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Temperature variability regulates the interactive effects of warming and pharmaceutical on aquatic ecosystem dynamics

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ABSTRACT

Climate warming and pharmaceutical contaminants have profound impacts on population dynamics and ecological community structure, yet the consequences of their interactive effects remain poorly understood. Here, we explore how climate warming interacts with pharmaceutical-induced boldness change to affect aquatic ecosystems, built on an empirically well-informed food-chain model, consisting of a size-structured fish consumer, a zooplankton prey, and a fish predator. Climate warming is characterized by both daily mean temperature (DMT) and diurnal temperature range (DTR) in our model. Results show that DMT and high levels of species' boldness are the primary drivers of community instability. However, their interactive effects can lead to diverse outcomes: from predator collapse to coexistence with seasonality-driven cycles and coexistence with population interaction-driven cycles. The interactive effects are significantly modulated by daily temperature variability, where moderate DTR counteracts the destabilizing interactive effects by increasing consumer reproduction, while large temperature variability considerably reduces consumer biomass, destabilizing the community at high mean temperatures. Our analyses disentangle the respective roles of DMT, DTR and boldness in mediating the response of aquatic ecosystems to the impacts from pharmaceutical contaminants in the context of climate warming. The interactive effects of the environmental stressors reported here underscore the pressing need for studies aimed at quantifying the cumulative impacts of multiple environmental stressors on aquatic ecosystems.

1. Introduction

Climate warming and pharmaceutical contaminants are two major threats to organisms, as both can directly induce a series of non-lethal to lethal impacts on individual organisms, particularly in aquatic communities (Sokolova & Lannig, 2008; Noyes et al., 2009; Hooper et al., 2013; Noyes & Lema, 2015; Verberk et al., 2016; Dinh et al., 2022). Previous studies have demonstrated that elevated temperatures can affect the structure and stability of populations and communities, for instance, by skewing population size distributions (Osmond et al., 2017; Forster et al., 2012; Ohlberger, 2013; Lindmark et al., 2022) through altering organisms' physiological rates (e.g., attack rate, metabolism rate, Pörtner & Farrell, 2008; Neuheimer et al., 2011; Lefevre et al., 2017). At the ecosystem level, these alterations manifest as changes in species' community structure (Zhang et al., 2017; Lindmark et al., 2019) and geographical distribution (Durant et al., 2007; Hannesson, 2007; Pinsky et al., 2013).

While much focus of climatic impacts on populations and ecological communities are being given to average temperature (e.g., daily mean temperature, abbreviated hereafter as DMT) (Ohlberger, 2013; Poloczanska et al., 2013; Pecl et al., 2017; Lindmark et al., 2019), temperature variability (e.g., diurnal temperature range, abbreviated hereafter as DTR) has received relatively less attention (Dee et al., 2020). However, empirical and theoretical studies have demonstrated that temperature variability could have a profound impact on both individuals and populations (Vasseur et al., 2014; Dee et al., 2020). In certain cases, its effects may even exceed the effects of the average temperatures (Helmuth et al., 2014) by for instance suppressing reproductive cycles (Rideout et al., 2005), leading to reproduction interruptions. Therefore, understanding the climatic consequences for ecological communities requires considering both temperature means and variability and their interactive effects.

In addition to climatic stressors, accumulating empirical evidence shows that a variety of pharmaceutical contaminants (e.g., oxazepam

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and fluoxetine, types of antidepressants) can be commonly found in aquatic systems affecting organisms by altering fish boldness (a behavioral trait) (Brodin et al., 2013; Saaristo et al., 2018) or by depressing organisms' physiological rates (Grzesiuk et al., 2023). Boldness, here defined as an animal's likelihood of risk-taking (White et al., 2013), is a key personality trait in animals (Réale et al., 2007). It is directly linked to foraging rates (positively) and predator avoidance (negatively), which not only influences species invasion success (Sales et al., 2023), but also has elusive effects on species body length, population biomass, reproduction and even ecosystem state shifts (Wang et al., 2021). For example, it has been documented that pharmaceutical exposure to fish (*Perca fluviatilis*) reduced its anti-predator behavior, and consequently increased its mortality (Brodin et al., 2013, 2014). Moreover, a recent study demonstrated that fluoxetine decreased the feeding rate of crucian carps on the herbivore *Daphnia magna*, thereby reducing predation mortality of *Daphnia magna* and ultimately increasing *Daphnia magna* population abundance (Grzesiuk et al., 2023). These examples suggest that pharmaceutical-induced boldness changes have a great potential to affect population dynamics, which can lead to a substantial biomass decline in fish populations (Kidd et al., 2014) and may further induce changes in ecosystem structure (Wang et al., 2021).

Despite the growing insights of climate warming and pharmaceutical contaminant effects on ecological populations and communities, the two environmental stressors are usually studied independently. This leads to a knowledge gap regarding how these two ubiquitous environmental stressors interactively affect community dynamics, which is particularly relevant to ecosystem management aiming at minimizing the adverse effects of multiple human activities that act simultaneously on ecosystems. Empirical evidence has already illustrated their joint effects, for instance, by reducing *Daphnia*'s reproductive success and population growth due to the synergistic effects of fluoxetine and DTR in a laboratory environment (Barbosa et al., 2017). Moreover, a recent field study demonstrated that perch exposed to oxazepam experienced increased anti-predator behavior rather than previously anticipated reduced anti-predator behavior in a lake experiment with fluctuating temperatures (Fahlman et al., 2021). While several possible reasons (e.g., shoaling, spatial and temporal scales) may account for this contrasting observation, the authors argued that the elusively interactive effects between temperature and pharmaceutical-induced boldness change may explain this.

In this study, we investigate how the interplay between pharmaceutical-induced boldness change, and climate warming (i.e., DMT and DTR) affects population/community dynamics. We employ an empirically well-calibrated, size-structured food chain model as a representative of a structurally simple aquatic ecosystem, where a consumer species (roach, *Rutilus rutilus*), feeding on a zooplankton species, is simultaneously fed upon by a predator species (Eurasian perch, *Perca fluviatilis*). We aim at answering two questions: (1) What are the interactive effects between DMT, DTR, and pharmaceutical-induced change in species' boldness on species coexistence and food chain stability? (2) What are the mechanisms underlying changes in community stability and its effects (positive and negative) on population biomass? The analyses presented in this study improve the understanding of the complex and interactive nature of anthropogenic forcing on aquatic ecosystems, and its implications for species population dynamics and coexistence.

2. Methods

We employed a well developed size-structured food chain model developed by de Roos and Persson (2002), which was extended in our previous work (Wang et al., 2021) to explicitly account for the impacts of environmental stressors (e.g., pharmaceutical contaminants) on species' boldness. Here, we continued to update it by integrating DMT and DTR into organisms' physiological rates in an analogous manner to previous studies (i.e., Lindmark et al., 2019; Dee et al., 2020). Furthermore, taking into account the factor that the consumer species exhibits a seasonal growth (Wyatt & Kennedy 1988; Velasco et al., 1989), and a seasonal reproduction (Hellawell, 1972; Mann, 1973; Papageorgiou, 1978; Velasco et al., 1989), we replaced the continuous reproduction (i.e., reproduction throughout the whole year) in above model by a seasonal reproduction. In the present work, we focused only on the growing season (including the reproductive period) for the reason being that biological activity can be negligible outside the growing season, and thus took the state of the system at the start of a growing season to be identical to that at the end of the previous one (Persson et al., 1998; Claessen et al., 2000).

The population dynamics of the size-structured food chain model with a seasonal reproduction (hereafter referred as seasonal reproduction model) in each growth season (150 days from $t_{start} = 0$ to $t_{end} = 150$ day) are governed by the following system of differential equations:

$$\begin{cases} \dfrac{\partial c(t,x)}{\partial t} + \dfrac{\partial (g(R,x)c(t,x))}{\partial x} = -\mu(x,R,P)c(t,x), & (1.1) \\ g(R,x_b)c(t,x_b) = \begin{cases} \displaystyle\int_{x_j}^{x_m} b(R,x)c(t,x)dxdt, t_{start} \le t \le t_{mid} \\ 0, t_{mid} \le t \le t_{end} \end{cases} & (1.2) \\ \dfrac{dR}{dt} = \rho\varepsilon_r(T_{env})(K-R) - \displaystyle\int_{x_b}^{x_m} \frac{\tau A(x)R}{1+\tau A(x)H(x)R} c(t,x)dx, & (1.3) \\ \dfrac{dP}{dt} = \left(\varepsilon \dfrac{\tau(a\varepsilon_a(T_{env}))B}{1+\tau(a\varepsilon_a(T_{env}))(T_h\varepsilon_h(T_{env}))B} - \delta\varepsilon_u(T_{env}) \right) P, & (1.4) \end{cases}$$

where the partial differential equation (1.1) describes the dynamics of the consumer species $c(t, x)$ by accounting for the ontogenetic growth in body size x , and the nonlocal boundary condition (eq.1.2) which describes the reproduction flux governed by the size- and resource-dependent birth rate of adult consumers. Here, reproduction in each growth season takes place in a period of 60 days from $t_{start} = 0$ to $t_{mid} =$ 60 day. Equations (1.3) and (1.4), respectively, describe the population dynamics of resource (R) and predator species (P). The resource species follows a semi-chemostat growth with a constant turnover in the absence of consumer species (de Roos et al., 1990), but its growth rate is reduced by predation of consumer species of all sizes in a manner of the Holling type II functional response. The predator species feeds only on small consumer individuals of sizes between x_b and x_v (i.e., vulnerable individuals, de Roos & Persson 2002), the total biomass of which is represented as B. Its population growth is of the Lotka-Volterra type with a Holling type II functional response and a temperature-dependent mortality. Detailed descriptions of the consumer life history are specified below with life-history equations and model parameters being summarized in Table 1 and 2, respectively.

Consumer individuals are born at size x_b, mature at size x_j and grow to the maximal size x_m under a sufficient food condition. Individual life history traits are featured by growth rates $g(R, x)$, mortality rates $\mu(R, P, x)$ and birth rates $b(R, x)$, all of which vary with individual body size and are dynamically dependent on resource biomass. The intake rate of a consumer species is the Holling type II functional response (N5 in Table 1) with a resource attack rate varying with body size in a form of dome shape that peaks at the body size w_{opt} (N4) (Persson et al., 1998). Handling time of a prey varies allometrically with body size (N11). Food is being assimilated with an efficiency ε_R and a fraction (1-κ) of the assimilated energy is used for gonad development if individuals are immature, and for offspring reproduction if individuals are mature (N7) (Kooijman, 1993). The remaining energy is first used to pay the maintenance costs which are composed of the basal and active metabolic costs (N3) (Andersen et al., 2018), and the surplus energy is then used for the growth of body size (N6). However, in case that maintenance costs fail to be covered, starvation mortality occurs (N9). In addition to the starvation mortality, consumer individuals further suffer from a constant natural background mortality, and a density-dependent mortality, which is only for the vulnerable juvenile consumers.

Table 1
The life-history forms of the consumer.

Interpretation	Equation	Num
Body mass	$w(x) = \beta x^3$	N1
Vulnerable biomass	$B = \int_{x_b}^{x_v} w(x)c(t,x)dx$	N2
Maintenance costs	$M(x) = \varepsilon_x(T_{env})\rho_s w(x)^{\rho_1} + \varepsilon_x(T_{env})\tau\rho_f w(x)^{\rho_2}$	N3
Attack rate	$A(x) = A_{\max}\varepsilon_a(T_{env})\left[\frac{w(x)}{w_{opt}}\exp\left(1-\frac{w(x)}{w_{opt}}\right)\right]^{\alpha}$	N4
Food intake rate	$F(x,R) = \varepsilon_R\frac{\tau A(x)R}{1+\tau A(x)H(x)R}$	N5
Growth rate in length	$g(x,R) = \begin{cases}\frac{1}{3\beta x^2}[\kappa F(x,R) - M(x)] & \kappa F(x,R) \geq M(x)\\ 0 & otherwise\end{cases}$	N6
Birth rate	$b(x,R) = \begin{cases} c_r(1-\kappa)F(x,R)w(x_b)^{-1} & x \geq x_j \\ 0 & otherwise\end{cases}$	N7
Mortality rate	$\mu(x,R,P) = \mu_0 + \mu_s + \mu_p$	N8
Starvation mortality	$\mu_s(x,R) = \begin{cases} s[M(x) - \kappa F(x,R)] & \kappa F(x,R) < M(x)\\ 0 & otherwise\end{cases}$	N9
Predation mortality	$\mu_p = \frac{\tau a\varepsilon_a(T_{env})P}{1+\tau(\varepsilon_a(T_{env})a)(T_h\varepsilon_h(T_{env}))B}$	N10
Digestion time	$H(x) = \varepsilon_h(T_{env})\xi_1 w(x)^{\xi_2}$	N11
Boldness function	$\tau = \begin{cases}\tau_J \in [0.38,1), & x_b \leq x \leq x_j,\\ \tau_A = 0.38, & x_j < x \leq x_m\end{cases}$	N12
Arrhenius correction	$\varepsilon_i(T_{env}) = e^{E_i\frac{T_{env}-T_0}{kT_0T_{env}}}\ i = a,h,r,x,u$	N13

Two parameters (τ and T_{env}) were added to the model to account for the impacts from the environmental stressors, which in this study are: pharmaceutical contaminants (i.e.,τ) and climate warming (i.e., DMT and DTR). The boldness parameter (τ) was first introduced by Andersen et al. (2018) and then adopted by Wang et al. (2021) to describe anthropogenic forcing (e.g., fishing and pharmaceutical contaminants)-induced boldness shifts in animals that could affect individual life-history traits (Arlinghaus et al., 2015, 2017). Mathematically, boldness is quantified by the single variable parameter τ (Andersen et al., 2018), which conceptually is the fraction of time (e.g., day) that a species uses for food searching activities. It varies from 0 to 1 where the larger this parameter, the higher the active metabolic costs (N3), and the higher the predation mortality (N10). At $\tau = 0$, individuals hide themselves in a refuge habitat and thus spend no time for searching food, and there is no active metabolic cost (N3) nor predation mortality (N10). Since the behavioral assays (e.g., locomotor activity and social interaction) of experimental studies demonstrated that juvenile individuals are usually more vulnerable to pharmaceutical exposure (Praskova et al., 2011; Dong et al., 2022), we considered here boldness changes induced by pharmaceutical contaminants only in juvenile consumer individuals (N12). In our previous study, an average level of boldness was estimated to be 0.38 under natural environmental conditions (Wang et al., 2021). We used this value as the default level of consumer boldness, but we also explored other levels of boldness (e.g., lower/higher than 0.38) induced by pharmaceuticals (e.g., Flutamide and Fluoxetine), which could virtually vary markedly away from the default value as indicated by recent laboratory studies (Brodin et al., 2013, 2017; Dzieweczynski et al., 2016, 2018; Vignet et al., 2015; Fig. S1).

In analogy to previous work (i.e., Lindmark et al., 2019; Dee et al., 2020), we further introduced a temperature parameter (T_{env}) to the three species in the model. This was achieved by multiplying their physiological rates with the Boltzmann-Arrhenius function (N13), where T_{env} indicates the environmental temperature, T_0 the reference temperature (8 °C), k the Boltzmann's constant and E_i the activation energy rate. The subscript indices i in the activation energy, respectively, indicate the attack rate E_a, the handling time of consumer E_h, the intrinsic growth rate of resource E_r, the metabolism cost E_x, and the predator mortality E_u. The environmental temperature T_{env} is described by a sinusoidal progression during daytime and a decreasing exponential curve during nighttime (eq. (2) (Fig. S2), depending on DMT and DTR (i.e., the maximal daily temperature (T_{max}) − the minimal daily temperature (T_{min})). DMT varies from 8 to 13 °C (Fahlman et al., 2021), and DTR from 0 to 6 °C based on empirical measurements from Northern Europe lakes (Fig. S3), with the sunrise time at t_{rise} (6:00), the sunset time at t_{set} (18:00), the day length D (12 h), the night length N (12 h), the time duration between solar noon and maximum air temperature p (1.5 h) and the nocturnal time constant λ (12 h) (Paaijmans et al., 2010)

$$\begin{cases} T_{env} = (DMT - \frac{DTR}{2}) + DTR\sin[\pi(t-12+D/2)/(D+2p)], & t_{rise} \leq t \leq t_{set}, \\ T_{env} = \frac{DMT - \frac{DTR}{2} - DMT\exp(-N/\lambda) + \frac{DTR}{2}\exp(-(t-t_{set})/\lambda)}{1-\exp(-N/\lambda)}, & t_{set} \leq t \leq t_{rise}. \end{cases} \quad (2)$$

Note that since we focus on the population dynamics during the growing seasons of fish species, we thus assume that the above mentioned three parameters (DMT, DTR and τ) are all constant during these seasons.

We numerically studied the interactive effects of boldness change (τ) and climate warming (DMT and DTR) on the food chain dynamics (Eq.1), using Matlab 2020. To this end, we ran the model (1) for

Table 2
Model parameters.

Symbols	Value	Unit	Interpretation
x_b	7	mm	Length at birth[a]
x_v	27	mm	Maximal length vulnerable to predator[a]
x_j	110	mm	Length at maturation[a]
x_m	300	mm	Maximal length[a]
μ_0	0.01	d^{-1}	Background death rate[a]
β	9.0×10^{-6}	g mm^{-3}	Proportionality of length to body size[a]
ρ	0.1	d^{-1}	Intrinsic growth rate of resource[a]
K	0.0003	g $liter^{-1}$	Resource carrying capacity[d]
ε_R	0.6	—	Conversion efficiency[c]
ε	0.01	—	Predator reproduction efficiency[d]
a	3.8×10^5	liter d^{-1}	Attack rate of predator[d]
T_h	0.175	d g^{-1}	Handing time of Roach[d]
δ	0.01	d^{-1}	Predator mortality[a]
ξ_1	5	d $g_2^{(1+\xi}$	Allometric constant in handing time function[b]
ξ_2	−0.8	—	Allometric exponent in handing time function[b]
ρ_1	0.77	—	Allometric exponent in background metabolic cost[d]
ρ_2	0.77	—	Allometric exponent in active metabolic cost[d]
ρ_s	0.033	$g_1^{(1-\rho}$ d^{-1}	Allometric constant in background metabolic cost[d]
ρ_f	0.033	$g_2^{(1-\rho}$ d^{-1}	Allometric constant in active metabolic cost[d]
α	0.6	—	Allometric exponent in pelagic attack rate[b]
A_{max}	1.5×10^5	liter d^{-1}	Maximum pelagic attack rate[b]
w_{opt}	50	g	Body size with maximum pelagic attack rate[b]
κ	0.7	—	Allocation coefficient[c]
c_r	0.5	—	Efficiency offspring reproduction[c]
s	1	d	Proportionality constant of starvation mortality rate[b]
k	8.62×10^{-5}	—	Boltzman's constant[c]
E_a	0.38	—	Activation energy of attack rate[e]
E_h	−0.26	—	Activation energy of handling time[e]
E_r	0.84	—	Activation energy of intrinsic growth rate[e]
E_x	0.69	—	Activation energy of metabolism[e]
E_u	0.45	—	Activation energy of predator mortality[f]
T_0	8	°C	Reference temperature
t_{end}	150	d	The period of growth season
t_{mid}	60	d	The end of reproduction
t_{start}	0	d	The beginning of reproduction

[a] de Roos and Persson (2002).
[b] de Roos and Persson (2001).
[c] Claessen and de Roos (2003).
[d] Wang et al. (2021).
[e] Binzer et al. (2016).
[f] Lindmark et al. (2019).

sufficient long time (i.e., 20000 days) such that we could ignore the transient dynamics for all considered combinations of τ, DMT and DTR in the present work. The ultimate states are dynamically fluctuating states due to the presence of DTR, but can vary substantially in terms of amplitudes, depending on the intensity of stressors (Fig. S4). Given the fluctuating states, community stability was measured by the amplitude variation of time-series solutions, where a larger amplitude indicates more unstable dynamics (Wang et al., 2014). Population characteristics (e.g., population biomass, growth rate, and reproduction rate) were obtained by averaging these characteristics based on the last 10 % of the simulated time steps.

Our model was validated by comparing modeled biomass change of juvenile perch exposed to pharmaceutical contaminants in the presence of a predator (Pike) in a semi-natural experiment (Lagesson et al., 2018) (Fig. S5). The results show that our model is able to reasonably foresee observed increased biomass for fish with moderate temperature fluctuation in a predator environment as well as with pharmaceutical exposure, and this observation appeared to be fairly robust even for a small perturbation with respect to the key physiological parameters of species, confirmed through a sensitivity parameter analysis (Fig.S6).

3. Results

3.1. Interactive effects of warming and contaminants on community stability

To examine how species coexistence and community stability vary with intensity of environmental stressors, climate warming (DMT and DTR), and pharmaceutical-induced boldness change (τ), we conducted simulations with varying parameters for these stressors, using a size-structured food chain model (Fig. 1). Within the parameter space, spanned by DTR and the boldness of juvenile consumers (Fig. 1A & B), small boldness is detrimental to species coexistence by promoting predator collapse, but intermediate levels of boldness benefit species coexistence (Fig. 1A). Moreover, species generally coexist either in seasonality-driven cycles (SDCs) with a period coincident with that of the growing season or in population interaction-driven cycles (PIDCs) (Fig. S4) with a period being longer than the growing season, the latter of which is more favored at high DMT (Fig. 1B). Similar observations occur when turning to the parameter space, spanned by DTR and DMT (Fig. 1C & D). Overall, community stability is primarily determined by DMT and boldness, and marginally affected by DTR, but the impacts of DTR on community biomass are remarkable, compared to DMT and boldness. Note in our analysis that both DTR and boldness varied independently from DMT, but nevertheless we have also explored three types (linear and nonlinear) of temperature-dependent boldness and temperature-dependent DTR, and found that our findings remain robust (Appendix S3).

3.2. Effects on population biomass and individual life history

At the population level, our results show biomass changes in consumer species under various combinations of climate warming intensity (DMT and DTR) and pharmaceutical-induced boldness change (Fig. 2). The results indicate that low levels of boldness and DMT are generally detrimental to consumer biomass, particularly at a high DTR level (Fig. 2C), whereas high levels of boldness and DMT promote consumer biomass, particularly at a low DTR level (Fig. 2A). Interestingly,

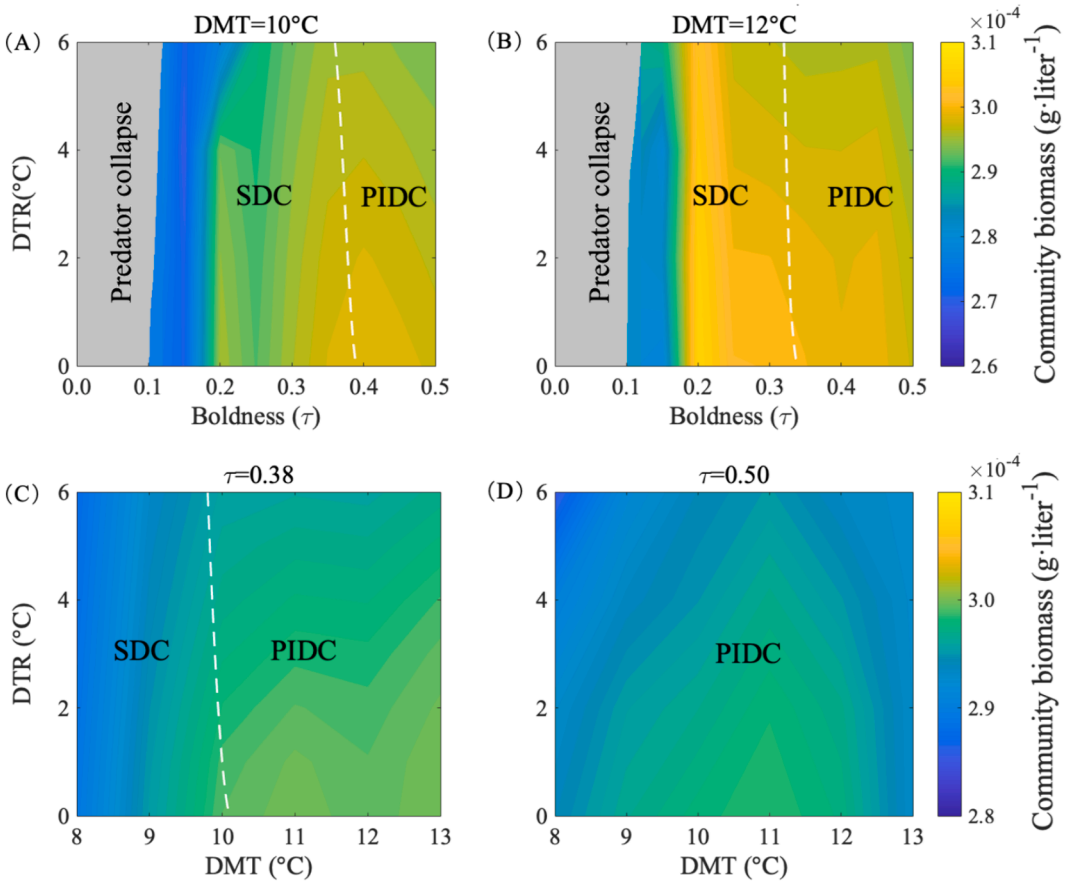

Fig. 1. Effects of the juvenile consumer boldness (panels A and B), the DMT (panels C and D), and the amplitude of DTR on community biomass (colorbar) are examined to determine community states that arise: predator collapse and species coexistence, and whether the coexistence state is in seasonality-driven cycles (SDC) with a period of 150 days or in population interaction-driven cycles (PIDC) with a period $>$ 150 days.

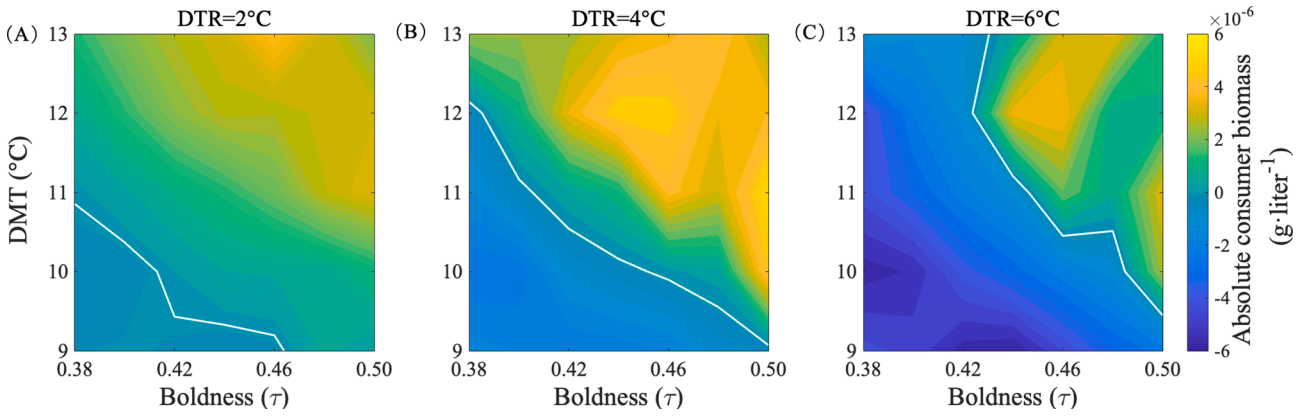

Fig. 2. Consumer biomass with increasing DTR relative to consumer biomass when DTR=0. The absolute change in biomass, expressed as plus/minus values, indicates the positive and negative contribution of DTR to the consumers. The white lines represent the zero contour lines, where areas above them indicate positive effects while areas below them negative effects. The impacts of DTR on the absolute consumer biomass at particular combinations of DMT and τ are exhibited in Fig. S9.

compared to biomass change at the community level, biomass change is more obvious at the population level, indicating that a high sensitivity of populations to warming and boldness change.

To shed light on the cascading effects of environmental stressors on species biomass, we looked at the relative changes in biomass of the three species types (Fig. 3), relative to the case where DTR=0. In general, a large DTR depresses the population biomass of consumers and predators, leading to increased resource biomass consequently, whereas a small DTR may benefit the population biomass of consumers and predators, particularly at high levels of boldness (Fig. 3B & C). This observation is even more evident at a high DMT (Fig. 3C).

Using the scenario of panel C in Fig. 3, we assessed the biomass changes for different consumer stages (e.g., the absolute proportion of vulnerable vs. invulnerable juveniles and adults) with increasing DTR (Fig. 4). Results show that the increased consumer biomass (stippled line) in Fig. 3 is mainly due to increased biomass of invulnerable individuals (not susceptible to predation). In addition, while DTR facilitates juvenile population growth, it inhibits adults, and the extent varies substantially with the levels of DTR. With increased DTR, invulnerable juveniles experience a steady increase in biomass, while adults undergo a rapid decline in population biomass. This observation in biomass change for different life stages is generally consistent with the other two panels (A and B) in Fig. 4 (see also Appendix S5).

Mechanisms behind the observed effects of DTR on population biomass were revealed when probing reproduction and growth rate of consumer individuals as a function of the intensity of the environmental

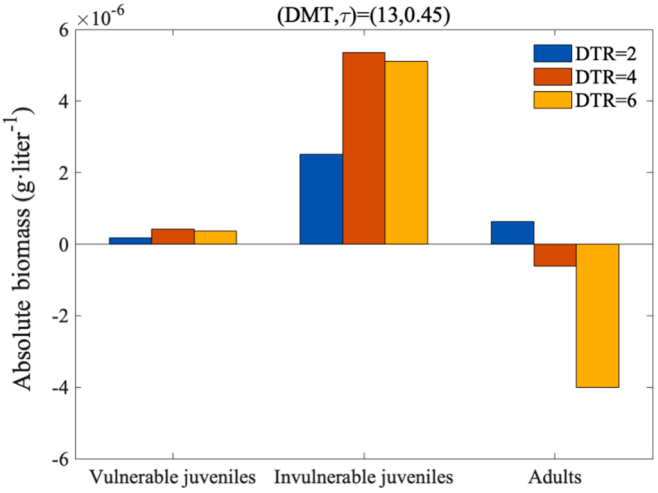

Fig. 4. Absolute population biomass for different life stages (vulnerable, invulnerable juveniles, adults) of consumers varies with increased DTR (see Fig. S10 for absolute biomass). Biomass is higher (lower) than the scenario of DTR=0 when the color columns are above (below) the baseline (horizontal line).

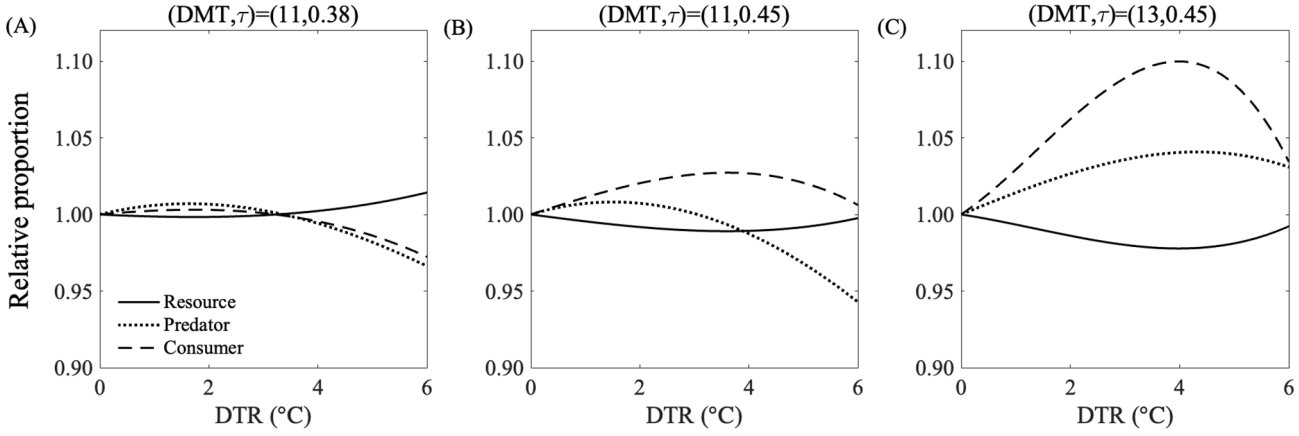

Fig. 3. Population biomass proportion of the three studied species, relative to the case of DTR=0, as a function of increased DTR under different combinations of DMT and boldness level (τ).

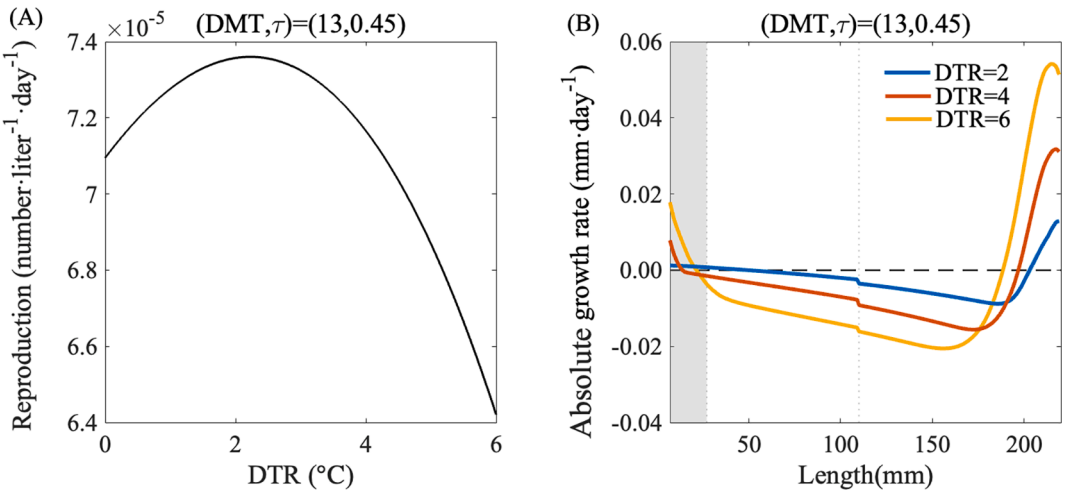

Fig. 5. Reproduction of adult consumers (A) and the absolute size-dependent growth rate of consumer individuals (B, the absolute growth rates in Fig. S11) with increased DTR. The growth is relative to the case of DTR=0 under the environmental condition (i.e., DMT=13, $\tau = 0.45$). In panel B, the shaded area represents vulnerable juvenile consumers (susceptible to predation).

stressors for the scenario of panel C in Fig. 3 (Fig. 5). Reproduction initially experiences a moderate increase and then a rapid decrease with elevated DTR. Additionally, the absolute growth rate increases for consumer individuals with body sizes between 7–27 mm and 190–220 mm but declines for other consumer individuals with body sizes outside these size ranges (Fig. 5B). A large DTR depresses population reproduction of the consumer species, leading to a substantial decline in vulnerable (size between 7–27 mm) individuals (Fig. 5A). This alleviates the competition pressure on their resource species, leading to increased resource uptake per individual, which promotes faster recruitment and growth into invulnerable consumer individuals (Fig. 4). Aggregated invulnerable juvenile consumers experience increased resource competition, and therefore display reduced growth rates.

4. Discussion

We used a size-structured food chain model to examine the responses of population and community dynamics to the interactive effects of climate warming and pharmaceutical-induced boldness change, and to explore the associated mechanisms underlying population biomass changes. Our study discloses the synergistic and antagonistic effects of DTR on community dynamics with respect to DMT and boldness, emphasizing that temperature variability deserves more attention in the context of climate warming (Poloczanska et al., 2013; Dee et al., 2020). Moreover, our results suggest that in the context of an expected 1.5–2 °C increase in global temperature over next 20 years (Kim & Bae, 2021), aquatic ecosystems may undergo an increase in population biomass (Fig. 2), but a regime shift in stability (Fig. 1C &D). Qualitatively similar results were found using the same model with continuous reproduction instead of seasonal reproduction (Appendix S6), indicating the generality of our findings.

4.1. The interactive impact on ecosystem level vs population level

At the community level, our study demonstrated that the effects of DMT and boldness change can lead to a diversity of outcomes, from predator collapse to species coexistence with SDCs and with PIDCs (Fig. 1, Fig. S4). The collapse of the predator species was due to the depensatory growth mechanism, or alternatively the emergent Allee effect (de Roos & Persson, 2002). Moreover, the SDCs were mainly driven by the seasonal reproduction (Fig. S4) while PIDCs were possibly the consequence of the classic paradox of resource enrichment in predator–prey communities (Rosenzweig, 1971), as inferred by the increased resource biomass (Fig. S21). Importantly, we found that the onset of unstable coexistence with PIDCs induced by DMT could be significantly advanced by enhancing boldness (Fig. 1C & D), and vice versa (Fig. 1A & B), indicating a significant synergistic effect between these parameters (Halpern et al., 2019).

It is worth mentioning that since different types of pharmaceutical contaminants may alter boldness in different directions, our boldness is virtually a bidirectional parameter that varies between 0 and 1 (Andersen et al., 2018). This bidirectional change can result in disparate outcomes. As illustrated in Fig. 1, increasing boldness promotes community instability, while decreasing boldness can result in predator collapse. Bidirectional boldness changes have also been reported in previous laboratory studies. For instance, the Siamese fighting fish showed contrasting boldness changes when exposed to Flutamide (Dzieweczynski et al., 2016) and Fluoxetine (Dzieweczynski et al., 2018), respectively. Furthermore, while a variety of pharmaceuticals have been demonstrated to induce boldness changes (Lagesson et al., 2018), the present work does not refer to any specific pharmaceuticals, but instead focuses on the change in boldness regardless of which pharmaceutical is considered. Hence, a comprehensive understanding of the interactive effects between anthropogenic stressors is important, as an amplified stressor may lower the resilience of the ecosystem to another stressor (Scheffer et al., 2015).

While high levels of DMT and boldness were the primary drivers of community instability, DTR displayed a considerable regulatory effect on population biomass (Fig. 2, Fig. 3, Fig. 4) by altering population reproduction rate (from a slight increase to begin with to a significant decline as DTR is further elevated) and the size-dependent growth rate of the consumer species (Fig. 5). A large DTR demonstrated an inhibitory effect (detrimental synergistic effect) (Fig. 2C & Fig. 3), which was primarily a consequence of the impact of DTR on population reproduction (Fig. 5A). The changes in consumer biomass primarily manifested as an increase in invulnerable juvenile individuals and a rapid decrease in adult individuals (Fig. 4). The accumulation of invulnerable juvenile was due to the slower rate of their growth as well as the recruitment of vulnerable juveniles' fast growth (Fig. 5B). Our findings are in line with existing aquatic experimental studies. For instance, an experimental study indicated that a small DTR had the potential to enhance the population biomass of the Siberian sturgeon *Acipenser baerii* (Sadati et al., 2011), while a large DTR exerted the opposite effects in the Arctic charr *Salvelinus alpinus* (Lyytikainen & Jobling 1998). Our study thus calls for addressing DTR in aquatic ecosystems to improve our ability to judge the severity of climate warming.

4.2. The mechanism

The potential mechanism underlying the positive or negative influence of DTR on species life history traits (Fig. 5) can be understood as follows. In nature, ambient temperatures undergo daily fluctuations, which may pose greater challenges for ectotherms compared to the exposure from increased average temperatures (Vasseur et al., 2014). Exposure to daily fluctuating temperatures (DTR) is energetically costly (Colinet et al., 2015) and may consequently influence how organisms respond to contaminants (Verheyen et al., 2022). Therefore, fluctuating temperatures (e.g., DTR) play a crucial role in regulating warming (DMT) and pharmaceutical-induced boldness change. Furthermore, theoretical studies indicate that DTR, determined by daily maximum temperature (DMT_{max}) and daily minimum temperature (DMT_{min}), is a key driving factor in the climatological processes (Vinnarasi et al., 2017). As most species generally have optimum temperature ranges T_{opt} that allow for maximal production (Constantine, 1987; Sadati et al., 2011), species' ontogenetic developments are inhibited when experiencing abnormal DMT_{max} and $DMT_{min.}$ Thus, a large DTR makes it likely for species to exceed their optimum temperature ranges (Brander, 2010), increasing their vulnerability to extreme temperature (Briga & Verhulst 2015; Frölicher et al., 2018). Nevertheless, moderate DTR can maintain temperature at optimal levels, thereby enhancing species resilience to pharmaceutical exposure, mitigating the negative effects in individual development and population productivity (García et al., 2015; Martino et al., 2021; Aulsebrook et al., 2022).

4.3. Linking theoretical to empirical studies

In a recent lake experimental study with fluctuating temperature, effects on the survival and growth rate of oxazepam-exposed perch failed to be detected (Lagesson et al., 2018; Fahlman et al., 2021), contrary to the *a priori* anticipation that oxazepam contaminants reduced anti-predator behavior (Klaminder et al., 2014; Brodin et al., 2017). Without rigorous testing, the authors of this study suggested that daily temperature variability likely masked the response of pharmaceutical contaminants on fish (Saaristo et al., 2019). Indeed, given the complex impacts of environmental stressors on organisms in natural environment and the differences from laboratory assays, monitoring the ecological effects of pharmaceutical contaminants on fish population dynamics is challenging *in situ*. Nonetheless, as an echo to their suggested explanation, our results demonstrate that fluctuating temperatures might indeed mask the weak responses of perch to oxazepam exposure, implying that neglecting DTR may lead to a biased prediction of the harmful impacts of warming and pharmaceutical contaminants on species.

5. Limitations

Caution must be taken when applying our results to deep aquatic ecosystems. In the present work, we assumed a spatially uniform DMT for studied ecosystems, regardless of their water depths. Thus, global warming can possibly lead to an increasing mismatching between DMT and the optimal temperature of fish that developed in a pre-warming environment. In nature, fish live in a thermally stratified environment, and can position themselves further down in water body to maintain the best matching between environmental temperature and their optimal temperature (Pörtner & Farrell, 2008). Nevertheless, the trade-off for such thermal stratum shift might be a declined access to the food resources inhabiting their previous thermal stratum. Our work may be more relevant for ecosystems without obvious thermal stratification, such as shallow lakes, the most abundant freshwater ecosystems on Earth (Verpoorter et al., 2014), which are of an average depth below than 3 m (Cheruvelil et al., 2022).

In conclusion, our findings contribute to a holistic understanding of how the interaction between temperature rise and pharmaceutical-induced behaviour change predominantly affects species coexistence and community stability. Daily temperature fluctuations (DTR) act as a regulator of species population responses to pharmaceutical contaminants, where moderate DTR may boost the positive effects and alleviate the negative effects of pharmaceutical contaminants. On the contrary, large temperature fluctuations (DTR) can act as a catalyst aggravating the negative effects and advancing the onset of regime shift from a state with SDC to with PIDC. Our study calls for future studies to move beyond the focus on single environmental stressors, acknowledging that multiple stressors interact in shaping population and community dynamics.

CRediT authorship contribution statement

Guangjing Qian: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Dan Wu:** Methodology, Investigation. **Lai Zhang:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Susanne Kortsch:** Writing – review & editing, Supervision.

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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Author contributions

LZ conceived this study. GJQ wrote the manuscript with inputs from LZ and SK, and further performed numerical simulations and analysis. All authors contributed to the discussion of the results and the final text.

Data Accessibility

Data supporting the finds of this study have been stated in the body of the paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtbi.2024.111948.

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