit intraspecific variability in their temperature traits (de Boer et al., 2005) and some species can be cryptic, with genotypes occupying different ecological niches (Luo et al., 2017). This may be evidenced in our analyses of the bicoastal HAB species *Margalefidinium polykrikoides*, where we found variability in the HAB thermal niche and HAB mean niche between Atlantic and Pacific populations (**Figure S5**). Though this analysis could only be conducted for one species, our results suggest there may be value in assessing ecotypes when developing regional forecasting models, as species traits may not always be representative of local populations. This also highlights how single-strain experiments conducted in a lab may not capture the whole species response (Boyd et al., 2013; Fu et al., 2012) and methods such as ours, which evaluate diverse natural communities, serve as a valuable complement to laboratory studies. Our ensemble approach also considered different samplings of the data and different algorithms to assess the uncertainty in our models. These methods thus provide valuable information on the role of temperature as a driver of HABs.

5. Conclusions

By pairing environmental data with historical HAB records, we increased the value of existing databases for management purposes (Wells et al., 2020) and used models to better define the HAB-temperature relationship for several species, a critical need in species forecasting (Kearney and Porter, 2009; Wells et al., 2015). From our analyses and literature compilation, we documented the thermal traits of 31 HAB species. This includes laboratory-based assessments of the fundamental niche for 25 species (57 strains) and model-derived estimates of the realized niche for 18 species, characterized in this study. For 12 species, there is overlap, providing a unique opportunity to compare traits under both field and experimental conditions. These traits may be used to identify or predict changes in geographic ranges or "windows of increased opportunity" that are associated with warming temperatures (Gobler et al., 2017; Moore et al., 2008; Wells et al., 2020).

They may also be used to target monitoring efforts, lessening the economic burden of future HAB events.

CRediT authorship contribution statement

Stephanie I. Anderson: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Niall McGinty:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Alexa R. Sterling:** Writing – review & editing, Formal analysis, Data curation. **James D. Hagy III:** Writing – review & editing, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2026.103180.

Data availability

The HAEDAT HAB event data used in this analysis are available via https://www.obis.org or http://haedat.iode.org. NOAA OISST weekly means are available from the Physical Sciences Laboratory (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.html) along with the NARR reanalysis products for DSR flux and wind (https://psl.noaa.gov/data/gridded/data.narr.html). NASA OISSS data are available from The Physical Oceanography Distributed Active Archive Center (https://podaac.jpl.nasa.gov/dataset/OISSS_L4_multimission_7day_v2). Collated data from this study and code to repeat or replicate these analyses has been made available through a GitHub repository (https://github.com/USEPA/HAB_thermal_traits) and archived on Zenodo (https://doi.org/10.5281/zenodo.21398667). A summary of thermal trait values, as discerned from the literature and with our ensemble models, is included with this manuscript.

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