Towards effective management of the marine-origin *Prymnesium parvum* (Haptophyta): A growing concern in freshwater reservoirs?

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A B S T R A C T

Freshwater ecosystems are highly susceptible to harmful algal blooms (HABs), which are often caused by monospecific dense blooms. Effective preventive management strategies are urgently needed to avoid wide-ranging and severe impacts often resulting in costly damage to resources and unsustainable management options. In this study, we utilized SDM techniques focused on *Prymnesium parvum*, one of the most notorious HABs species worldwide. We first compare the climatic space occupied by *P. parvum* in North America, Europe and Australia. Additionally, we use MaxEnt algorithm to infer, for the first time, the potentially suitable freshwater environments in the aforementioned ranges. We also discuss the risks of invasion in reservoirs – prone habitats to persistent blooms of pests and invasive phytoplanktonic species. Our results show populations with distinctive niches suggesting ecophysiological tolerances, perhaps reflecting different strains. Our model projections revealed that the potential extent for *P. parvum* invasions is much broader than its current geographic distribution. The spatial configuration of reservoirs, if not sustaining dense blooms due to non-optimal conditions, favors colonization of multiple basins and ecoregions not yet occupied by *P. parvum*. Our models can provide valuable insights to decision-makers and monitoring programs while reducing the resources required to control the spread of *P. parvum* in disturbed habitats. Lastly, as impact magnitude is influenced by toxicity which in turn varies between different strains, we suggest future studies to incorporate intraspecific genetic information and fine-scale environmental variables to estimate potential distribution of *P. parvum*.

1. Introduction

Harmful algal blooms (HABs) pose a persistent threat to aquatic biodiversity, presenting a conservation challenge with extensive impacts to ecosystem services, human health, and the economy (Lewitus et al., 2012). These blooms can thrive in a wide range of environmental conditions (i.e. temperature and precipitation; Becker et al., 2009; Jeppesen et al., 2014; Paerl and Huisman, 2008; Reinl et al., 2023) and arise from the prolific growth of various taxa, such as Cyanobacteria, dinoflagellates, and haptophytes (Balaji-Prasath et al., 2022). These taxa can present "pest behavior", become invasive or remain in an even unconclusive status (Acosta et al., 2015; Litchman, 2010; Ruiz et al., 1997). In freshwater environments, HABs have led to the degradation of water quality, impacting diverse uses like drinking water and recreational activities (Aguilera et al., 2023). Moreover, climate-induced disturbances are expected to interact synergistically, jeopardizing the availability of clean freshwater resources (Boretti and Rosa, 2019), while also potentially reducing the resistance to successively introduced non-native species (Glibert, 2020; Glibert et al., 2011; Macêdo et al., 2021a). Consequently, the management of HABs becomes a multivariate and intricate challenge (Glibert, 2020; Hallegraeff, 2010).

Management options can utilize robust statistical approaches to assist cost-efficient management based on prevention and anticipation of impacts (Erratt et al., 2022). At regional and global scales, species distribution models (SDMs) have proven to be a valuable technique for identifying areas with suitable environmental conditions based on occurrence records and associated temperature and precipitation patterns (Liu et al., 2022; Pearson et al., 2006). Temperature plays a crucial

role in phytoplankton survival and physiological performance, directly influencing their distribution (Kramer et al., 2017; Xia et al., 2021). Similarly, precipitation impacts nutrient availability, salinity, and vertical temperature stratification, thereby affecting the growth of algae (Jeppesen et al., 2009; Stockwell et al., 2020). These factors (surrogates for water conditions) jointly contribute to shaping the potential distribution of multiple aquatic species, including phytoplanktonic groups (Jensen et al., 2017; Macêdo et al., 2021; Meriggi et al., 2022). The lack of direct estimates of water variables (Ficklin et al., 2014; McGarvey et al., 2018) maked them useful constraints in SDM predictions with demonstrated high niche overlap when comparatively using climatic surrogates and instream measurements (McGravey et al., 2018).

The golden algae, *Prymnesium parvum* (Carter, 1937) has widely expanded its distribution through inland water reservoirs and *rivers* (Brooks et al., 2011; Hambright et al., 2014; Remmel and Hambright, 2012; Southard et al., 2010). Despite its marine and coastal origin (Hambright et al., 2015), catastrophic episodes have raised increasing concerns regarding freshwater resources, leading to severe mass mortality problems in water supply systems and rivers (Johnsen et al., 2010; Southard et al., 2010). *Prymnesium parvum* has euryhaline features persisting under varying salinity concentrations e.g. 5–35 ppm (Kaartvedt et al., 1991; Richardson and Patiño, 2021). While Australian strains tend to reach optimal growth at higher salinity, direct or indirect human-driven alterations affects water bodies favoring blooms of *P. parvum,* e.g. in the case of water diversion with sudden drops in salinity (Barone et al., 2010) or alterations in precipitation regimes (Roelke et al., 2011; German Environment Agency - UBA, 2022; Sobieraj and Metelski, 2023). The first reported case of a *P. parvum* bloom that led to fish mortality occurred in 1985 in the south-central region of the United States, specifically in the Pecos River in Texas (James and De La Cruz, 1989). Since then, *P. parvum* has spread rapidly across both southern and northern regions of the USA, invading lakes and rivers (Roelke et al., 2011; Brooks et al., 2011; Hambright et al., 2010). As far as we know, no previous study attempt to predict the potential distribution of this highly impactful algae.

Once favorable conditions are met for *P. parvum*, it is also suggested that the intensity of dispersal (i.e. propagule pressure) becomes a determining factor in the success of this species (Acosta et al., 2015). Similarly to other pervasive species, *P. parvum* can enhance recruitment and spread throughout inland alterations (e.g. dams, diversions and artificial channels; Havel et al., 2005; Morgan et al., 2001) Macêdo et al., 2021a; 2021b). Aquatic non-native species from marine environments like *P. parvum* are more prone to invade freshwater ecosystems than *vice versa* (Casties et al., 2016). Anthropogenically created freshwater ecosystems like reservoirs serve a variety of purposes such as irrigation, store drinkable water for domestic and industrial means but are particularly prone to invasions as aquatic non-native species can be introduced through a variety of means, such as accidental introductions via shipping or intentional introductions for aquaculture or recreational fishing purposes (Hallegraeff and Bolch, 1991).

Here, we used SDMs to visualize and predict the potential distributional patterns of *P. parvum* across three largely impacted regions: North America, Europe and Oceania. We also used available data on current dam constructions across these regions to identify matches between the climatic suitability and the potential facilitators for establishment and spread. In addition, we identify important climatic variables underpinning invasion pathway of *P. parvum* in the face of the current tendency of global warming and salinization of freshwaters (Kaushal et al., 2021; Raitsos et al., 2010; Robinson et al., 2020). In doing so, we aim to inform environmental management to avoid or mitigate ecological catastrophes (Granéli et al., 2012; Svendsen et al., 2018) and safeguard ecosystem services and health of nature and people utilizing freshwater reservoirs across target invaded systems.

2. Material and methods

Species records were gathered from the Global Biodiversity Information Facility (www.gbif.org), Ocean Biodiversity Information System (www.obis.org) and literature search as complementary sources. We collated a total of 102 *Prymnesium parvum* after removal of duplicates and spatial thinning by 5 km using spthin library (Aiello-Lammens et al., 2015) (Fig. 1; Supplementary Table S1). For environmental predictors, we pre-selected five from all 19 bioclimatic variables in the geodata R package from historical monthly climatic data (1970–2000) monthly temperature and precipitation values at a 5 km^2 resolution (Fick and Hijmans, 2017).

For the development of our SDM for the subject species, we carefully selected bioclimatic variables based on the species' known ecological preferences and physiological constraints, as well as empirical evidence from related studies. Minimal temperature of the coldest month (bio6), provides insights into the potential regions where the species could survive during the coldest periods: the species, originating from coastal marine areas, demonstrates a particular sensitivity to cold temperatures that might impact its ability to overwinter in freshwater environments (Manning and La Claire, 2010). Mean diurnal range (bio2): As the species shifts from coastal to more interior inland waters, its exposure to daily temperature fluctuations is expected to increase. Precipitation variables (bio14, bio17, bio19): precipitation plays a pivotal role in determining water quality, particularly parameters like electrical conductivity (or salinity) and nutrient concentrations (Granéli et al., 2012; Kaushal et al., 2021). Precipitation of the driest month (bio14): This metric gauges the species' resilience to extremely dry periods, potentially indicating its adaptation to higher salinities and altered nutrient conditions. Precipitation of the driest quarter (bio17): a broader temporal scale metric, it offers insights into seasonal drought conditions that might influence the species' distribution. Precipitation of the coldest quarter (bio19): Considering that the species is more prevalent in blooms during temperate climates, understanding precipitation during colder months can provide crucial insights into bloom dynamics in relation to nutrient availability and temperature (Paerl and Huisman, 2008; Reinl et al., 2023). Multicollinearity among efcalculating variance inflation factor (VIF; $r < 0.7$) statistics (Zeng et al., 2016), which resulted in the selection of four variables used in our models, formally: (bio2, bio6, bio14, bio19).

First, we compared climatic niches directly in a multivariate space following Broennimann et al. (2012). For such comparisons, we used a principal component analysis (PCA-env *sensu* Broennimann et al., 2012) calibrated on the available environmental background of the three target populations (Supplementary Fig. S1). We calculated niche overlaps between climatic spaces using the comparative metric Schoener's *D* (Warren et al., 2008) and niche similarity to assess whether the niches are more (or less) similar than expected. Further, we used the Maximum Entropy (MaxEnt), a presence only model (uses pseudo-absences to compensate) that tries to minimize a *gain* function (similar to deviance) to maximize the entropy (uniform distribution of uncertainty in geographical space) (Phillips et al., 2006). Modeling procedure was carried out in R language and environment version 4.2.1 (R Core Team, 2023) using the sdm R package (Naimi and Araújo, 2016). As invasive species distributions are not in equilibrium with their environment making transferability in space and time are limited (Liu et al., 2022), we used global distribution (both native and non-native ranges), thus capturing the maximum climatic amplitude of the species. We randomly set 10,000 background points generated across the globe following evidence-based recommendations for large-scale modeling (Barbet-Massin et al., 2012). Models were trained with a bootstrapping method, indicated when the species has a low number of registers, with 20 repetitions. Models were calibrated using 75% of the data and evaluated using the remaining 25%.

Model performance was assessed by traditional metrics the Area Under the Receiver Operating Curve (AUC; Franklin, 2010), (2) True
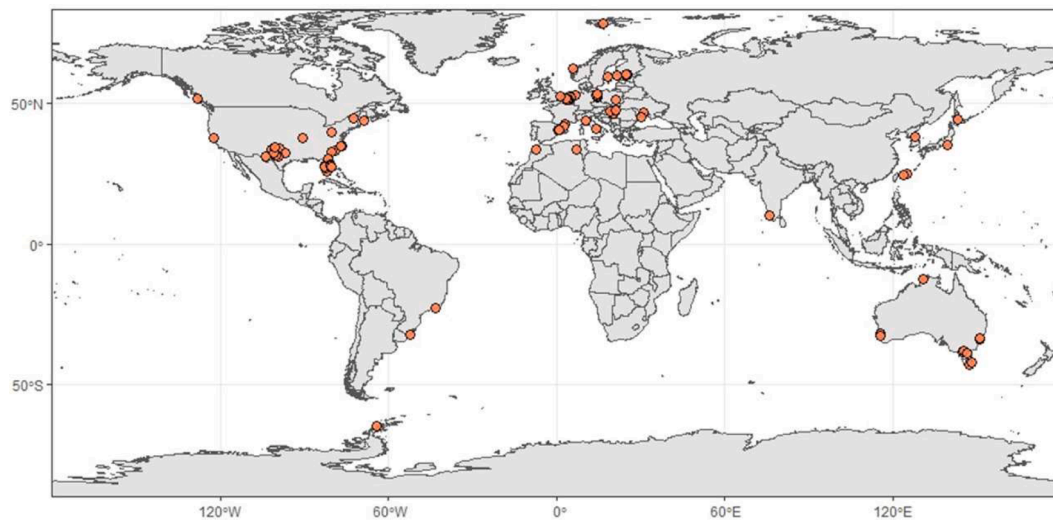
Fig. 1. Distribution records of *Prymnesium parvum*.

Skills Statistics (TSS; Allouche et al., 2006). The threshold used was the one that maximizes both sensitivity and specificity i.e. max(ss+sp). In addition, we used the Boyce index which is highly indicated for MaxEnt (Hirzel et al., 2006), and represents how well the predictive suitability for true positive cases (i.e., presence points) differ from a random set of predictions (i.e., background points). The Boyce index details the average agreement between the predicted suitability and observed values, which ranges from −1 (no agreement) to 1 (perfect agreement), with values close to zero indicating that the prediction is no better than random as determined by the corresponding function in ecospat R package (Boyce et al., 2002). To determine the presence/absence binary map we used the max(ss+sp) as the cut-off value (Liu et al., 2005). MaxEnt response curves were extracted and back-transformed to raw values for interpretation. Specifically, we focused our model visualization on the North American, European and Oceania, where the species has raised severe concerns.

We included data on a number of operating freshwater reservoirs gathered from Mulligan et al. (2020) aiming to more accurately predict prone freshwater environments at risk of *P. parvum* establishment. For visualization of priority areas for regional management, we plot reservoirs vulnerable for *P. parvum* invasions i.e., suitable reservoirs indicated by binary models, yet represented as having low, moderate or high probabilities values.

3. Results

Our multivariate niche analysis showed very low niche overlap between all pairwise population comparisons. When comparing both European and Australian populations, climatic niche overlaps showed to be higher than expected by chance ($p = 0.04$) based on available environmental backgrounds. However, the reciprocal comparison (2 to 1) showed contrasting result ($p = 0.051$) (Table 1). The first two axes of PCA-env accounted for 74% of the environmental variation in the studied areas (55% in the first axis; 24% in the second axis) (see also

Supplementary Fig. S2; S3).

SDMs accurately predicted presences (sensitivity) and pseudo-absences (specificity) of *P. parvum* in North America, Europe, and Oceania, with final models presenting high evaluation metrics (Table 2). Variable importance estimates showed that the minimum temperature of the coldest month (i.e. bio 6) was the most relevant environmental predictors (Fig. 2; Table 3). The other three variables used in our models showed similar importance percentages, with bio14 slightly leading. Increasing precipitation resulted in drastic reduction of occurrence probabilities values of *P. parvum*, suggesting preference for drier localities (Fig. 2). Daily thermal stability (bio2) increased the probability of occurrence whereas Peak relative suitability for minimum temperature of the coldest month was 0 and 6 °C.

The final probability of the occurrence map shows suitable areas for the occurrence of *P. parvum* in many areas of Europe, whereas it has more restricted potential in distribution in North America and Oceania (Fig. 3). Areas with very high occurrence probabilities > 0.75 were concentrated in areas where *P. parvum* has been recorded in blooms, particularly in coastal areas of Florida, central Europe and southeast Australian coast. Also in interior areas such as the Great Lakes and Texans waterbodies and localities in eastern Germany as well as South western Poland, indicating areas where *P. parvum* may have already colonized or where future invasions may occur. The map also highlighted areas with zero or low occurrence probability [max(ss+sp) <0.38] in all three regions (Fig. 3a, b).

Areas suitable for *P. parvum* (Fig. 3d-f) corresponded to those with dense number of reservoirs of medium and large magnitudes in areas with varying degree of suitability. Reservoirs in France, Germany, UK, Poland; North of Spain and Italy were found to be at high risk of *P. parvum* invasions whereas in the United State high risk areas were, Texas, Oklahoma, Kansas and Missouri. Finally, Southeastern Australia were also highly suitable for *P. parvum* establishment.

4. Discussion

In the Anthropocene, characterized by unprecedented global

Table 1

Niche comparisons between ranges (North America, Europe and Australia). Niche overlap are given as *D* index and results from niche similarity hypotheses (p-values) are given for comparisons in the two possible directions of the test.

1→2	*D*	Similarity 1→2	Similarity 2→1
North America-Europe	0.012	0.248	0.208
North America-Australia	0.032	0.149	0.139
Europe-Australia	0.045	**0.049**	0.051

Table 2

Performance metrics of final models projected in North America, Europe and Oceania. TSS= True Skill Statistics, AUC= Area Under the Receiving Operator Curve and, CBI= Continuous Boyce Index.

	Sensitivity	Specificity	TSS	AUC	CBI
Final model	89%	90%	0.79	0.94	0.94±0.02
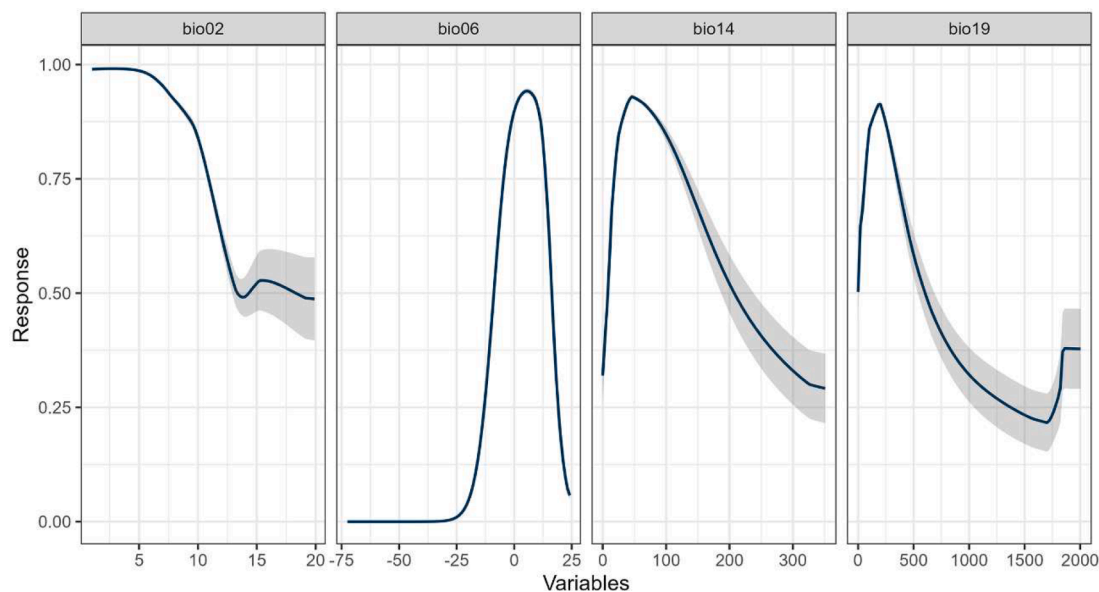
Fig. 2. Response curves showing the relationships between the probability of presence of *P. parvum*. Values shown are average over 20 replicate runs; gray shades margins show standard deviation. Mean diurnal range (bio2), minimal temperature of the coldest month (bio6), precipitation of driest month (bio14), and precipitation of coldest quarter (bio19).

Table 3
Relative variable importance in the MaxEnt models for *P. parvum* assessed through permutation based on two metrics (Pearson correlation and AUC). Mean diurnal range (bio2), minimal temperature of the coldest month (bio6), precipitation of driest month (bio14), and precipitation of coldest quarter (bio19).

Method Variables	Correlation%	AUC%
Bio2	18.8	6.2
Bio6	74.1	70.3
Bio14	30.5	10.2
Bio19	12.3	3.3

environmental and climate changes, decision-making regarding harmful algal bloom (HAB) management has become increasingly complex. Regardless of the invasive or native status of these blooms, early detection and rapid response remain the most cost-efficient options (Erratt et al., 2022; Reaser et al., 2020; Xia et al., 2018). This is in agreement with research efforts focused on filling gaps on geographical range and distribution of blooms (Aguilera et al., 2023; Reinl et al., 2023), verifying efficiency of methods for early detection (Macêdo et al., 2021a,b; Luo et al., 2022; Meriggi et al., 2022), and synthesize cost estimates (Macêdo et al., 2022). To the best of our knowledge, our study is the first in predicting potential distribution of the harmful *Prymnesium parvum*, with our SDMs suggesting a broader potential distribution of *P. parvum*.

Overall, the hypothesis of similarity between climatic niches was rejected for almost all pairwise comparisons due to very low and randomly distributed overlaps. Such niche differentiation can be due to physiologic plasticity and/or different patterns of strains encountered in these regions (Binzer et al., 2019) which can contain even higher genetic variation. These results are aligned with recent analysis of geographically diverse strains indicating taxonomic crypticity in *P. parvum* (Wisecaver et al., 2023). Future research should, therefore, consider exploring the underlying processes of niche evolution e.g. niche expansion as has been identified in other phytoplankton species (Soininen et al., 2019; Macêdo et al., 2021b), perhaps using a more comprehensive molecular data on strains types to train distribution models.

When managing microorganism's invasion, major unknowns refer to

crypt**icity of functions (see Jarić et al., 2019). For example, *P. parvum* exhibits mixotrophic behavior, utilizing various nutritional strategies such e.g., as photo-autotrophy and phagotrophy (Carvalho and Granéli, 2010), but also physiological plasticity and genetic diversity (Granéli et al., 2012; Binzer et al., 2019). These features can be selected by long-term environmental changes, heterogeneity and disturbances, thus offering major scope for niche differentiation as found by Macêdo et al. (2021)b for *Ceratium furcoides*. Given the enormous development of analytical tools to address fundamental questions in ecology, our study suggests investigated the overlap between the spatial niche of the different model strains as *n*-dimensional hypervolumes, and to quantify their reciprocal intersection (i.e. overlap; Fig. 4). Formal hypothesis could address whether possible overlaps result in direct competition, causing one strain to increase its toxicity

When considering the SDM projections, low temperature has been suggested as a critical environmental factor that might restrict the expansion of *P. parvum* to higher latitudes. Although rare episodes were previously reported (e.g. in Brazil; Alves-de-Souza et al., 2017; Manning and La Claire, 2010), the temperature limitations shown in the response curves are consistent with studies which recorded growth inhibition and lysis in warm waters (30–35°C; Shilo and Aschner, 1953; McLaughlin, 1958). The Danish and Norwegian strains of *P. parvum* tested by Larsen et al. (1998) exhibited a maximum growth rate at 15 °C, yet tolerating a wide temperature range of 5 to 30 °C. Outbreaks were also reported at temperatures between 15 and 23.5°C (Sabour et al., 2000). Although the wide thermal tolerances may support that *P. parvum* is a eurythermal organism, complexities due to a temperature and salinity interplay may be crucial for population dynamics and altering the magnitude of observale impacts (Baker et al., 2007; 2009). For example, the estimated optimal temperature for growth decreased with decreasing salinity (Baker et al., 2009). At low salinities, the negative effect of low temperatures on growth of *P. parvum* are weakened which may partially explain its high suitability in the winter months in inland waters of Texas State, United States (Roelke et al., 2011; VanLandeghem et al., 2015). These findings are also consistent with recent reports of blooms at very low temperatures, including ice-cold environments and below the ice (Reinl et al., 2023). In addition, lower biological resistance of recipient communities is expected at low temperatures, lower grazing pressure by toxin-resistant zooplankton and the pathogenic effects of viruses (Acosta et al., 2015; Hambright et al., 2015, 2010; Schwierzke et al.,
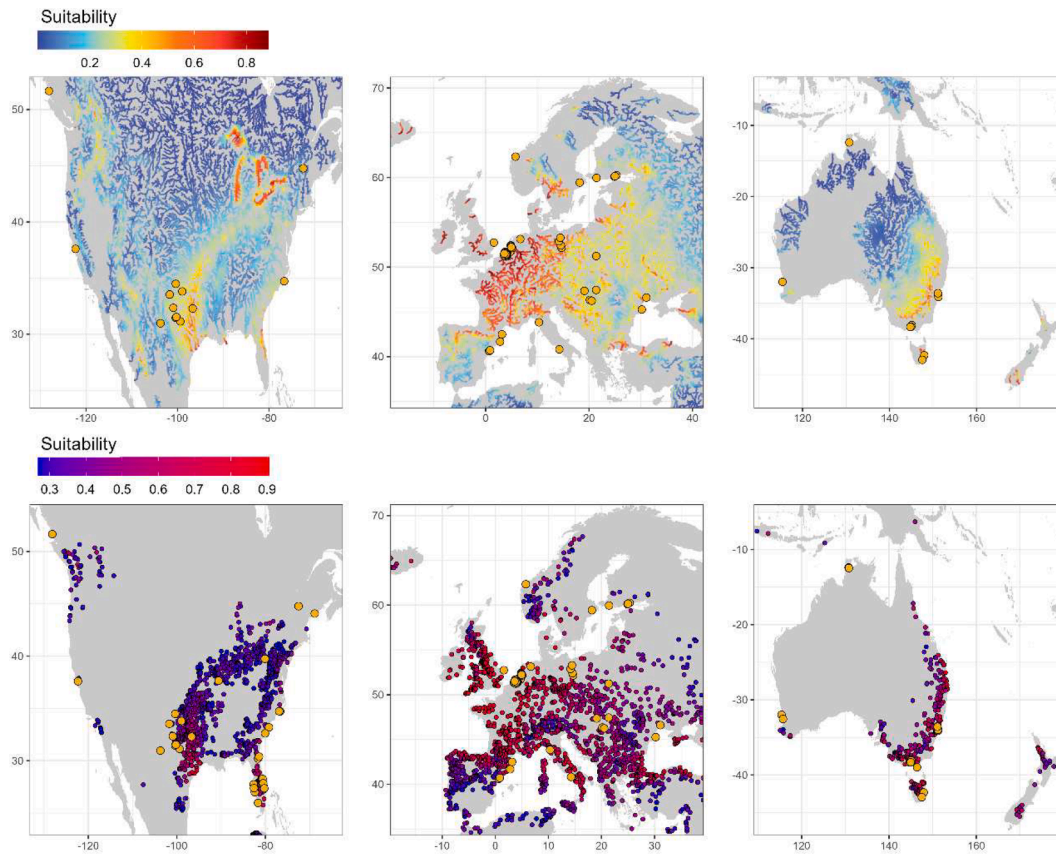
Fig. 3. *Prymnesium parvum* (Haptophyte) SDMs probability of occurrence map for North America (a), Europe (b) and Oceania (c) based on presence data from 102 sites and climatic grid-based variables. Yellow circles represent current records of *P. parvum*. Risk assessment across suitable dammed habitats is represented for the same aforementioned regions, respectively (d, e, and f). Reservoirs are shown as smaller circles with blue-red color gradients. Note that although all reservoirs represent suitable locations defined by the binary model (cut-off > 0.38), they also show varying suitability (blue=low, red=high).
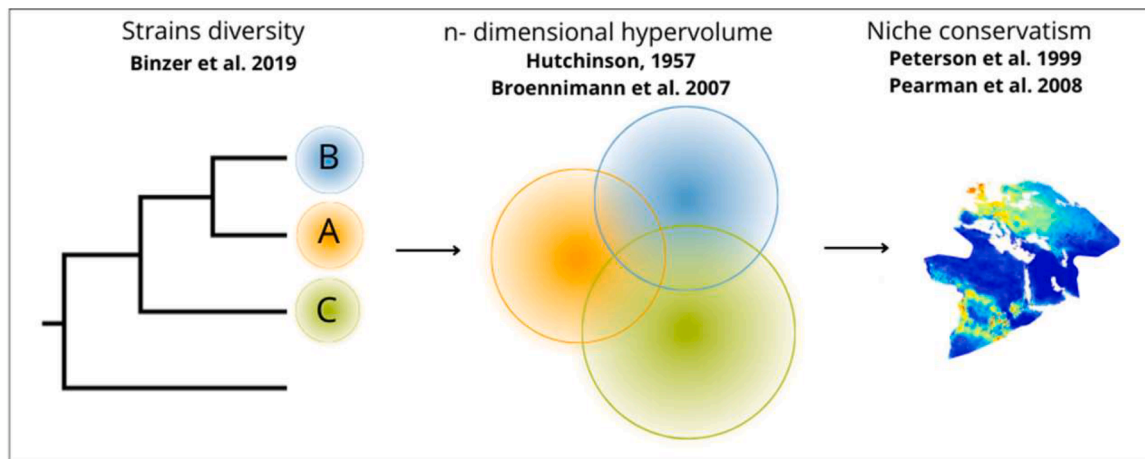
Fig. 4. Conceptual figure suggesting the utilization evolutionary and ecological knowledge for better inform management of *Prymnseium parvum*. Phylogenetic data, which influences toxicity and environmental tolerances, together with comparative computational analysis of niche can help elucidate geographic patterns of *Prymnesium* strains.

2010). Moreover, certain phytoplankton species can effectively outcompete *P. parvum*. For instance, its blooms are typically absent when cyanobacteria are present. Thus, in the reservoirs of Australia's East Coast, where our models indicated high suitability, cyanobacterial dominance might be preventing *Prymnesium* outbreaks.

Our models also suggested that drier climates can favor the establishment of *P. parvum*. This conjecture is supported by a recent study in Poland which documented a recent massive fish mortality in the River

Oder in the late summer in 2022 (Sobieraj and Metelski, 2023). The findings presented in the technical report indicated that the Oder fish die-off was triggered by multi-causal mechanisms, yet the elevated conductivity of more than 1900 µS/cm encouraged the rapid growth of the brackish water alga *P parvum* to a very high density of individuals. Climate conditions such as high evaporation rates and low levels of precipitation, that are also anticipated in the future, can add complexity to the predictability of *P. parvum* outbreaks. This is beacuse of the role of

salinity being particularly important due to *P. parvum* being a marine species that is already at the limit of its salinity tolerance in reservoirs (Hambright et al., 2014) and with most recorded blooms occurring when salinity exceeds 1.7 practical salinity units (psu; Hambright et al., 2015). Not only ions which increase salinity in freshwaters but also concentrations of substances dissolved in water will continue to lead to complex interactions under water, thereby highlighting the importance of context dependencies in invaded freshwaters.

The habitat relatedness of *P. parvum* to artificial systems, such as reservoirs, may enhance its spread across larger ranges. This is possible due to water diversion projects undertaken to improve water security in regions with semi-arid climate or urban areas with fast population growth (Lasserre, 2006; Clayton et al., 2021). Dams can facilitate the establishment of harmful algae even in climatically unsuitable areas - if local variables of relevance for *P. parvum* growth are present (e.g. high concentrations of herbicides, carbon dioxide or wetland cover suppression; Clayton et al., 2021; Tábora-Sarmiento et al., 2022). In reservoirs, the management of harmful algal blooms, including those from *P. parvum*, requires careful consideration of nutrient imbalances and their potential effects on allelopathy (Granéli and Johansson, 2003). Traditional methods of controlling cyanobacteria, such as phosphorus and nitrogen reduction and thus, N:P ratio disruption, in lakes and reservoirs, can inadvertently trigger the toxin production of *Prymnesium* (VanLandeghem et al., 2015; Granéli and Johansson, 2003). Studies have shown that allelopathic effects are increased under nutrient limitation, and when *P. parvum* cultures with unbalanced nutrient conditions, such as very high or very low N:P ratios, produce allelopathic compounds (Sobieraj and Metelski, 2023). Also, the production of toxins by *P. parvum* tends to increase under sub-optimal growth conditions, which often coincide with the formation of blooms (reviewed in Granéli et al., 2012; Granéli and Salomon, 2010). Furthermore, lowland reservoirs are often situated in catchments that are affected by agricultural land use and urbanization, resulting in elevated nutrients and pollutants run-off that favors blooms (Clayton et al., 2021). Also, coastal areas, which also showed high suitability to *P. parvum,* raise concern about the conservation of estuaries and brackish environments. By complementing climatic variables with information on the nutrient status of reservoirs waters - mainly those most closely related to *P. parvum* ecology e.g. nitrogen - we will be able to identify both areas of high risk for invasion and areas where impacts can be of high magnitude, thereby of concern to multiple water uses related to agriculture, food industry, fisheries, recreational and potable sources.

The studied regions are prominent in biological invasions with multi-million dollars undertaken to control or mitigate impacts of invasive species (Cuthbert et al., 2022; Ricciardi, 2006). High probability of occurrence was found in the Great Lakes basin of North America, an already largely invaded freshwater ecosystem (Ricciardi and MacIsaac, 2022). In North American lakes for example, the invasion of other species *Bythotrephes longimanus Limnoperna fortunei* can cause loss of ecosystem services e.g. water quality changes and transparency reduction, which in turn can alter N:P balance via direct effects or management options (Reynolds and Aldridge, 2021; Walsh et al., 2017), thus favoring more toxic blooms and rising management complexity. Beyond this important ecosystem in North America, an impressive high number of freshwater reservoirs were classified as highly suitable to *P. parvum*. If not representing a severe risk of blooms with plausible catastrophic impacts, these findings indicate that it is highly probable that *P. parvum* will spread due to the connectivity of inland water ecosystems. Yet, previous studies stated that the transfer of species between different salinity habitats is asymmetrical, with a colonization of freshwater habitats by marine and brackish species becoming increasingly common in recent years, but not *vice versa* (Grigorovich et al., 1998; Paiva et al., 2018). Last but not least, the emergence of new introduction pathways (e.g. new international shipping routes, inland water diversion and dam projects and hydrological alterations) will likely facilitate the dispersal of the species to neighboring localities (Macèdo et al., 2021a; Litchman,

2010; Yang et al., 2023).

5. Conclusion

Our results rejected the hypothesis of niche conservatism in *P. parvum* populations stablished in North America, Europe, and Australia. This finding has important implications on the effective management and assessments of invasion risk, raising discussions on plausible underlying mechanisms shaping its invasiveness due to i.e. physiological tolerances of different strains and invasibility and the high suitability in prone invadable freshwater habitats (reservoirs). We showed the potential distribution of *P. parvum* is larger than perceived by observational studies posing a severe risk to freshwater ecosystems in North America, Europe, and Australia. Our results also narrow down the number of reservoirs that must be subjected to continuous and monitoring protocols, which should also include multiparametric evaluation of water quality to favor the understanding of the role of context dependencies in the success and magnitude of impacts caused by this toxin-producing algae.

CRediT authorship contribution statement

RLM conceived and designed, and performed the analyses. RLM and OR collected the data and wrote the original draft.

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.

Data availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2023.102513.

References

Acosta, F., Zamor, R.M., Najar, F.Z., Roe, B.A., Hambright, K.D., 2015. Dynamics of an experimental microbial invasion. Proc. Natl. Acad. Sci. 112, 11594–11599. https://doi.org/10.1073/pnas.1505204112.

Aguilera, A., Almanza, V., Haakonsson, S., Palacio, H., Benitez Rodas, G.A., Barros, M.U. G., Capelo-Neto, J., Urrutia, R., Aubriot, L., Bonilla, S., 2023. Cyanobacterial bloom monitoring and assessment in Latin America. Harmful Algae 125, 102429. https://doi.org/10.1016/j.hal.2023.102429.

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545. https://doi.org/10.1111/ecog.01132.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Alves-de-Souza, C., Benevides, T.S., Santos, J.B.O., Von Dassow, P., Guillou, L., Menezes, M., 2017. Does environmental heterogeneity explain temporal β diversity

of small eukaryotic phytoplankton? Example from a tropical eutrophic coastal lagoon. J. Plankton Res. 39, 698–714. https://doi.org/10.1093/plankt/fbx026.

Baker, J.W., Grover, J.P., Brooks, B.W., Ureña-Boeck, F., Roelke, D.L., Errera, R., Kiesling, R.L., 2007. Growth and toxicity of Prymnesium parvum (Haptophyta) as a function of salinity, light, and temperature. J. Phycol. 43, 219–227. https://doi.org/10.1111/j.1529-8817.2007.00323.x.

Baker, J.W., Grover, J.P., Ramachandrannair, R., Black, C., Valenti, T.W., Brooks, B.W., Roelkec, D.L., 2009. Growth at the edge of the niche: An experimental study of the harmful alga Prymnesium parvum. Limnol. Oceanogr. 54, 1679–1687. https://doi.org/10.4319/lo.2009.54.5.1679.

Balaji-Prasath, B., Wang, Y., Su, Y.P., Hamilton, D.P., Lin, H., Zheng, L., Zhang, Y., 2022. Methods to control harmful algal blooms: a review. Environ. Chem. Lett. 20, 3133–3152. https://doi.org/10.1007/s10311-022-01457-2.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Barone, R., Castelli, G., Naselli-Flores, L., 2010. Red sky at night cyanobacteria delight: the role of climate in structuring phytoplankton assemblage in a shallow, Mediterranean lake (Biviere di Gela, southeastern Sicily). Hydrobiologia 639, 43–53. https://doi.org/10.1007/s10750-009-0016-2.

Becker, V., Huszar, V.L.M., Crossetti, L.O., 2009. Responses of phytoplankton functional groups to the mixing regime in a deep subtropical reservoir. Hydrobiologia 628, 137–151. https://doi.org/10.1007/s10750-009-9751-7.

Binzer, S.B., Svenssen, D.K., Daugbjerg, N., Alves-de-Souza, C., Pinto, E., Hansen, P.J., Larsen, T.O., Varga, E., 2019. A-, B- and C-type prymnesins are clade specific compounds and chemotaxonomic markers in Prymnesium parvum. Harmful Algae 81, 10–17. https://doi.org/10.1016/j.hal.2018.11.010.

Boretti, A., Rosa, L., 2019. Reassessing the projections of the World Water Development Report. NPJ Clean Water 2, 15. https://doi.org/10.1038/s41545-019-0039-9.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Modell. 157, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C. H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecol. Biogeogr. 21, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x.

Brooks, B.W., Grover, J.P., Roelke, D.L., 2011. Prymnesium parvum: An emerging threat to inland waters. Environ. Toxicol. Chem. 30, 1955–1964. https://doi.org/10.1002/etc.613.

Carvalho, W.F., Granéli, E., 2010. Contribution of phagotrophy versus autotrophy to Prymnesium parvum growth under nitrogen and phosphorus sufficiency and deficiency. Harmful Algae 9, 105–115. https://doi.org/10.1016/j.hal.2009.08.007.

Casties, I., Seebens, H., Briski, E., 2016. Importance of geographic origin for invasion success: A case study of the North and Baltic Seas versus the Great Lakes-St. Lawrence River region. Ecol. Evol. 6, 8318–8329. https://doi.org/10.1002/ece3.2528.

Clayton, J.B., Patiño, R., Rashel, R.H., Tábora-Sarmiento, S., 2021. Water quality associations and spatiotemporal distribution of the harmful alga Prymnesium parvum in an impounded urban stream system. J. Urban Ecol. 7 https://doi.org/10.1093/jue/juab011.

Cuthbert, R.N., Diagne, C., Hudgins, E.J., Turbelin, A., Ahmed, D.A., Albert, C., Bodey, T. W., Briski, E., Essl, F., Haubrock, P.J., Gozlan, R.E., Kirichenko, N., Kourantidou, M., Kramer, A.M., Courchamp, F., 2022. Biological invasion costs reveal insufficient proactive management worldwide. Sci. Total Environ. 819, 153404 https://doi.org/10.1016/j.scitotenv.2022.153404.

Erratt, K.J., Creed, I.F., Trick, C.G., 2022. Harmonizing science and management options to reduce risks of cyanobacteria. Harmful Algae 116, 102264. https://doi.org/10.1016/j.hal.2022.102264.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Ficklin, D.L., Barnhart, B.L., Knouft, J.H., Stewart, I.T., Maurer, E.P., Letsinger, S.L., Whittaker, G.W., 2014. Climate change and stream temperature projections in the Columbia River basin: habitat implications of spatial variation in hydrologic drivers. Hydrol. Earth Syst. Sci. 18, 4897–4912. https://doi.org/10.5194/hess-18-4897-2014.

Franklin, J., 2010. Mapping Species Distributions. Cambridge University Press. https://doi.org/10.1017/CBO9780511810602.

German Environment Agency - UBA. 2022. Fish die-off in the Oder River, August 2022 Status report as of 2022. Available online from: https://www.bmuv.de/fileadmin/Daten_BMU/Download_PDF/Binnengewaesser/Bericht_-_Fischsterben_in_der_Oder_20220929_en_bf.pdf.

Glibert, P.M., 2020. Harmful algae at the complex nexus of eutrophication and climate change. Harmful Algae 91, 101583. https://doi.org/10.1016/j.hal.2019.03.001.

Glibert, P.M., Fullerton, D., Burkholder, J.M., Cornwell, J.C., Kana, T.M., 2011. Ecological Stoichiometry, Biogeochemical Cycling, Invasive Species, and Aquatic Food Webs: San Francisco Estuary and Comparative Systems. Rev. Fish. Sci. 19, 358–417. https://doi.org/10.1080/10641262.2011.611916.

Granéli, E., Edvardsen, B., Roelke, D.L., Hagström, J.A., 2012. The ecophysiology and bloom dynamics of Prymnesium spp. Harmful Algae 14, 260–270. https://doi.org/10.1016/j.hal.2011.10.024.

Granéli, E., Johansson, N., 2003. Increase in the production of allelopathic substances by Prymnesium parvum cells grown under N- or P-deficient conditions. Harmful Algae 2, 135–145. https://doi.org/10.1016/S1568-9883(03)00006-4.

Granéli, E., Salomon, P.S., 2010. Factors Influencing Allelopathy and Toxicity in Prymnesium parvum 1. J. Am. Water Resour. Assoc. 46, 108–120. https://doi.org/10.1111/j.1752-1688.2009.00395.x.

Grigorovich, I.A., Pashkova, O.V., Gromova, Y.F., van Overdijk, C.D.A., 1998. Bythotrephes longimanus in the Commonwealth of Independent States: Variability, distribution and ecology. Hydrobiologia 379, 183–198. https://doi.org/10.1023/A:1003427117034.

Hallegraeff, G.M., 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. J. Phycol. 46, 220–235. https://doi.org/10.1111/j.1529-8817.2010.00815.x.

Hallegraeff, G.M., Bolch, C.J., 1991. Transport of toxic dinoflagellate cysts via ships' ballast water. Mar. Pollut. Bull. 22, 27–30. https://doi.org/10.1016/0025-326X(91)90441-T.

Hambright, D., Beyer, J.E., Easton, J.D., Zamor, R.M., Easton, A.C., Hallidayschult, T.C., 2015. The niche of an invasive marine microbe in a subtropical freshwater impoundment. ISME J 9, 256–264. https://doi.org/10.1038/ismej.2014.103.

Hambright, K.D., Easton, J.D., Zamor, R.M., Beyer, J., Easton, A.C., Allison, B., 2014. Regulation of growth and toxicity of a mixotrophic microbe: implications for understanding range expansion in Prymnesium parvum. Freshwater Science 33, 745–754. https://doi.org/10.1086/677198.

Hambright, K.D., Zamor, R.M., Easton, J.D., Glenn, K.L., Remmel, E.J., Easton, A.C., 2010. Temporal and spatial variability of an invasive toxigenic protist in a North American subtropical reservoir. Harmful Algae 9, 568–577. https://doi.org/10.1016/j.hal.2010.04.006.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Modell. 199, 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.

Havel, John E., Lee, Carol Eunmi, Vander Zanden, M.Jake, 2005. Do Reservoirs Facilitate Invasions into Landscapes? Bioscience 55, 518–525.

James, T.L., De La Cruz, A., 1989. *Prymnesium parvum* Carter (Chrysophyceae) as a suspect of mass mortalities of fish and shellfish communities in western Texas. Texas J. Sci. 41, 429–430.

Jarić, I., Heger, T., Castro Monzon, F., Jeschke, J.M., Kowarik, I., McConkey, K.R., Pyšek, P., Sagouis, A., Essl, F., 2019. Crypticity in Biological Invasions. Trends Ecol. Evol. 34, 291–302. https://doi.org/10.1016/j.tree.2018.12.008.

Jensen, L.Ø., Mousing, E.A., Richardson, K., 2017. Using species distribution modelling to predict future distributions of phytoplankton: Case study using species important for the biological pump. Mar. Ecol. 38, e12427. https://doi.org/10.1111/maec.12427.

Jeppesen, E., Kronvang, B., Meerhoff, M., Søndergaard, M., Hansen, K.M., Andersen, H. E., Lauridsen, T.L., Liboriussen, L., Beklioglu, M., Özen, A., Olesen, J.E., 2009. Climate Change Effects on Runoff, Catchment Phosphorus Loading and Lake Ecological State, and Potential Adaptations. J. Environ. Qual. 38, 1930–1941. https://doi.org/10.2134/jeq2008.0113.

Jeppesen, E., Meerhoff, M., Davidson, T.A., Trolle, D., Søndergaard, M., Lauridsen, T.L., Beklioglu, M., Brucet, S., Volta, P., González-Bergonzoni, I., Nielsen, A., 2014. Climate change impacts on lakes: an integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes. J. Limnol. 73 https://doi.org/10.4081/jlimnol.2014.844.

Johnsen, T.M., Eikrem, W., Olseng, C.D., Tollefsen, K.E., Bjerknes, V., 2010. Prymnesium parvum : The Norwegian Experience 1. J. Am. Water Resour. Assoc. 46, 6–13. https://doi.org/10.1111/j.1752-1688.2009.00386.x.

Kaartvedt, S., Johnsen, T.M., Aksnes, D.L., Lie, U., Svendsen, H., 1991. Occurrence of the Toxic Phytoflagellate Prymnesium parvum and Associated Fish Mortality in a Norwegian Fjord System. Can. J. Fish. Aquat. Sci. 48, 2316–2323. https://doi.org/10.1139/f91-272.

Kaushal, S.S., Likens, G.E., Pace, M.L., Reimer, J.E., Maas, C.M., Galella, J.G., Utz, R.M., Duan, S., Kryger, J.R., Yaculak, A.M., Boger, W.L., Bailey, N.W., Haq, S., Wood, K.L., Wessel, B.M., Park, C.E., Collison, D.C., Aisin, B.Y., 'aaqob, I., Gedeon, T.M., Chaudhary, S.K., Widmer, J., Blackwood, C.R., Bolster, C.M., Devilbiss, M.L., Garrison, D.L., Halevi, K., Kese, G.Q., Quach, E.K., Rogelio, C.M.P., Tan, M.L., Wald, H.J.S., Woglo, S.A., 2021. Freshwater salinization syndrome: from emerging global problem to managing risks. Biogeochemistry 154, 255–292. https://doi.org/10.1007/s10533-021-00784-w.

Kramer, A.M., Annis, G., Wittmann, M.E., Chadderton, W.L., Rutherford, E.S., Lodge, D. M., Mason, L., Beletsky, D., Riseng, C., Drake, J.M., 2017. Suitability of Laurentian Great Lakes for invasive species based on global species distribution models and local habitat. Ecosphere 8. https://doi.org/10.1002/ecs2.1883.

Larsen, A., Bryant, S., Båmstedt, U., 1998. Growth rate and toxicity of Prymnesium parvum and Prymnesium patelliferum (haptophyta) in response to changes in salinity, light and temperature. Sarsia 83, 409–418. https://doi.org/10.1080/00364827.1998.10413700.

Lasserre, F., 2006. Managing Water Diversion from Canada to the United States: An Old Idea Born Again? Int. J. 62, 81. https://doi.org/10.2307/40204247.

Lewitus, A.J., Horner, R.A., Caron, D.A., Garcia-Mendoza, E., Hickey, B.M., Hunter, M., Huppert, D.D., Kudela, R.M., Langlois, G.W., Largier, J.L., Lessard, E.J., RaLonde, R., Jack Rensel, J.E., Strutton, P.G., Trainer, V.L., Tweddle, J.F., 2012. Harmful algal blooms along the North American west coast region: History, trends, causes, and impacts. Harmful Algae 19, 133–159. https://doi.org/10.1016/j.hal.2012.06.009.

Litchman, E., 2010. Invisible invaders: non-pathogenic invasive microbes in aquatic and terrestrial ecosystems. Ecol. Lett. 13, 1560–1572. https://doi.org/10.1111/j.1461-0248.2010.01544.x.

Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x.

Liu, C., Wolter, C., Courchamp, F., Roura-Pascual, N., Jeschke, J.M., 2022. Biological invasions reveal how niche change affects the transferability of species distribution models. Ecology 103. https://doi.org/10.1002/ecy.3719.

Luo, N., Huang, H., Jiang, H., 2022. Establishment of methods for rapid detection of Prymnesium parvum by recombinase polymerase amplification combined with a lateral flow dipstick. Front. Biosci.-Landmark 9. https://doi.org/10.3389/fmars.2022.1032847.

Macêdo, R.L., Clara Sampaio Franco, A., Russo, P., Collart, T., Mammola, S., Jeppesen, E., Wyss Castelo Branco, C., Neves dos Santos, L., Rocha, O., 2021. Climate and landscape changes enhance the global spread of a bloom-forming dinoflagellate related to fish kills and water quality deterioration. Ecol. Indic. 133, 108408 https://doi.org/10.1016/j.ecolind.2021.108408.

Macêdo, R.L., Franco, A.C.S., Kozlowsky-Suzuki, B., Mammola, S., Dalu, T., Rocha, O., 2022. The global social-economic dimension of biological invasions by plankton: Grossly underestimated costs but a rising concern for water quality benefits? Water Res. 222, 118918 https://doi.org/10.1016/j.watres.2022.118918.

Macêdo, R.L., Russo, P., Corrêa, R.F., Rocha, O., dos Santos, L.N., Branco, C.W.C., 2021. The drifting dinoflagellate Ceratium furcoides (Levander) Langhans 1925: fundamental niche shift during global invasion. Hydrobiologia 848, 2105–2117. https://doi.org/10.1007/s10750-020-04495-5.

Manning, S.R., La Claire, J.W., 2010. Prymnesins: Toxic Metabolites of the Golden Alga, Prymnesium parvum Carter (Haptophyta). Mar. Drugs 8, 678–704. https://doi.org/10.3390/md8030678.

McGarvey, D.J., Menon, M., Woods, T., Tassone, S., Reese, J., Vergamini, M., Kellogg, E., 2018. On the use of climate covariates in aquatic species distribution models: are we at risk of throwing out the baby with the bath water? Ecography 41, 695–712. https://doi.org/10.1111/ecog.03134.

McLaughlin, J.J.A., 1958. Euryhaline Chrysomonads: Nutrition and Toxigenesis in Prymnesium parvum, with Notes on Isochrysis galbana and Monochrysis lutheri. J. Protozool. 5, 75–81. https://doi.org/10.1111/j.1550-7408.1958.tb02529.x.

Meriggi, C., Drakare, S., Polaina Lacambra, E., Johnson, R.K., Laugen, A.T., 2022. Species distribution models as a tool for early detection of the invasive Raphidiopsis raciborskii in European lakes. Harmful Algae 113, 102202. https://doi.org/10.1016/j.hal.2022.102202.

Morgan, J.A.T., Dejong, R.J., Snyder, S.D., Mkoji, G.M., Loker, E.S., 2001. Schistosoma mansoni and Biomphalaria : past history and future trends. Parasitology 123, 211–228. https://doi.org/10.1017/S0031182001007703.

Mulligan, M., van Soesbergen, A., Sáenz, L., 2020. GOODD, a global dataset of more than 38,000 georeferenced dams. Sci. Data 7, 31. https://doi.org/10.1038/s41597-020-0362-5.

Naimi, B., Araújo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39, 368–375. https://doi.org/10.1111/ecog.01881.

Paerl, H.W., Huisman, J., 2008. Blooms Like It Hot. Science 320, 57–58. https://doi.org/10.1126/science.1155398 (1979).

Paiva, F., Barco, A., Chen, Y., Mirzajani, A., Chan, F.T., Lauringson, V., Baltazar-Soares, M., Zhan, A., Bailey, S.A., Javidpour, J., Briski, E., 2018. Is salinity an obstacle for biological invasions? Glob. Chang. Biol. 24, 2708–2720. https://doi.org/10.1111/gcb.14049.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson, A., 2006. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34, 102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Raitsos, D.E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, A. M., Theocharis, A., Papathanassiou, E., 2010. Global climate change amplifies the entry of tropical species into the eastern Mediterranean Sea. Limnol. Oceanogr. 55, 1478–1484. https://doi.org/10.4319/lo.2010.55.4.1478.

Reaser, J.K., Burgiel, S.W., Kirkey, J., Brantley, K.A., Veatch, S.D., Burgos-Rodríguez, J., 2020. The early detection of and rapid response (EDRR) to invasive species: a conceptual framework and federal capacities assessment. Biol. Invas. 22, 1–19. https://doi.org/10.1007/s10530-019-02156-w.

Reinl, K.L., Harris, T.D., North, R.L., Almela, P., Berger, S.A., Bizic, M., Burnet, S.H., Grossart, H., Ibelings, B.W., Jakobsson, E., Knoll, L.B., Lafrancois, B.M., McElarney, Y., Morales-Williams, A.M., Obertegger, U., Ogashawara, I., Paule-Mercado, M.C., Peierls, B.L., Rusak, J.A., Sarkar, S., Sharma, S., Trout-Haney, J.V., Urrutia-Cordero, P., Venkiteswaran, J.J., Wain, D.J., Warner, K., Weyhenmeyer, G. A., Yokota, K., 2023. Blooms also like it cold. Limnol. Oceanogr. Lett. 8, 546–564. https://doi.org/10.1002/lol2.10316.

Remmel, E.J., Hambright, K.D., 2012. Toxin-assisted micropredation: experimental evidence shows that contact micropredation rather than exotoxicity is the role of Prymnesium toxins. Ecol. Lett. 15, 126–132. https://doi.org/10.1111/j.1461-0248.2011.01718.x.

Reynolds, S.A., Aldridge, D.C., 2021. Impacts of invasive quagga mussels (Dreissena rostriformis bugensis) on reservoir water quality, as revealed by progressive-change BACIPS analysis. Water Res. 197, 117105 https://doi.org/10.1016/j.watres.2021.117105.

Ricciardi, A., 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Divers. Distribut. 12, 425–433. https://doi.org/10.1111/j.1366-9516.2006.00262.x.

Ricciardi, A., MacIsaac, H.J., 2022. Vector control reduces the rate of species invasion in the world's largest freshwater ecosystem. Conserv. Lett. 15, e12866 https://doi.org/10.1111/conl.12866.

Richardson, E.T., Patiño, R., 2021. Growth of the harmful alga, Prymnesium parvum (Prymnesiophyceae), after gradual and abrupt increases in salinity. J. Phycol. 57, 1335–1344. https://doi.org/10.1111/jpy.13172.

Robinson, T.B., Martin, N., Loureiro, T.G., Matikinca, P., Robertson, M.P., 2020. Double trouble: the implications of climate change for biological invasions. NeoBiota 62, 463–487. https://doi.org/10.3897/neobiota.62.55729.

Roelke, D.L., Grover, J.P., Brooks, B.W., Glass, J., Buzan, D., Southard, G.M., Fries, L., Gable, G.M., Schwierzke-Wade, L., Byrd, M., Nelson, J., 2011. A decade of fish-killing Prymnesium parvum blooms in Texas: roles of inflow and salinity. J. Plankton Res. 33, 243–253. https://doi.org/10.1093/plankt/fbq079.

Ruiz, G.M., Carlton, J.T., Grosholz, E.D., Hines, A.H., 1997. Global Invasions of Marine and Estuarine Habitats by Non-Indigenous Species: Mechanisms, Extent, and Consequences. Am. Zool. 37, 621–632. https://doi.org/10.1093/icb/37.6.621.

Sabour, B., Loudiki, L.M., Oudra, B., Oubraim, S., Fawzi, B., Fadlaoui, S., Chlaida, M., Vasconcelos, V., 2000. Blooms of Prymnesium parvum associated with fish mortalities in a hypereutrophic brackish lake in Morocco. Harmful Algae News 21. An IOC Newsletter on Toxic Algae and Algal Blooms The Intergovernmental Oceanographic Commission of UNESCO.

Schwierzke, L., Roelke, D.L., Brooks, B.W., Grover, J.P., Valenti, T.W., Lahousse, M., Miller, C.J., Pinckney, J.L., 2010. Prymnesium parvum Population Dynamics During Bloom Development: A Role Assessment of Grazers and Virus 1. J. Am. Water Resour. Assoc. 46, 63–75. https://doi.org/10.1111/j.1752-1688.2009.00391.x.

Shilo, M., Aschner, M., 1953. Factors governing the Toxicity of Cultures containing the Phytoflagellate Prymnesium parvum Carter. J. Gen. Microbiol. 8, 333–343. https://doi.org/10.1099/00221287-8-3-333.

Sobieraj, J., Metelski, D., 2023. Insights into Toxic Prymnesium parvum Blooms as a Cause of the Ecological Disaster on the Odra River. Toxins (Basel) 15, 403. https://doi.org/10.3390/toxins15060403.

Soininen, J., Jamoneau, A., Rosebery, J., Leboucher, T., Wang, J., Kokociński, M., Passy, S.I., 2019. Stream diatoms exhibit weak niche conservation along global environmental and climatic gradients. Ecography 42, 346–353. https://doi.org/10.1111/ecog.03828.

Southard, G.M., Fries, L.T., Barkoh, A., 2010. Prymnesium parvum : The Texas Experience 1. J. Am. Water Resour. Assoc. 46, 14–23. https://doi.org/10.1111/j.1752-1688.2009.00387.x.

Stockwell, J.D., Doubek, J.P., Adrian, R., Anneville, O., Carey, C.C., Carvalho, L., De Senerpont Domis, L.N., Dur, G., Frassl, M.A., Grossart, H., Ibelings, B.W., Lajeunesse, M.J., Lewandowska, A.M., Llames, M.E., Matsuzaki, S.S., Nodine, E.R., Nõges, P., Patil, V.P., Pomati, F., Rinke, K., Rudstam, L.G., Rusak, J.A., Salmaso, N., Seltmann, C.T., Straile, D., Thackeray, S.J., Thiery, W., Urrutia-Cordero, P., Venail, P., Verburg, P., Woolway, R.I., Zohary, T., Andersen, M.R., Bhattacharya, R., Hejzlar, J., Janatian, N., Kpodonu, A.T.N.K., Williamson, T.J., Wilson, H.L., 2020. Storm impacts on phytoplankton community dynamics in lakes. Glob. Chang. Biol. 26, 2756–2784. https://doi.org/10.1111/gcb.15033.

Svendsen, M., Andersen, N., Hansen, P., Steffensen, J., 2018. Effects of Harmful Algal Blooms on Fish: Insights from Prymnesium parvum. Fishes 3, 11. https://doi.org/10.3390/fishes3010011.

Tábora-Sarmiento, S., Patiño, R., Portillo-Quintero, C., Coldren, C., 2022. Air, land, and water variables associated with the first appearance and current spatial distribution of toxic Prymnesium parvum blooms in reservoirs of the Southern Great Plains, USA. Sci. Total Environ. 836, 155567 https://doi.org/10.1016/j.scitotenv.2022.155567.

VanLandeghem, M.M., Farooqi, M., Southard, G.M., Patiño, R., 2015. Associations between Water Physicochemistry and Prymnesium parvum Presence, Abundance, and Toxicity in West Texas Reservoirs. J. Am. Water Resour. Assoc. 51, 471–486. https://doi.org/10.1111/jawr.12262.

Walsh, J.R., Lathrop, R.C., Vander Zanden, M.J., 2017. Invasive invertebrate predator, Bythotrephes longimanus, reverses trophic cascade in a north-temperate lake. Limnol. Oceanogr. 62, 2498–2509. https://doi.org/10.1002/lno.10582.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution (N. Y.) 62, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.

Wisecaver, J.H., Auber, R.P., Pendleton, A.L., Watervoort, N.F., Fallon, T.R., Riedling, O. L., Manning, S.R., Moore, B.S., Driscoll, W.W., 2023. Extreme genome diversity and cryptic speciation in a harmful algal-bloom-forming eukaryote. Curr. Biol. 33, 2246–2259. https://doi.org/10.1016/j.cub.2023.05.003. .e8.

Xia, Z., Barker, J.R., Zhan, A., Haffner, G.D., MacIsaac, H.J., 2021. Golden mussel (Limnoperna fortunei) survival during winter at the northern invasion front implies a potential high-latitude distribution. Divers. Distrib. 27, 1422–1434. https://doi.org/10.1111/ddi.13289.

Xia, Z., Johansson, M.L., Gao, Y., Zhang, L., Haffner, G.D., MacIsaac, H.J., Zhan, A., 2018. Conventional versus real-time quantitative PCR for rare species detection. Ecol. Evol. 8, 11799–11807. https://doi.org/10.1002/ece3.4636.

Yang, N., Hou, X., Li, Y., Zhang, H., Wang, J., Hu, X., Zhang, W., 2023. Inter-basin water diversion homogenizes microbial communities mainly through stochastic assembly processes. Environ. Res. 223, 115473 https://doi.org/10.1016/j.envres.2023.115473.

Zeng, Y., Low, B.W., Yeo, D.C.J., 2016. Novel methods to select environmental variables in MaxEnt: A case study using invasive crayfish. Ecol. Modell. 341, 5–13. https://doi.org/10.1016/j.ecolmodel.2016.09.019.