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ADVANCES IN CLADOCERA RESEARCH

Benchmarking toxic effects on *Daphnia magna* of the *Prymnesium parvum* strain causing the 2022 Oder River fish kill

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Abstract Harmful algal blooms (HABs) caused by *Prymnesium parvum* pose significant threats to aquatic ecosystems, as exemplified by the massive fish kill in the Oder River in 2022. In addition to fish kills, *P. parvum* can affect zooplankton populations that play a crucial role in top-down control of algae. We measured immobilization of *Daphnia magna* to compare the toxicity of the *P. parvum* strain that caused the 2022 Oder fish kill (ODER1, known to produce B-type prymnesins) with two well-studied *P. parvum* strains, UTEX2797 (known to produce A-type prymnesins), and RCC3427 (known to produce C-type prymnesins). *D. magna* neonates were exposed to a range of cell concentrations of the three *P. parvum* strains, and immobility was recorded after 24, 48, and 72 h. Overall, immobilization increased with increasing *P. parvum* cell concentrations and exposure times for all three strains. The ODER1 strain caused 100% immobilization of *D. magna* at a cell concentration of 200,000 cells/mL after 72 h. The two other *P. parvum* strains caused significantly higher immobilization at lower cell concentrations, with 100% immobilization at 25,000 cells/mL after 48 h for UTEX2797 and 10,000 cells/mL after 24 h for RCC3427. Our findings highlight strain-specific toxicity of *P. parvum* on zooplankton. Identifying the dominant prymnesin type of local *P. parvum* populations may be crucial to predict toxic bloom effects on zooplankton communities.

Keywords Haptophyte · Strain-specific toxicity · Zooplankton · Top-down control · Harmful algal blooms

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Introduction

Worldwide, harmful algal blooms (HABs) are increasing in frequency, duration, and intensity, mainly due to eutrophication, climate change, and hydrological changes linked to anthropogenic activities (Feng et al., 2024; Wang et al., 2025). These

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blooms pose major threats to aquatic ecosystems, causing oxygen depletion, habitat degradation, and biodiversity loss (Glibert, 2020; Igwaran et al., 2024). The decomposition of excessive algal biomass from HABs often results in hypoxia, creating dead zones that disrupt aquatic food webs (Glibert, 2020). Some bloom-forming algae can destabilize ecosystem structures by producing potent toxins that harm fish, molluscs, and other aquatic organisms (Burkholder et al., 2018; Igwaran et al., 2024). The economic and societal impacts of HABs are severe (Igwaran et al. 2024; Mancera Pineda et al., 2024), with regional estimates of billions of dollars in annual losses due to lost revenues, healthcare costs, and increased water treatment expenses (Heil & Muni-Morgan, 2021).

Prymnesium parvum, a mixotrophic haptophyte that primarily occurs in marine and brackish waters (Tábora-Sarmiento et al., 2022), is a well-studied HAB-forming species with a global distribution (Lutz-Carrillo et al., 2010). Its blooms have raised significant concern also in freshwater systems, due to their increasing frequency and devastating ecological and economic impact (Roelke et al., 2016; Macêdo et al., 2023). *P. parvum* is known to produce a suite of toxins collectively called prymnesins, which display hemolytic, ichthyotoxic, neurotoxic, and cytotoxic effects, with the largest impact on gill breathing organisms (Manning & La Claire, 2010). Fish are particularly vulnerable to these toxins due to their constant exposure through gill respiration. The toxin is suspected to increase gill permeability, disrupt ion balance, and induce excessive mucus production, ultimately leading to respiratory distress and mass mortality (Ulitzur & Shilo, 1966; Clinton et al., 2021). A large-scale bloom of *P. parvum* in the lower Oder River at the border of Germany and Poland in summer 2022 resulted in the mortality of over 360 tons of fish, mussels, and snails, significantly impacting local fisheries and biodiversity (Free et al., 2023; Szlauer-Łukaszewska et al., 2024). Similar mass fish kills in association with *P. parvum* blooms have been reported in freshwater and brackish ecosystems worldwide, raising concerns about its expanding distribution (Edvardsen & Paasche, 1998; Roelke et al., 2016).

The severity of toxic blooms varies across HAB events and across the *P. parvum* strains involved, as their toxicity is influenced by differences in prymnesin composition. Three major prymnesin types, A, B, and C, have been identified, with varying degrees of ichthyotoxicity (Blossom et al., 2014; Binzer et al., 2019; Anestis et al., 2021). A-type prymnesins are the most potent ichthyotoxins, C-type prymnesins exhibit intermediate toxicity, and B-type prymnesins are generally the least toxic to fish gill (RTgill-W1) and human colon (HCEC-1CT) epithelial cells, based on a molar estimation (Varga et al., 2024). A number of environmental factors such as pH, irradiance/sunlight, temperature, salinity, and nutrient availability impact the growth of *P. parvum* as well as its toxin production (Hill et al., 2020; Medić et al., 2022). Certain strains producing B- and C-type prymnesins, such as strain K0081 from Denmark and strain RCC1436 from France, have been shown to cause high fish mortality in bioassays. Overall, data suggest that toxicity is influenced by both toxin composition and environmental conditions (Blossom et al., 2014; Medić et al., 2022). These variations in toxin production complicate the evaluation and prediction of bloom severity and its ecological consequences.

Prymnesium parvum toxins not only affect fish but also pose a significant threat to zooplankton, impacting their growth, reproduction, and survival (Nejstgaard & Solberg, 1996; Remmel et al., 2011; Witt et al., 2019; Szklarek et al., 2024). Exposure to *P. parvum* has been associated with shifts in zooplankton community structure, favoring taxa that selectively avoid ingesting toxic cells (Remmel et al., 2011; Witt et al., 2019). For example, the rotifers *Brachionus plicatilis* and *Notholca laurentiae* persisted during a *P. parvum* bloom in Lake Koronia, Greece (Michaloudi et al., 2009), whereas the water flea *Daphnia magna,* a strong ecological interactor, appears particularly susceptible (Witt et al., 2019). A recent study documented high *D. magna* mortality in laboratory exposures to *P. parvum* bloom-affected waters preserved from the 2022 Oder River ecological disaster (Szklarek et al., 2024). While these studies document the effects of *P. parvum* on zooplankton, and most have tested responses across different cell concentrations, these experiments typically used a single strain, and none have directly compared toxicity among strains under standardized common garden conditions. As a result, the interactive effects of strain variation and cell concentration remain insufficiently understood. Investigating how these interactions influence zooplankton survival is critical for

assessing the broader ecological consequences of blooms.

The current study aims to characterize strain-specific effects of *P. parvum* at increasing cell concentrations on *D. magna* neonate's mortality, assessed as immobility. Previous studies have reported strain-specific toxicity in fish (Blossom et al., 2014) and differential cytotoxic responses in rainbow trout gill cells and human colon cells, ranking cytotoxic potencies of prymnesin toxin types as A > C > B (Varga et al., 2024). By comparing three *P. parvum* strains, each producing one of the three known prymnesin types**,** we expected UTEX 2797 (A-type) to induce the strongest immobilization, RCC 3427 (C-type) a moderate level, and ODER1 (B-type) the lowest level in *D. magna* neonates under identical exposure conditions. Although physiological differences between *D. magna* and fish/human cell lines may influence sensitivity, we expected prymnesin's disruption of membrane integrity and ion regulation (Ulitzur and Shilo, 1966) to produce similar toxicity patterns in *D. magna*. Our focal strain was the ODER1 strain, a B-type prymnesin producer isolated during the 2022 Oder River bloom that caused extensive fish mortality. We used UTEX 2797 (A-type) and RCC 3427 (C-type) as well-characterized reference strains representing different prymnesin toxin types.

Material and methods

Prymnesium strains and culture

The three *P. parvum* strains used in this experiment originated from different ecosystems and produce different toxin types (Table 1). The strain UTEX2797 originated from the Texas Colorado River at US Hwy 183, Texas, USA, a semiarid region that experiences nutrient enrichment and salinity fluctuations, conditions that frequently support harmful algal blooms in the area (Robertson et al., 2020). This strain is also listed in the UTEX Culture Collection as "UTEX LB 2797" and has previously been cited under this designation (Hill et al., 2020). The Oder strain (ODER1) was isolated from the Oder River in Germany on August 19, 2022, during the massive fish kill (Kuhl et al., 2024). The Oder River is highly regulated and eutrophic and has been affected by salt emissions from coal and ore mining in the upper catchment (Krodkiewska et al., 2022). The strain RCC3427 was collected from Norman Bay off the coast of Wilsons Promontory National Park, Victoria, Australia. This region is characterized by a temperate maritime climate, stable salinity, and moderate nutrient levels with minimal human impact (Young et al., 2023). This strain is also listed in the Rostoff Culture Collection as "UIO55" and "K-0252" and is often cited as "K-0252" (Anestis et al., 2021).

Prior to the experiments, all strains were cultured under identical conditions for two weeks and cell concentrations monitored to ensure they were in the

Table 1 Characteristics of the three strains used in this experiment, including toxin type and origin. Isolation locations are approximations, based on information from culture collections and Kuhl et al. (2024)

Strain name	Toxin type	Origin	Isolation year	Isolation location	Environment
UTEX2797	A	Texas Colorado River at US Hwy 183, Texas, USA	2001 Maintained in the UTEX Culture Collection	30.245552° N, 97.691498° W	Freshwater/Brackish
ODER1	B	Oder River, Germany	2022 Maintained at Leibniz Institute of Freshwater Ecology and Inland Fisheries	52.583881° N, 14.646773° E	Freshwater/Brackish
RCC3427	C	Norman Bay, Australia	1987 (Scandinavian Culture Collection in Copenhagen, now moved to Roscoff Culture Collection in France)	39.04° S, 146.31° E	Marine/Brackish

exponential growth phase. The cells were cultivated in Erlenmeyer flasks (150 mL) containing f/2 media (Guillard & Ryther, 1962) adjusted to 4 ppt salinity using artificial sea water made from dissolving pharmaceutical pure sea salts for marine aquaria in laboratory grade ultrapure water. Cultures were maintained at 20 °C on a gyrorotary shaker (175 rpm) under a 16:8 light/dark photoperiod with a light intensity of 100 µmol photons m^2 s^{-1}.

Daphnia magna clone and culture

The *D. magna* clone Pond28_05 used for the experiment was isolated in 2021 from a rural pond in Müncheberg, Germany (52.5156°N, 14.1263°E). The clone was maintained at 20 °C under a 14:10 light/dark cycle for several generations. Animals were kept at a density of 1 individual per 100 mL in 24 h aged tap water (pH 7.14, specific conductance 864 µS/cm, dissolved oxygen 9.16 mg/L) which provides suitable and stable culture medium for *D. magna*. The medium was refreshed and cultures fed 1×10^5 cells/mL *Acutodesmus obliquus* (equivalent to 1 mg C/L) three times per week. Neonates $\leq$ 24 h old from the third brood were used for the experiments.

Experimental setup

The experimental treatments consisted of the three *P. parvum* strains at six cell concentrations (5,000; 10,000; 25,000; 50,000; 10,0000; and 20,0000 cells/mL, chosen for their ecological relevance to blooms of these strains). For each stock culture, initial cell concentration was determined using a hemocytometer (Alam et al., 2019) and diluted to the desired concentrations using f/2 media. In Texas reservoirs, blooms of *P. parvum* have been documented at 40,000–60,000 cells/mL in Possum Kingdom Reservoir, 80,000–100,000 cells/mL in Lake Granbury Reservoir, and 140,000–170,000 cells/mL in Lake Whitney Reservoir (Roelke et al., 2011). Although the strains responsible for these Texas blooms were not identified and no field cell concentration data exist for RCC3427, these values were used to inform our test concentrations. For ODER1 in the Oder River, cell concentrations were reported in August 2022 at approximately 109,400 cells/mL, peaking at 116,900 cells/mL, and reaching up to 141,000 cells/mL further downstream at Hohenwutzen (Schulte et al., 2022).

D. magna neonates were exposed to the *P. parvum* cell suspensions immediately following dilution from the culture stocks. Each dilution of the three cultures was pipetted into 6-well plates in random order. Each concentration was replicated four times, with each replicate consisting of five *D. magna* neonates in 10 mL of the exposure solution following OECD Test Guideline 202 (OECD, 2004). In total, 78 experimental units were prepared (3 *Prymnesium* strains × 6 concentrations × 4 replicates = 72, plus 6 control replicates [f/2 medium only]). Neonates were not fed during the test period and mortality was monitored at 24, 48, and 72 h by scoring immobility as the absence of movement within 15 s, including antenna activity, and lack of response to a gentle tap on the well as an external stimulus (OECD, 2004). OECD guidelines specify 48 h as the standard endpoint, but we extended observations to 72 h to evaluate longer exposure effects. The experimental plates were maintained on a flat surface under controlled laboratory conditions at 20 °C with a 14:10 h light/dark cycle.

Statistical analysis

All analyses were performed in R software, version 4.3.0 (R CoreTeam, 2024). The effects of *P. parvum* strain, cell concentrations, exposure time, as well as their interactions on *D. magna* immobilization were analyzed using a generalized linear model (GLM) with a quasibinomial distribution and a logit link function in the R base package *stats*. Strains and exposure time were included as categorical predictors, while cell concentration was treated as a continuous predictor. To explicitly compare the *P. parvum* strains, we ran an additional GLM with only strain as a predictor (this was because tests involving RCC3427 produced unreliable estimates due to complete (≈100%) immobilization across certain treatments). Model adequacy was confirmed using Q-Q residual plots and by assessing overdispersion through the dispersion parameter, ensuring that model assumptions were met. Pairwise comparisons between strains and exposure times were conducted using estimated marginal means derived from the GLM via the *emmeans* package (version 1.10.0; Lenth et al., 2021). Plots were produced using the R package *ggplot2* version 3.5.1 (Wickham et al., 2016).

Results

All three *P. parvum* strains caused immobilization in *D. magna* at low cell concentrations (5000–10,000 cells/mL). *P. parvum* strain identity, cell concentration, experimental exposure time, the two-way interaction of strain × concentration, and the three-way interaction of strain × concentration × time, all significantly influenced *D. magna* immobility (Table 2). The overall mean immobilization in the control group was 0% at 24 and 48 h, fully meeting the OECD validity criterion of ≤ 10% immobilization at the end of the 48 h test. Although beyond the OECD test time, 72 h mean control immobilization was 6%, which is still below 10% and therefore does not compromise interpretation of treatment effects. The control group was excluded from the post hoc comparisons due to complete absence of mortality at 24 h and 48 h, and minimal mortality at 72 h, which would result in complete separation and unstable parameter estimates in the model**.**

Overall mean immobilization across all time points and concentrations was highest for the C-type strain RCC3427 (mean immobilization 97%, Fig. 1c), followed by the A-type strain UTEX2797 (mean immobilization 84%, Fig. 1a), and was the lowest for the B-type strain ODER1 (mean immobilization 36%, Fig. 1b). Post hoc comparisons confirmed that all three *P. parvum* strains caused significantly higher immobilization of *D. magna* compared to the control (all $p < 0.05$). Among strains, ODER1 caused significantly lower immobilization than UTEX2797 (estimate = -2.30 ± 0.27 SE, z = − 8.64, $p < 0.0001$; logit scale) and RCC3427 (estimate = -4.09 ± 0.48 SE, z = –8.57, $p < 0.0001$). In addition, RCC3427 caused significantly higher immobilization than UTEX2797 (estimate = 1.79 ± 0.50 SE, z = 3.60, $p = 0.0018$). Mean immobilization increased with increasing cell concentration and over time for all three strains (Fig. 1a–c, Table 2). However, 100% immobilization was observed at different time points and cell concentrations for all three strains. For strain UTEX2797, 100% immobilization was observed at 50,000 cells/mL after 24 h, and at 25,000 cells/mL after 48 h and 72 h (Fig. 1a). At 200,000 cells/mL of the ODER1 strain, 55% immobilization occurred after 24 h, 70% after 48 h, and 95% after 72 h (Fig. 1b). For strain RCC3427, 100% immobilization was observed at 10,000 cells/mL after 24 h and 85% immobilization at 5000 cells/mL after 48 and 72 h (Fig. 1c). Pairwise comparisons among strains at each time point showed that UTEX2797 caused significantly higher immobilization than ODER1 at 24, 48, and 72 h; estimable results are presented in Supplementary Material 1.

Table 2 Results of the type II analysis of deviance for the generalized linear model on the effects of strain, cell concentration, exposure time, and their interactions on *D. magna* immobilization

Effect	LR Chisq	df	p
Strain	576.80	3	< 0.0001***
Concentration	127.31	1	< 0.0001***
Time	33.63	2	< 0.0001***
Strain: concentration	50.10	2	< 0.0001***
Strain: time	3.52	6	0.741
Concentration: time	3.84	2	0.147
Strain: concentration: time	15.22	4	0.004**

Significance: *** $p < 0.001$, ** $p < 0.01$

Discussion

The three studied *P. parvum* strains caused high immobilization in *D. magna* at relatively low cell concentration, with immobilization increasing consistently with cell concentration and experimental exposure time. Toxicity was also highly strain-specific, with RCC3427 causing the highest and ODER1 causing the lowest mortality in *D. magna*. Although this study did not analyze prymnesin types and concentrations produced by these strains, prior research has identified the ODER1 strain as producing B-type prymnesins, whereas strains UTEX2797 and RCC3427 are linked to A- and C-type prymnesins, respectively (Binzer et al., 2019; Kuhl et al., 2024). These prymnesins differ in their ichthyotoxicity and cytotoxicity, with A-type being the most potent, C-type exhibiting intermediate toxicity, and B-type being the least toxic (Blossom et al., 2014; Rasmussen et al., 2016; Varga et al., 2024). In our study, the RCC3427 and UTEX2797 strains both exerted strong impacts on *D. magna*, with RCC3427 being more toxic, and the ODER1 strain being markedly less toxic. While our observations thus partially align with the expected toxicity ranking (A > C > B), we cannot unequivocally link the observed differences to toxin

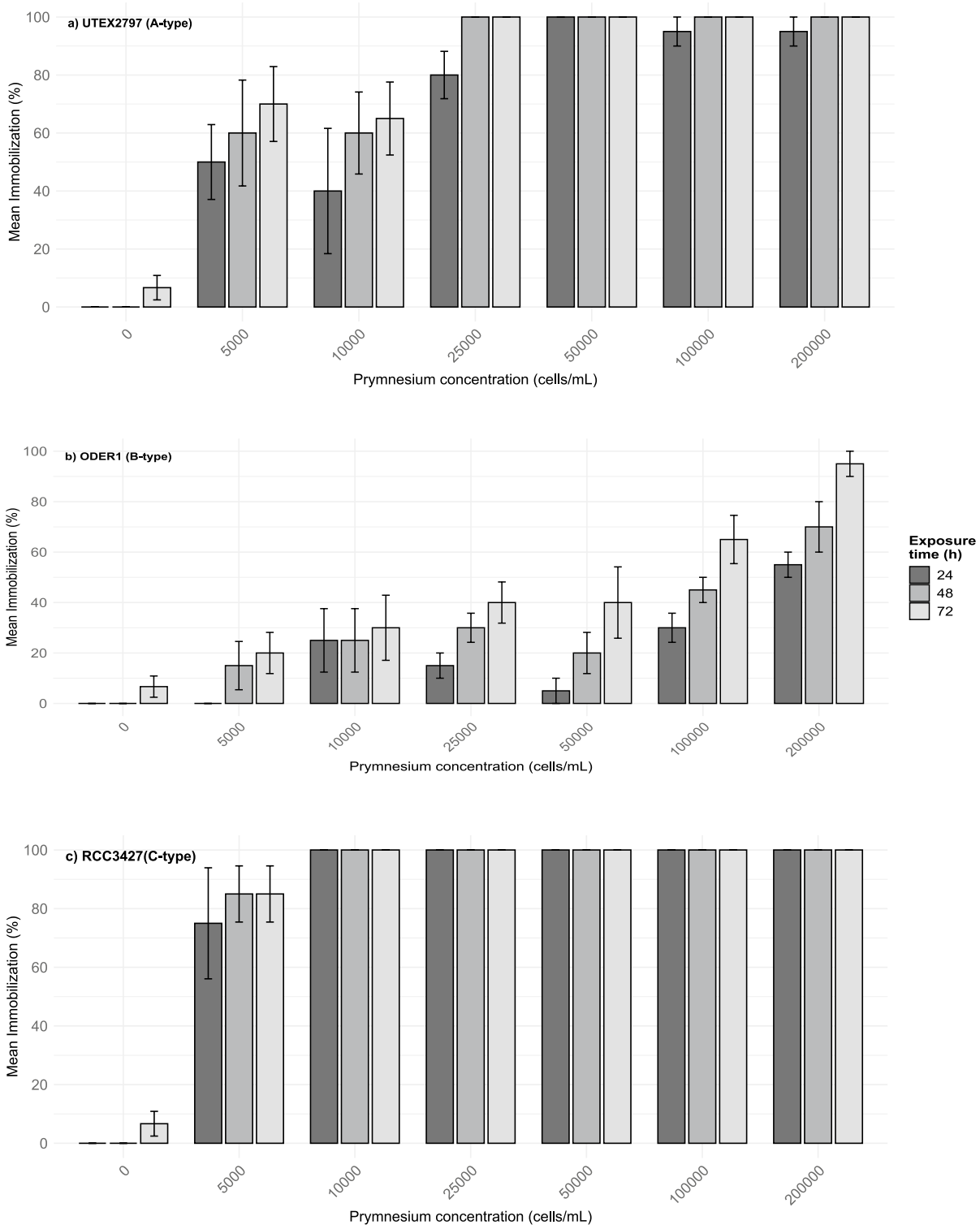


Fig. 1 Mean immobilization (%) of *D. magna* exposed to three *P. parvum* strains: **a** UTEX2797, **b** ODER1, and **c** RCC3427 after 24, 48, and 72 h. Each bar represents mean immobilization ± standard error. Each condition was tested in four replicate wells, with five neonates per well

type, as we tested only one strain per type (Blossom et al., 2014; Varga et al., 2024).

Variations in toxicity within the same prymnesin type have been reported in previous studies. For instance, while our study, in line with expectations, identified the B-type prymnesins producing ODER1 strain as the least toxic, Blossom et al. (2014) reported that strain K0081, which is also producing B-type prymnesins, was among the most toxic to rainbow trout (*Oncorhynchus mykiss*) in a comparative analysis that also involved strains RCC191 and RCC1436 (C-type prymnesins), UTEX2797 (A-type prymnesins), and K0374 (B-type prymnesins)**.** Strains classified under the same toxin type can vary substantially in their prymnesin content and associated toxicity. Medić et al. (2022) compared two B-type prymnesin producing strains, K-0081 and K-0374, and showed that under high irradiance (550 µmol photons m^{-2} s^{-1}), the cellular prymnesin quota in K-0081 was approximately 30-fold higher than in K-0374, while the maximum production rate was only about three-fold higher. This difference highlights that *P. parvum* toxicity goes beyond simple prymnesin classification and depends critically on toxin abundance influenced by environmental conditions.

Moreover, evolutionary familiarity likely plays a key role in shaping *D. magna*'s response to *P. parvum* (Lange et al., 2023). Populations lacking a coevolutionary history with specific *P. parvum* strains may suffer elevated mortality due to the absence of adaptive defences. Although no direct evidence yet exists for such dynamics in the *Prymnesium–Daphnia* system, the *Daphnia–Microcystis* system has demonstrated that genotype-by-genotype interactions, i.e. specific combinations of *Daphnia* clones and *Microcystis* strains, significantly influence mortality outcomes, reflecting local adaptation and a geographic mosaic of coevolution (Lemaire et al., 2012).

The least toxic in our assay, the ODER1 *P. parvum* strain, still caused *D. magna* mortality at cell concentrations that are low compared to the cell concentrations observed in blooms. During the 2022 Oder fish kill, *P. parvum* concentrations averaged approximately 109,400 cells/mL and peaked at 116,900 cells/mL, while even higher concentrations of up to 141,000 cells/mL were measured further downstream at Hohenwutzen (Schulte et al., 2022). As a result, the *P. parvum* bloom likely caused a strong impact on the zooplankton community in the Oder River, but this cannot be verified due to the lack of zooplankton samples prior to and after the bloom.

Strain UTEX2797, which caused 100% immobilization in *D. magna* at 50,000 cells/mL after 24 h in our study, did not cause mortality to microalgae *Teleaulax acuta* even at 100,000 cells/mL (Blossom et al., 2014). However, this strain was very toxic to trout, causing 100% mortality of the fish at just 25,000 cells/mL (Blossom et al., 2014). Although previous studies documented *P. parvum* blooms without specifying strain identity, we believe that UTEX2797 is one of the strains responsible for *P. parvum* blooms in Texas, e.g., in Lake Whitney, Lake Granbury, and Lake Possum Kingdom, based on its origin in the Texas Colorado River and its prevalence in Texas-focused research (Barkoh et al., 2010; Roelke et al., 2011). These blooms have led to widespread fish kills, with reported cell densities reaching up to 170,000 cells/mL in Lake Whitney (Roelke et al., 2011). In the case of strain RCC3427, specific bloom history and natural cell concentration data is not readily available. Its high toxicity at relatively low cell densities (<5,000 cells/mL) in our laboratory experiments suggests that its proliferation in natural environments could pose substantial ecological risks, even before reaching the high cell concentrations typically associated with *P. parvum* blooms.

While our study provides valuable insights into the toxicity of the ODER1 strain for *D. magna*, benchmarking it against the toxicity of two other strains (RCC3427 and UTEX2797), further investigation is required to fully understand the impact of *P. parvum* on zooplankton. Our experiments were conducted under controlled laboratory conditions, which allowed us to show the effects of different strains on *D. magna* but cannot fully capture the natural complexity of *P. parvum* bloom dynamics. In natural systems, *P. parvum* bloom toxicity is shaped by microbial interactions, nutrient availability, cell densities, water chemistry fluctuations, and hydrodynamic conditions (Medić et al., 2022). This might lead to complex dynamic changes in toxicity, which we have reduced to a single condition. Moreover, only one strain per prymnesin type was tested, which limits our ability to generalize toxicity patterns across prymnesin types. Future studies incorporating multiple strains per type will be essential to validate these trends.

Additionally, our experiment was conducted at 4 ppt salinity, a level favorable for *P. parvum* growth

and toxin production. Although immobilization in control treatments was low, we cannot fully exclude the possibility that salinity (4 ppt) interacted with toxin exposure to affect *D. magna* immobilization. We did not include a freshwater (0 ppt) treatment because *P. parvum* cannot grow or produce toxins under freshwater conditions (Larsen et al., 1998), making such exposures ecologically irrelevant. Third, we used *D. magna* as a model system, but the Oder River zooplankton hosts mostly small to very small zooplankton taxa at relatively low densities (Kahsay et al.,in prep). Finally, we only used one clone of *D. magna* for our assay. Genotype-by-genotype interactions, where different *D. magna* clones exhibit varying resistance or sensitivity that can be *P. parvum* strain-dependent might influence bloom outcomes in natural systems. Ideally, such a study on *Daphnia–Prymnesium* interactions should involve both multiple *Daphnia* clones as well as a wider set of *Prymnesium* strains than used in the current study.

Our results indicate that although the ODER1 strain was the least toxic among those tested, it still caused substantial immobilization in *D. magna* at cell concentrations below those typically encountered during natural blooms. This finding highlights that even strains with moderate toxicity can cause serious ecological damage, disrupting zooplankton populations and initiating potential trophic cascades. In broader ecological contexts, *P. parvum* blooms are known to impair or eliminate critical zooplankton grazers, which reduces grazing pressure on phytoplankton populations. This disturbance can foster unchecked algal proliferation, alter nutrient cycling, diminish water clarity, and disrupt energy flows across trophic levels, thereby destabilizing aquatic ecosystems. Recognizing the ecological risks of even moderately toxic *P. parvum* strains is therefore essential for predicting and mitigating the broader impacts of *P. parvum* blooms on freshwater ecosystems.

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Data availability The data supporting the findings of this study are available upon request from the corresponding author.

Declarations

Conflict of interest The authors declare that they have no competing financial or non-financial interests related to this work.

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