Received: 18 August 2021 | Revised: 22 November 2021 | Accepted: 11 January 2022

DOI: 10.1002/ecs2.4062

ARTICLE

Coastal and Marine Ecology

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Increases in temperature and freshwater inputs will shift grazing patterns of a coastal mesograzer on foundation species

Maximilian Berthold[1,2] | **Christian Porsche**[3] | **Antonia Hofmann**[3] | **Petra Nowak**[3]

[1]Applied Ecology and Phycology, University of Rostock, Rostock, Germany

[2]Phytoplankton Ecophysiology, Mount Allison University, Sackville, New Brunswick, Canada

[3]Aquatic Ecology, University of Rostock, Rostock, Germany

Correspondence
Maximilian Berthold
Email: maximilian.berthold@uni-rostock.de

Funding information
Bundesministerium für Bildung und Forschung, Grant/Award Number: 03F0737A

Handling Editor: Rochelle D. Seitz

Abstract

Foundation species, and the roles that they play in structuring ecosystems, are threatened by global change. For example, charophytes are a refuge for zooplankton and stabilize sediments, but they are also a food source for various animal species (water birds, fishes, and invertebrates). Particularly, the introduction of new species, such as *Gammarus tigrinus*, into the Baltic Sea led to yet not understood changes in the food web. Furthermore, future projections point to increased water temperatures and freshwater inputs affecting species capacity to acclimatize to changing abiotic factors. In this study, we investigated the influence of temperature and salinity on the grazing pressure of *G. tigrinus* on two charophyte species: *Chara aspera* and *Chara tomentosa*. The grazing experiments were conducted in a full-factorial design with the factors salinity (3–13 g kg^{-1}), temperature (5–30°C), and charophyte species. Grazing rates were determined as mass deviation within 48 h considering biomass changes in the presence and absence of gammarids. Grazing rates were further used to calculate charophyte losses in two coastal lagoons with different salinity concentrations for recent and future time periods. Increasing freshwater inputs can buffer charophyte biomass loss at higher temperatures. Gammarids had a higher grazing impact on *C. aspera* than on *C. tomentosa*. The potential grazing peak of about 24°C is not yet reached in these coastal waters but may be reached in the near future as shown by our future projection results. However, a temperature increase and decrease in salinity will cause a shift in seasonal individual grazing patterns from summer to spring and autumn. An increase in temperature and freshwater input can lead to a shift in optimal habitats for *G. tigrinus* in the future. These interactions between abiotic and biotic factors will affect the future spatial distribution that charophytes can exploit as foundation species.

KEYWORDS
Chara aspera, *Chara tomentosa*, climate change, *Gammarus tigrinus*, invasive species

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

INTRODUCTION

Global climate change imposes several interacting effects on aquatic organisms. Besides the increase in water temperature, there may be regionally altered hydrological flow regimes that alter timing and amount of freshwater input into coastal waters. Native species get stressed by this development and ecosystems may be more susceptible to invasive species colonization. The Baltic Sea is such a system prone to eutrophication and global climate change, due to already increased sea surface temperatures, compared with other oceans worldwide (Reusch et al., 2018). The Baltic Sea is subject to large phytoplankton blooms since decades, with the riparian states working to reduce the impact of nutrient runoff to the sea (HELCOM, 2018; Janssen et al., 2004). Similarly, the coastal water bodies of the Baltic Sea were impacted by eutrophication and shifts on primary producer dominance, which means from submerged macrophytes to phytoplankton (Schiewer, 2007).

Charophytes are widely distributed in fresh and brackish water ecosystems (e.g., Schubert & Blindow, 2003). During the last decades, charophytes received attention not only as indicator species for oligotrophic water bodies but also as pioneer species for post-eutrophied water bodies (e.g., Melzer, 1999; Schubert & Blindow, 2003). It was assumed that charophytes have several turbidity-reducing traits, for example, by decreasing the resuspension of particulate matter, and direct (dissolved nutrients) and indirect (refuge for zooplankton) competition with phytoplankton (Kufel & Kufel, 2002). Therefore, recolonization with those species could create feedback mechanisms, favoring a macrophyte-dominated stable state. These traits make charophytes interesting foundation species as habitats are colonized regardless of trophic status (Schubert et al., 2018). Algae of the Characeae family are currently listed as "endangered species" in several European areas (Auderset Joye & Schwarzer, 2012; Blazencic et al., 2005; Gärdenfors, 2010; Stewart & Church, 1992), and they are also under pressure in the Baltic Sea. Comparisons of historical and recent distributions in the northern Baltic Sea show that *Chara aspera* and *Chara tomentosa* were between 8% and 86% times less abundant in the most recent transects (Pitkänen et al., 2013). Besides eutrophication-related issues, salinity and/or temperature changes may influence successful recolonization in the future.

Salinity changes in brackish water are such a factor, where increased salinity prevents the growth of macrophyte species (Lindner, 1972). *Chara aspera* is assumed to increase their distribution under increasing freshwater inputs (Torn, Peterson, & Herkül, 2020). However, the interacting effects of temperature–salinity changes on charophytes are less known.

Furthermore, restoration measures may be hampered by global climate change and the effects of increasing water temperature and freshwater inputs. There are hypotheses that not only abiotic parameters but also top-down control (such as grazing) may affect the restoration of the pristine trophic state and macrophyte recolonization (Körner & Dugdale, 2003; Östman et al., 2016). Besides grazing from native species (Körner & Dugdale, 2003), there is also an increasing grazing pressure of invasive species, for example, introduced through ballast water of ships. One of these species is the gammarid *Gammarus tigrinus* (Sexton, 1939), a successful new species introduced from North America to European waters (Berezina, 2007). This gammarid was described to colonize shallow waters, especially within reed, and soft-bottom systems of the Baltic Sea (Daunys & Zettler, 2006; Kotta et al., 2011). Amid global climate change, invasive species can alter known food web interactions and may counteract recolonization of former native primary producers (Puntila, 2016). However, even these species are subject to global climate change and changes in the abiotic environment may support these invasive species even further (Kelley, 2014). The spatial distribution of *G. tigrinus* is assumed to increase with increases in water temperature and freshwater inputs in the Baltic Sea (Torn, Herkül, et al., 2020).

The question evolves, if recolonization of macrophytes is not only hampered by abiotic factors, such as temperature and salinity, but additionally by grazing pressure of (newly introduced) grazers. This grazing pressure likely changes throughout the year and may result in high-stress situations, where pressures of salinity and temperature amplify with grazing. *Gammarus tigrinus* and charophytes occur within the same depth distribution, and grazing can potentially happen. It was hypothesized that there is either a combination of factors (abiotic and biotic) that amplify mass loss on charophytes or that some abiotic factors quench each other; for example, lower salinity amplifies/buffers effects of higher temperatures. We tested the impact of salinity and temperature, as well as their interactions on biomass change of charophytes in the presence and absence of grazers. These results also allow to discuss future developments within coastal water bodies, for example, at increasing water temperatures or changing freshwater inputs. Coastal water bodies are likely to be more affected by such events due to their relatively shallow water column and close coupling with the adjacent land.

We chose the Darss-Zingst lagoon system (DZLS) as model ecosystem for the southern Baltic Sea, due to its salinity and trophic gradient and decade-long monitoring record (see Berthold, 2016; Schiewer, 2007). Even though today nutrient concentrations decreased to a comparable level of the 1930s, no dense macrophyte cover was able to

form in the DZLS (Berthold, Karsten, et al., 2018; Gessner, 1957; Paar et al., 2021). Indeed, the maximum depth distribution of charophytes has not increased significantly in the DZLS during the last years, and charophytes are found only in very shallow waters, where light is not limiting (Piepho, 2017). To account for this development, we combined the laboratory-determined grazing potentials with field-based growth patterns of submerged macrophytes of the DZLS and projected them with future salinity and temperature developments in these waters.

MATERIAL AND METHODS

Experimental design

We chose a full-factorial design with three factors (Appendix S1: Figure S1). One factor related to species and included two levels (*C. aspera* and *C. tomentosa*). The other two factors were each with four levels: water temperature (9, 15, 24, and 30°C) and salinity (3, 5, 7, and 13 g kg^{-1}). These salinity levels represent the salinity gradient from the western Belt Sea to the Gulf of Finland, covering most of the Baltic Sea area (HELCOM, 2010). The water temperature levels represent the blooming period of shallow coastal waters (+1°C in winter to +22°C in summer; Schiewer, 2007), with 30°C as prospective endpoint of possible charophyte growth.

The DZLS is formed by four consecutive shallow lagoons and shows a salinity and trophic gradient from the main river inflows Recknitz and Barthe (inner and middle part, salinity of 1–6 g kg^{-1}, eutrophic) to the open Baltic Sea (salinity of 10–12 g kg^{-1}, mesotrophic; Schumann et al., 2006). Salinity varies from 4 to 6 g kg^{-1} at the respective sampling locations in the Bodstedter Bodden (54°22′30.5″ N, 12°34′14.9″ E) and around 6–8 g kg^{-1} in the Grabow (54°22′2.3″ N, 12°48′27″ E) (Schumann et al., 2006). During the experiment, two charophyte species were used, *C. aspera* and *C. tomentosa*. Both species are common in the Baltic Sea, with *C. aspera* covering the widest salinity range among charophytes (Blindow, 2000). Along the west coast of Sweden, *C. aspera* is regularly found at sites with salinities up to 15 g kg^{-1} (temporarily up to 20 g kg^{-1}), but it is also common in freshwater (Blindow, 2000; Hasslow, 1931). *Chara tomentosa* is among the largest charophyte species and can be found in freshwaters all over the world. Only in the Baltic Sea, *C. tomentosa* also occurs in brackish water, with a salinity range between 0 and 7.5 g kg^{-1} (Björkman, 1947; Torn et al., 2003). Gammarids were derived from the Aquaculture section in Born of the State Research Centre for Agriculture and Fishery Mecklenburg-Vorpommern. This research facility is located at the DZLS and uses brackish water from the lagoon with a salinity of 4–6 g kg^{-1}. Gammarids were identified by morphology and genetic analyses (see Appendix S1: Genetic Analyses).

Charophytes were extracted as intact plants from the DZLS and then cultured in beakers (volume 500 ml) following the culture design described by Wüstenberg et al. (2011). Each beaker contained sediment containers (volume 64 ml) with acid-rinsed, phosphorus-enriched sediment (6 g P kg^{-1} sediment). Mineral growth media were prepared to culture charophytes (Pohl et al., 1987; Wüstenberg et al., 2011), but were adjusted to the respective salinities by adding marine salt (Instant Ocean; Aquarium Systems, Sarrebourg). Salinity was checked with a salinometer (Multiline P4, WTW). Each of the 16 combinations was replicated eight times with gammarids (=grazing treatment) and in the absence of gammarids (=control) (Appendix S1: Figure S1). Gammarids were pre-acclimatized to experimental conditions by culturing them at the respective temperature and salinity combinations. Ten to 20 individuals were simultaneously cultured per temperature–salinity combination, aerating all cultures. Charophytes were added as food supplement, as well as resting surface for the gammarids.

Charophytes were wet-weighed and set into beakers filled with sediment and growth media of the respective salinity. Controls consisted of one charophyte, whereas grazing treatments consisted of one charophyte and five gammarids in one beaker. Control and grazing treatments were exposed to light intensities between 80 and 120 µmol photons m^{-2} s^{-1} using fluorescent tubes (Philips, TLD 36W/950). Each replicate run lasted for about 48 h. Replicates were run in blocks over a period of 4 weeks per *Chara* species. Two of the eight replicates per salinity–temperature combinations were conducted simultaneously to spread and randomize replicate runs over the 4-week period. According to previous studies on growth of charophytes (Nowak et al., 2018), we did not expect significant growth responses of *C. aspera* and *C. tomentosa* over the course of 2 days. However, it was expected to find significant mass deviations when gammarids were present.

Charophytes were wet-weighed after each replicate run to calculate mass differences. Dead gammarids were counted at the end of each replicate run and replaced for the next replicate run. If possible, the same gammarids were used throughout all replicate runs. Equations (1)–(3) were used to extract grazing rates of gammarids from growth rates of charophytes during the experiments. Grazing rates were treated with an error propagation to account for experimental variability.

Equation (1) subtracts the mean effect of biomass change of the control (C) from the treatment, which also includes grazing (T):

$$G_i = T_i - \overline{C}\,\{i = 1...n. \quad (1)$$

Equation (2) standardizes the grazing effect from prior formula (z-score):

$$GZ_i = \frac{(G_i - \overline{G})}{\sigma_G}\,\{i : 1...n. \quad (2)$$

Equation (3) calculates the mean of pure grazing and includes its error caused by the experiment:

$$Gf_i = \overline{G} + GZ_i \times \sqrt{\left|\left(\sigma_T^2 - \sigma_C^2\right)\right|}\,\{i : 1...n, \quad (3)$$

T = treatment, C = control, G = detrended grazing, G_z = standardized grazing, G_f = grazing with included experimental error, and n = number of replicates.

Field sampling and analyses

In addition, we used elemental and biomass composition of submerged macrophytes from the DZLS, to compare the experimentally derived grazing rates with the actual ecosystem. Field sampling was conducted in the Bodstedter Bodden and the Grabow in 2014, as part of the BACOSA project. Interestingly, the Bodstedter Bodden has on average a lower salinity of 2 g kg^{-1}, than the Grabow, coinciding with future salinity projections (Neumann & Friedland, 2011). This difference may be used as model validation as if grazing rates of the present Bodstedter Bodden represent future grazing rates in the Grabow. Submerged macrophytes were sampled throughout the year, first in 54 × 54 cm plots, and in 25 × 25 cm plots later during the year at nine different depths. Here, three sampling locations were pooled into three depth zones, according to water depth and proximity to the reed belt. Water depths for both stations varied with water levels in the respective lagoons and were shallow (30–60 cm), intermediate (60–90 cm), and deep (90–120 cm). Sampled macrophytes were separated on the genus level. Whole plants, including roots, were wet-weighed and then dried at 60°C for 24 h. Afterward, dry mass (DM) was reweighed again to calculate water content. The dried plant material was ground with a ball mill. The powder was treated with 1 M HCl to remove inorganic carbon residues and then weighed in a tin container (1 × 0.5 cm). These samples were analyzed for their carbon and nitrogen contents using an elemental analyzer (vario EL III). The analyzer was calibrated using acetanilide (~5 mg per sample).

Aliquots of dried plant material were weighed in crucibles and combusted at 550°C for 4 h. The ash was reweighed to calculate ash-free DM. Ashes were used to determine total phosphorus content (mg P g^{-1} DM), using an acid persulfate extraction (see Berthold et al., 2015).

Data analyses

We further used the experimental grazing data to calculate grazing rates based on salinity and water temperature at two sites of the DZLS. The data set failed to show homogeneity of the residuals and was therefore Box–Cox power-transformed (*bcnPower* function, R package "*car*"; Fox & Weisberg, 2019). Finally, general linear models (*glm* function, R package "stats"; R Core Team, 2013) and generalized additive models (GAM, *gam* function, R package "*mcgv*"; Wood, 2011), both with Gaussian distributional assumptions, were compared by the Akaike information criterion (AIC, R package "stats"; R Core Team, 2013) and the Bayesian information criterion (BIC, R package "*stats*"; R Core Team, 2013), choosing the model with low AIC and BIC values. We chose the GAM (with knots, $k = 16$) as the best model to reflect the experimental data (see *Results*). To our knowledge, recent studies on seasonal population dynamics of *G. tigrinus* are currently missing in our study system, as elsewhere in the Baltic Sea. However, recent field studies found 5–2200 individuals (ind) per square meter (gammarids on genus level) in the DZLS and the adjacent western Rügen lagoon system. Largest, but fewest animals were found early in the year (22–28 mg ind^{-1}), with decreasing mass, but increasing abundance in summer (3.5 mg ind^{-1}) (M. Paar, personal communication). These patterns point to the same seasonal development as described in Chambers (1977). If we assume that *G. tigrinus* constitutes 20% of the local gammarid population in the DZLS (Zettler, 2001), we get a population size of up to 450 ind m^{-2}. These numbers are in agreement with first described abundance of *G. tigrinus* of 300–500 ind m^{-2} in the phytal and reed belt of the DZLS (Zettler, 1995), or 30–110 ind m^{-2} in the Neva Estuary (Baltic Sea; Berezina, 2007).

We used again a GAM to calculate the seasonal population development of *G. tigrinus* and normalized the predicted seasonal data to have a maximum of 1. Then, we used this normalized prediction to calculate population densities with a maximum of 400 ind m^{-2} (Zettler, 1995; M. Paar, personal communication; Appendix S1: Fig. S5). These population numbers were combined with the individual grazing rates of the temperature–salinity model with field data from the two sites of the DZLS (Equation 4) to calculate seasonal grazing rates. We used a fixed grazing preference of 20% macrophyte share in gammarid diets, which means grazing rates were multiplied by a factor of 0.2 (Pellan et al., 2016). Furthermore, we used the GAM to

predict the charophyte development as a function of sampling date ($k = 8$) at two sites of the DZLS. We calculated daily biomass increase and subsequently added gammarid grazing rates to determine the potential gross biomass production per site (see *Results* and *Discussion*).

Equation (4) calculates the seasonal grazing rates per square meter and day for specific sites:

$$\mathrm{Graz}_t = G_{\mathrm{GAM}_t}\{T_t; S_t\} \times \delta_t \times 0.2\,\{t : 1...n, \qquad (4)$$

t = day of the year, Graz_t = grazing at day t (in milligrams per square meter per day), G_{GAMt} = modeled grazing rate of one individual at time t with given temperature (T) and salinity (S) from specific site at time t, δ_t = population density at time t (in individuals per square meter), 0.2 = reflects the 20% fixed grazing preference, and n = length of the year in days.

RESULTS

Growth and survival rate

Starting biomasses of *C. aspera* in control and treatment beakers ranged from 50 to 300 mg, with the most macrophytes being within the range of 100–175 mg (70%). After 2 days, biomass distribution of *C. aspera* in control beakers stayed relatively the same, but proportions of smaller and larger plants (biomass) increased. Biomass of *C. aspera* decreased with increasing temperature at all salinities, but strongest at salinities >7 g kg^{-1}. On the contrary, biomass stayed almost constant at lower temperature, even at higher salinities (Appendix S1: Table S2 and Figure S3). These results indicate that negative effects on *C. aspera* biomass by increasing temperatures were slightly dampened by increasing freshwater share.

Starting biomass of *C. tomentosa* in control beakers ranged from 75 to 600 mg, and 40% of all macrophytes were within the range of 100–125 mg at the beginning. Contrary to *C. aspera*, the biomass of *C. tomentosa* in treatment beakers was close to a normal distribution with 50% of all macrophytes being within the range 175–225 mg at the beginning. The biomass distribution of *C. tomentosa* in control beakers stayed almost the same, but with a trend to smaller biomasses, indicating minor biomass losses even without grazing. Biomass of *C. tomentosa* stayed very constant at almost every temperature–salinity combination. There was a possible growth at temperatures of 15–24°C at salinities of 7 g kg^{-1} (Appendix S1: Figure S3). These results indicate that increasing temperature, but not salinity changes, was the major driver of *C. tomentosa* biomass. If control beaker results of both charophyte species were combined, the area with stable biomass over 2 days expands from 10 to 25°C and salinities of 7–13 g kg^{-1}. Furthermore, increased freshwater inputs may buffer *Chara* sp. biomass at increasing temperatures. In total, these results indicate an overall stable experimental approach, as significant growth was not expected within 2 days.

Two thirds of the time (65%), all gammarids survived at all temperature–salinity–macrophyte combinations in treatment beakers. Additionally, 30% of the time, only one gammarid died during incubation. These results indicate overall stable culture conditions and the capability of these gammarids to survive a wide range of temperature–salinity gradients.

Gammarid grazing on charophytes

Biomass in treatment beakers decreased in all combinations and beakers. Differences in control beakers were always significant, regardless of charophyte species or treatment (see Appendix S1: Table S2). Grazing rates ranged between 1 and 10 mg FM ind^{-1} gammarid d^{-1} on *C. aspera*, already accounting for biomass changes in control beakers. Grazing rates peaked at 24°C and tended to be higher with increasing salinities (Appendix S1: Figure S4). Increased freshwater shares negatively affected grazing rates even at higher temperatures. Grazing rates ranged between 1 and 5 mg FM ind^{-1} gammarid d^{-1} on *C. tomentosa* and peaked again at 24°C for all salinity levels but with a tendency to slightly lower salinity compared with grazing rates on *C. aspera*. Interestingly, highest grazing rates per charophyte species fell into temperature ranges where charophytes already showed highest loss rates in control beakers. Grazing rates depended therefore on both acclimation capacity of gammarids and charophytes at the respective salinity–temperature levels. In general, grazing rates on *C. aspera* were up to two times higher than *C. tomentosa*. Pooled grazing rates of both charophyte species were on average up to 5.5 mg ind^{-1} d^{-1}.

Field data results and model

Seasonal daily grazing rates within the ecosystem would range from 0.1 up to 5 mg FM ind^{-1} d^{-1}, when applying the grazing model on field observations of temperature and salinity of Grabow and Bodstedter Bodden (Figure 1). Grazing rates would peak during summer and be lowest at winter at the two sampling stations of the DZLS (see Figure 1). *Gammarus tigrinus* was originally collected in April/May, where grazing rates are not at its peak. Nonetheless, gammarids grazed twice as much at 24°C in our treatments, as would be expected from their initial collection time in April and May.

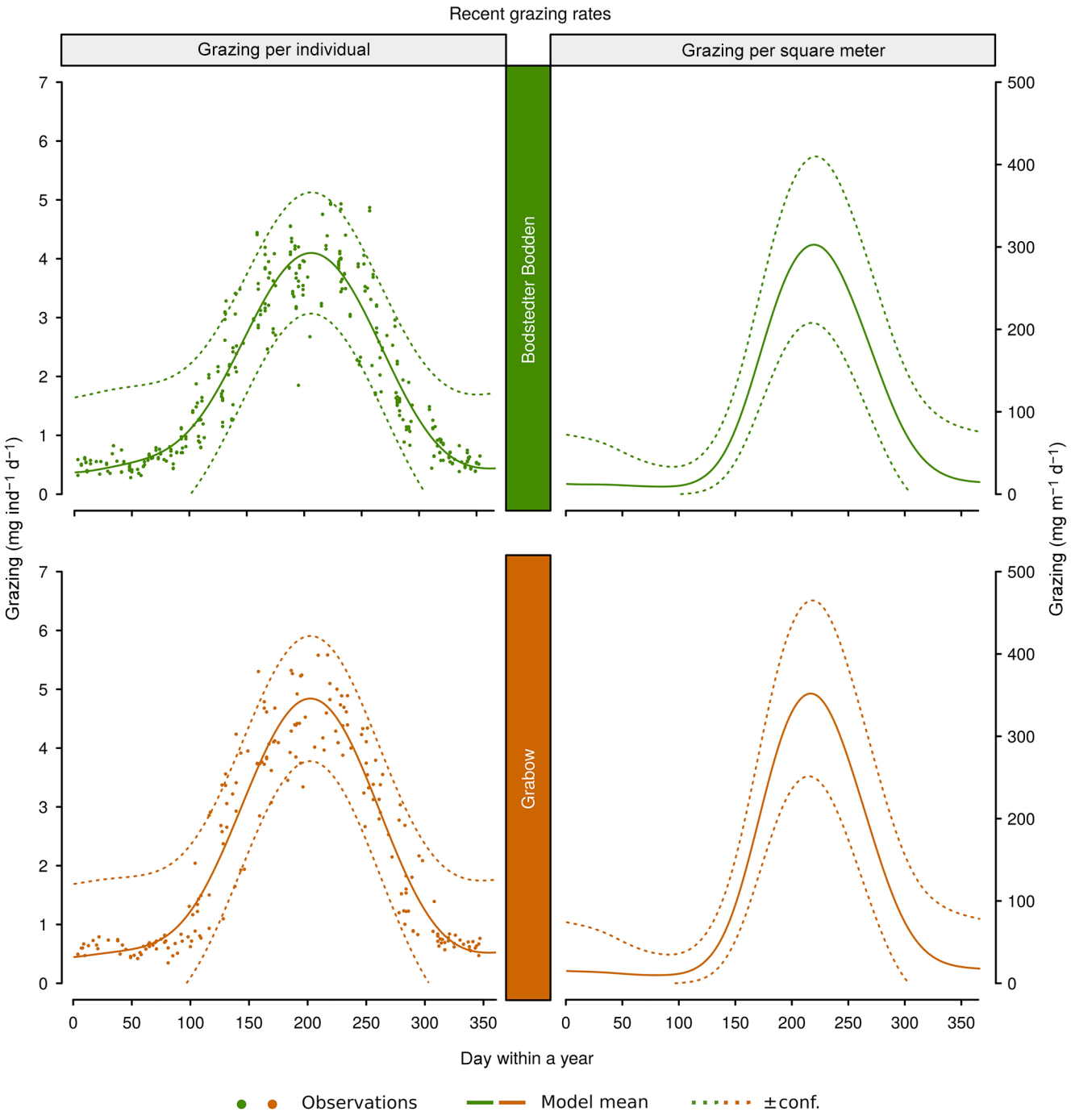


FIGURE 1 Seasonal losses of *Chara* sp. biomass by grazing of *Gammarus tigrinus* in the Bodstedter Bodden (upper panel) and Grabow (lower panel) over the years of 2000–2018. The losses of *Chara* sp. biomass by individual grazing (points) were modeled (generalized additive model) depending on temperature and salinity conditions at the respective time point in the water body (left). Grazing per square meter (right) was calculated as the product of the individual grazing model (left) and the seasonal population development of *Gammarus tigrinus* (Appendix S1: Figure S5) with a maximum abundance of 400 individuals/m^2. The solid line represents the mean, and the dotted line, the 95% CI

These findings indicate acclimation processes. The modeled grazing rates differed significantly between both stations ($p < 0.001$, paired Mann-Whitney U test), even though the difference in salinity is only 2 g kg^{-1}.

Charophyte biomass was highest in the shallow areas, close to the reed belt at both sampling sites (Figure 2). Biomass in the shallow zone peaked in July in the less eutrophic Grabow, and in October in the highly eutrophic Bodstedter Bodden. On the contrary, charophyte biomass was higher in the Bodstedter Bodden at intermediate distances/water depths compared with the Grabow. However, Grabow biomass peaked during summer,

whereas biomass in the Bodstedter Bodden became depressed during that time. Charophytes were only found in very little biomasses in the deeper water areas at both sampling locations, indicating a possible light limitation from shallow to deep.

Charophyte biomass would have been up to 15%–50% higher at shallow and intermediate depths, if macrophyte growth is corrected for seasonal gammarid grazing (Figure 2). Additionally, gammarid grazing would follow charophyte biomass peaks at the respective stations. The yearly potential grazing rate for *G. tigrinus* on charophytes ranges from 37.2 to 42.5 g FM m^{-2}, considering regional salinity and temperature patterns within the DZLS.

Future projections on temperature and freshwater input increase in the period of 2050–2100

The projected grazing rates vary significantly from today's grazing rates ($p < 0.001$, paired Mann-Whitney U test), when considering future temperature and freshwater input increase in this region (Neumann & Friedland, 2011; van der Linden & Mitchell, 2009). Individual grazing rates would increase in spring and autumn at both stations, but grazing rates in the Grabow being at least twice as high as in the Bodstedter Bodden (Figure 3, Appendix S1: Figure S6). Furthermore, individual grazing rates would probably drop during summer, as water

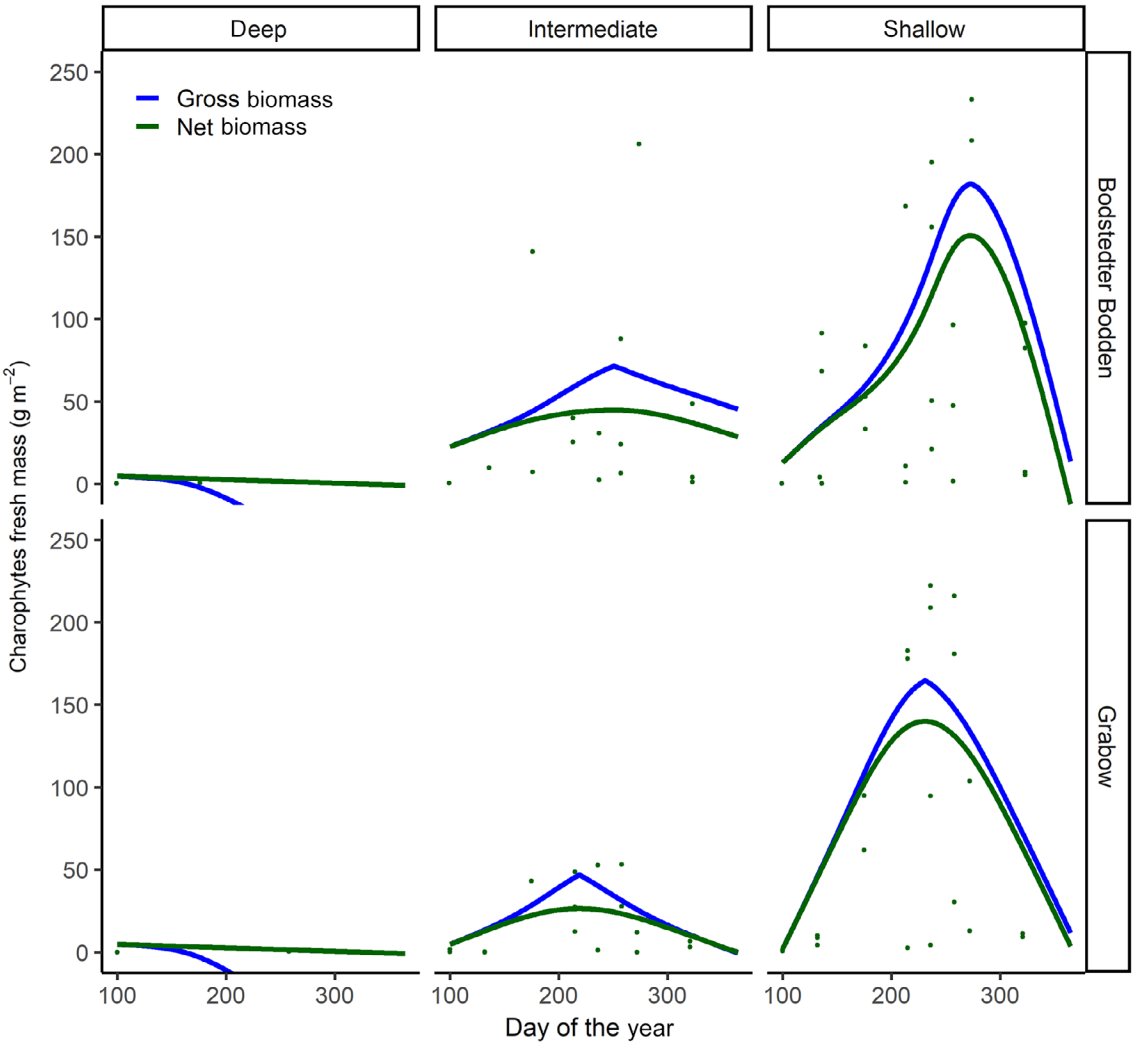


FIGURE 2 Charophyte fresh mass in gram per square meter at two sampling locations of the Darss-Zingst lagoon system along a water depth/distance to reed belt transect. Shallow depth, 30–60 cm close to the reed belt; intermediate depth, 60–90 cm distance to the reed belt; and deep depth, 90–120 cm farthest distance to the reed belt. Net biomass represents model-fitted values (generalized additive model) of observed charophyte biomass. Green points represent observed charophyte biomass at the respective day. Gross biomass represents the sum of net biomass plus biomass possibly lost by abiotic influenced seasonally resolved *Gammarus tigrinus* grazing

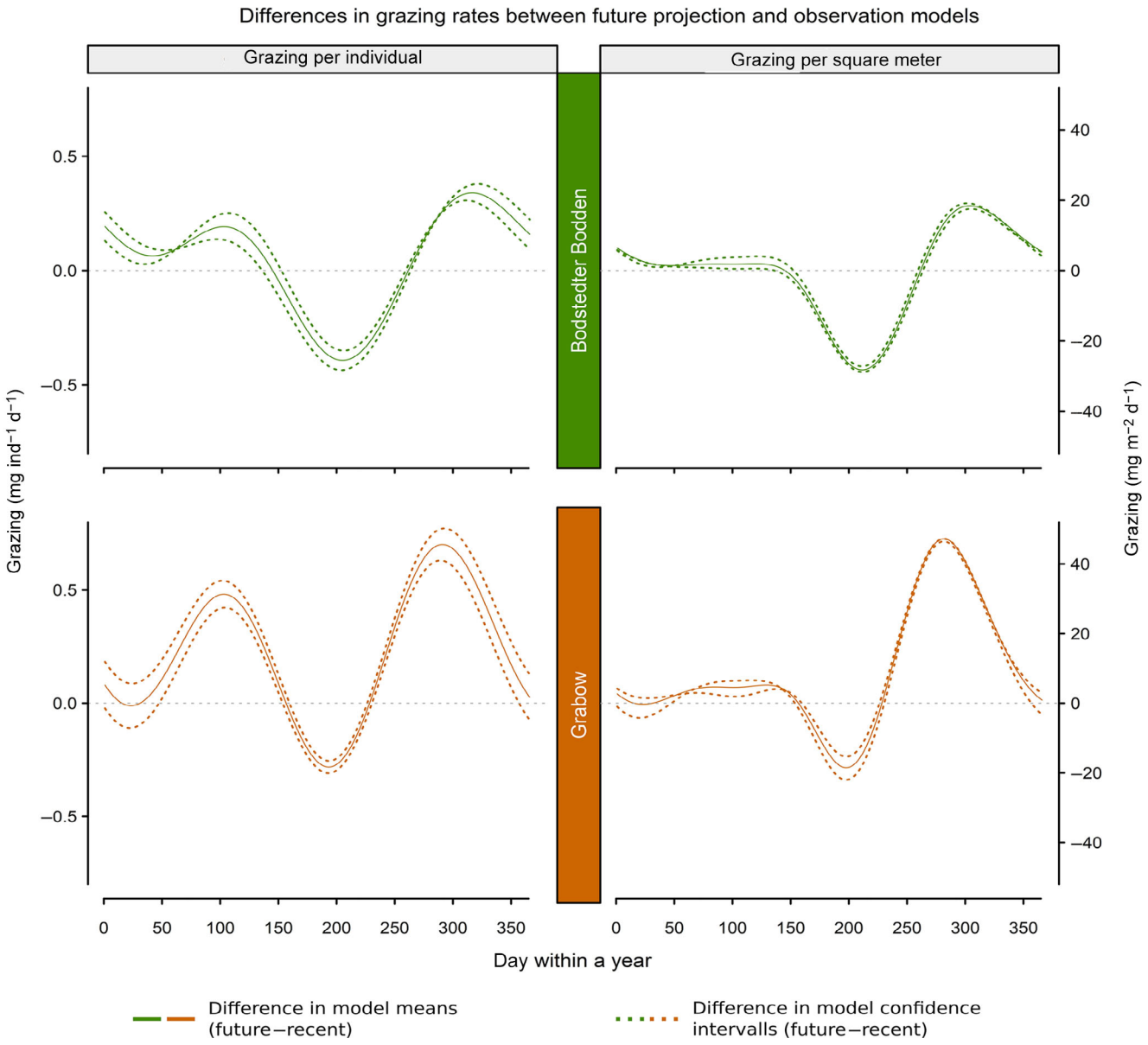


FIGURE 3 Differences in future-to-current grazing rates of *Gammarus tigrinus* on *Chara* sp. in the Bodstedter Bodden (upper panel) and Grabow (lower panel). Projections were calculated with a delta change approach of recent data with projected changes. Data from 2000 to 2018 were modified in temperature (+2.75 K) and salinity (−1.75 g kg^{-1}) as described in Neumann and Friedland (2011) and van der Linden and Mitchell (2009). Losses of *Chara* sp. biomass by individual grazing were modeled depending on the modified temperature and salinity conditions at the respective time point in the water body (left). Grazing per square meter (right) was calculated as the product of the individual grazing model (left) and the seasonal population development of *Gammarus tigrinus* (Appendix S1: Figure S5) with a maximum abundance of 400 individuals/m^2. The solid line represents the mean, and the dotted line, the 95% CI. Absolute losses for recent and projected conditions are presented in Appendix S1: Figure S6

temperatures will fall out of optimum ranges for *G. tigrinus*. These differences in future grazing rates are caused by earlier warmer temperatures, and lower salinities, increasing future individual grazing pressure in the Grabow (Table 1). However, this double peak is not apparent, when the seasonal population structure is included. Areal grazing rates would not be different during spring and even lower during summer. However, grazing rates would strongly increase during autumn at both stations. This peak is caused by the late population peak of gammarids, and the increased temperature in future projections. This grazing pattern would likely affect charophytes in the turbid Bodstedter Bodden, as they showed the highest biomass during autumn.

TABLE 1 Sum of losses of *Chara* sp. biomass in different coastal water bodies (CWB) by individual grazing or by grazing at one square meter (m^2) with respect to the seasonal population pattern of *Gammarus tigrinus* (Appendix S1: Supplement Figure S5) with a maximum abundance of 400 individual/m^2

CWB	Base	Recent (mg $year^{-1}$)	Projected (mg $year^{-1}$)	$\Delta_{(proj.-rec.)}$ (mg $year^{-1}$)	Δ/rec. (%)
Bodstedter Bodden	ind	672.6	687.3	14.7	2.2
Grabow	ind	768.3	847.9	79.6	10.4
Bodstedter Bodden	m^2	36,132.5	35,860.5	−272	−0.8
Grabow	m^2	41,014.9	44,230.3	3215.5	7.8

Note: These were calculated for the Bodstedter Bodden and the Grabow for the recent data and for the future projection.
Abbreviations: proj., projected; rec., recent.

DISCUSSION

Charophyte growth and gammarid grazing rates in our experiment and in the field depend on changes in the abiotic environment. However, grazing rates are simultaneously influenced by available food sources for gammarids, occurrence of competing species and predators, or ultimately habitat choice and niche occupation.

In this study, temperature increase and salinity experiments lasted only for 2 days. Charophytes of control beakers showed only little, if any biomass increase, and cannot be used for long-term growth projections. There are complex interactions between abiotic factors (e.g., salinity, temperature, light climate) that influence charophyte growth, and these effects depend on species-specific characteristics, local environmental conditions, and probably locally adapted subpopulations (Auderset Joye & Rey-Boissezon, 2015; Blindow et al., 2009; Rojo et al., 2017). Distinct *C. aspera* populations can show different growth optima depending on the habitat (freshwater and brackish), which is translated by changing photophysiological characteristics at varying salinities (Blindow et al., 2003; Blindow & Schütte, 2007). Likewise, water temperature shapes charophyte populations, which may result in local biomass decreases in *C. aspera*, *C. tomentosa*, and *C. vulgaris* if temperature increases more than 2°C (Auderset Joye & Rey-Boissezon, 2015; Choudhury et al., 2019). Even our short-term experiments may confirm these results, as both charophyte species lost most biomass at temperatures above average summer habitat temperatures (>24°C). However, interactions of abiotic factors do not necessarily induce synergistic effects in charophytes (Puche et al., 2018; Rojo et al., 2017). Our short-term growth controls showed synergistic effects on charophyte growth rates for different temperature and salinity conditions (Appendix S1: Figure S4). Further studies are needed to clarify long-term charophyte changes in the face of increasing water temperatures and decreasing salinities, especially among locally adapted subpopulations.

Several physiological reactions, such as survivability or oxygen consumption of *G. tigrinus* on salinity and temperature changes, have already been described in the literature (Dorgelo, 1973, 1974; Koop & Grieshaber, 2000). *Gammarus tigrinus* survives within a broad salinity–temperature spectrum, where only full marine or freshwater conditions show highest mortalities. Furthermore, potential synergetic effects were observed with higher temperatures buffering higher salinities, with survival rates 10 times lower at 5°C than at 25°C (Dorgelo, 1974).

Grazing rates in our study suggest similar findings, as lowest temperatures strongly lowered grazing rates, regardless of salinity. There was also a tendency to higher grazing rates, at higher salinity/temperature combinations, compared with high salinity/low temperatures, indicating a grazing optimum at higher temperatures. Ion regulation in *G. tigrinus* happens fast and can regulate sudden high ionic stress to a variety of ions (Na, Cl, and K) without compensation losses. However, hypoosmotic, which means low-salinity conditions, cause increased NO_3 inflow into *G. tigrinus* hemolymph, probably causing decreased survivability (Koop & Grieshaber, 2000). The growth media for charophytes in our experiment had elevated NO_3 concentrations (3 mM KNO_3; Pohl et al., 1987). This elevated NO_3 concentration may have caused lower grazing rates at lower salinities in our study.

Besides abiotic factors, population structure influenced the grazing rates of gammarids. Populations of *G. tigrinus* were described to turnover at least three times per year, with a peak of large animals (6–9 mm) in spring, and a concomitant shift to smaller animals in late summer (2–4 mm) (Chambers, 1977). We used animals in the size range of 6–12 mm, which means large adults for all our experiments. This size class is only dominant by up to 60% until May and is almost completely replaced by smaller animals from June to September (Chambers, 1977). This pre-selection had likely an effect on the described grazing rates, as metabolic rates of *G. tigrinus* increase with lower weight in form of a power function (Normant et al., 2007). Gammarids in our study weighed from 10 to 90 mg wet mass ind^{-1} (data not

shown), whereas the gammarids of Normant et al. (2007) were caught in August and weighed only 5–25 mg wet mass ind^{-1}. Animals of our study should therefore show lower specific metabolic rates of 0.25–1.5 mW g^{-1} wet mass, compared with 1–3.5 mW g^{-1} wet mass in smaller gammarids (Normant et al., 2007). This lower metabolic rate had likely an impact on the grazing rates we found in this study, as grazing for metabolic upkeep is lower in large adult animals.

The results of this study indicate that the individual grazing rates of *G. tigrinus* will change over the next 50–100 years. During that time, the optimal properties of temperature and salinity for *G. tigrinus* will increase in spring and autumn months and decrease during summer months.

Springtime is a crucial period for charophyte sprouting, as the active growth of, for example, *C. tomentosa* takes place during a relatively short period at the beginning of summer (Torn et al., 2006). Furthermore, young sprouted charophytes show a higher elemental content per biomass than, for example, tracheophytes (Volkmann, 2016; Appendix S1: Figure S7), making them a preferred grazing opportunity (Kraufvelin et al., 2006). *Gammarus locusta* follows a preference for high-value plant material and selectively feeds on more nutrient-rich macrophytes, especially periphyton, and brown and green algae (Kraufvelin et al., 2006). If *G. tigrinus* shows similar grazing preferences, periphyton from tracheophytes would be the first choice followed by charophytes in the DZLS. Periphyton (Sañudo-Wilhelmy et al., 2004) and possibly charophytes (Kufel & Kufel, 2002) can take up large amounts of dissolved nutrient that occur frequently through diffuse runoff (Berthold, Karstens, et al., 2018). Tracheophytes in the DZLS and adjacent lagoons can show high colonization rates by epiphytes (Paar et al., 2021), offering an additional plant food source to gammarids. Nonetheless, charophytes in the DZLS showed higher C:N and N:P ratios than tracheophytes, making them more likely to gammarid grazing as high-value food (Appendix S1: Figure S7). Furthermore, this preselection of high-value food may explain the differences in grazing rates on *C. tomentosa* versus *C. aspera* found in this study. *Chara tomentosa* can show higher C:N ratios (44:1) than *C. aspera* (27:1), making it maybe a less favorable food source. *Chara aspera* showed in our study signs of early decay at higher temperatures, contrary to *C. tomentosa* (see Appendix S1: Figure S3 for trends in control beakers). Such beginning decay can weaken *C. aspera* and make it more susceptible to grazing (Buchsbaum et al., 1991), explaining the deviation of grazing rates between both charophytes along the temperature gradient found in this study.

The drop in grazing rates during future summer conditions is probably caused by suboptimum water temperatures in combination with lowered salinities. The impact on future summer grazing is more pronounced in the Bodstedter Bodden than in the Grabow. This difference is probably caused by even lower salinity concentrations in the Bodstedter Bodden, indicating that future increased freshwater input can lead to shifts of preferred habitats.

Food preferences can change throughout the year depending on gammarid life stage and temperature (Felten et al., 2008; Pellan et al., 2016). Plant biomass becomes increasingly important, when temperatures increase and can reach up to 20%–30% of total food consumed (Pellan et al., 2016). Grazing on charophytes can happen earlier in the year and lasts longer during autumn. This effect does not come into effect in our future projection model, as the current modeled population densities of gammarids are lowest in spring. Nonetheless, prolonged grazing may hamper charophytes sprouting in spring (*C. aspera*) and lower biomass of overwintering species (*C. tomentosa*) (Blindow et al., 2016; Torn et al., 2006).

Functional feeding in gammarids relies furthermore on population composition and food availability (Kelly et al., 2002). Other food sources such as detritus, plant litter, or matter of animals, such as chironomids, are usually important food sources during wintertime (Felten et al., 2008, Pellan et al., 2016). Sediment organic content can be as high as 20% in sediments of the DZLS (Berthold, Zimmer, et al., 2018). Sediment detritus was not an alternative source in our experiments, as we used only inorganic sand. Plant litter occurs abundantly within the reed belt during wintertime in the DZLS (Karstens et al., 2016). Our experimental results show therefore only a potential grazing rate, as we did not represent the variety and abundance of alternative food sources from within the ecosystem.

Furthermore, grazing rates depend on niche occupation and competition with native and other invasive species. *Gammarus tigrinus* can probably outcompete the native *G. salinus*, if both depend on *Pylaiella littoralis* in the northern Baltic Sea (Orav-Kotta et al., 2009). Both gammarids had the potential to exceed daily macrophyte production during summer (Orav-Kotta et al., 2009).

Gammarus tigrinus may be more tolerant against heatwaves and hypoxic conditions than native species (Lenz et al., 2011). These broader temperature acclimation abilities may help to permanently introduce *G. tigrinus* within the Baltic Sea, as sea surface temperature is already higher there than in other ocean parts (Reusch et al., 2018). Furthermore, the endurance of hypoxic conditions is an advantage in eutrophic coastal waters of the Baltic, as redox conditions within the reed belt and adjacent macrophyte stands can change fast (Berthold & Paar, 2021; Karstens et al., 2015), and an increase in nutrients is challenging for submerged macrophytes in the coastal water bodies of the southern Baltic

Sea (Paar et al., 2021), stressing habitats of native gammarids. On the contrary, an in silico study assumed that *G. tigrinus* has actually a narrower niche than native gammarids in the northern Baltic Sea (Herkül et al., 2016). These results are somewhat contradictory to other studies in this area (Korpinen & Westerbom, 2009; Kotta et al., 2011; Lenz et al., 2011) and may have not considered the impact of haplotype diversity (Baltazar-Soares et al., 2017), which means locally adapted populations of *G. tigrinus*. Different studies revealed high genetic variability of *G. tigrinus* in the Baltic Sea (Appendix S1: Table S1 and Figure S2; Kelly et al., 2006; Paiva et al., 2018) which indicated that the invasive species may have different tolerance and different limits to salinities due to spatially varying selection among populations.

The patchy macrophyte stands found in the DZLS, and in other eutrophic water bodies, may affect the occurrence of *G. tigrinus*, and therefore the grazing rates, especially in intermediate and deeper waters. Palaemonid prawns put a higher grazing pressure on *G. tigrinus* in unvegetated mesocosms than in vegetated ones (Kuprijanov et al., 2015). It is likely that *G. tigrinus* stays close to the reed belt, as described for this lagoon and other coastal waters (Zettler, 1995, 2001). This spatial distribution would further hamper charophyte recolonization, as the shallow areas in the DZLS are the only spots, where light availability is high enough to support charophyte biomass (see Figure 2; Piepho, 2017). In general, the increasing abundance of charophytes in coastal areas with increasing freshwater inputs can be compensated for by simultaneously increased gammarid grazing.

ACKNOWLEDGMENTS

The authors thank the State Agency for Environment, Nature Conservation and Geology Mecklenburg-Vorpommern for providing monitoring data and the Aquaculture section in Born of the State Research Centre for Agriculture and Fishery Mecklenburg-Vorpommern for providing gammarids. We also want to thank Dr. Ralf Bastrop for providing the respective primers and Dr. Martin Paar for providing us with recent data on gammarid distribution in the southern Baltic Sea.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Berthold et al., 2021) are available from Figshare: https://doi.org/10.6084/m9.figshare.15209202.

ORCID

Maximilian Berthold https://orcid.org/0000-0003-1985-6426

REFERENCES

Auderset Joye, D., and A. Rey-Boissezon. 2015. "Will Charophyte Species Increase or Decrease Their Distribution in a Changing Climate?" *Aquatic Botany* 120: 73–83.

Auderset Joye, D., and A. Schwarzer. 2012. In *Red List Characeae. Threatened Species in Switzerland. Status 2010*, 1st ed., edited by D. Auderset Joye and A. Schwarzer. Geneva: Federal Office for the Environment FOEN, Laboratoire d'écologie et de biologie aquatique (LEBA), University of Geneva.

Baltazar-Soares, M., F. Paiva, Y. Chen, A. Zhan, and E. Briski. 2017. "Diversity and Distribution of Genetic Variation in Gammarids: Comparing Patterns between Invasive and Non-Invasive Species." *Ecology and Evolution* 7: 7687–98.

Berezina, N. A. 2007. "Expansion of the North American Amphipod *Gammarus tigrinus* Sexton, 1939 to the Neva Estuary (Easternmost Baltic Sea)." *Oceanologia* 49: 129–35.

Berthold, M. 2016. *The Influence of Phosphorus on the Eutrophication Process in the Darß-Zingst Bodden Chain*. Rostock: University of Rostock.

Berthold, M., U. Karsten, M. von Weber, A. Bachor, and R. Schumann. 2018. "Phytoplankton Can Bypass Nutrient Reductions in Eutrophic Coastal Water Bodies." *Ambio* 47: 146–58.

Berthold, M., S. Karstens, U. Buczko, and R. Schumann. 2018. "Potential Export of Soluble Reactive Phosphorus from a Coastal Wetland in a Cold-Temperate Lagoon System: Buffer Capacities of Macrophytes and Impact on Phytoplankton." *Science of the Total Environment* 616–617: 46–54.

Berthold, M., and M. Paar. 2021. "Dynamics of Primary Productivity in Relation to Submerged Vegetation of a Shallow, Eutrophic Lagoon: A Field and Mesocosm Study." *PLoS One* 16: e0247696.

Berthold, M., C. Porsche, A. Hofmann, and P. Nowak. 2021. "Temperature-Salinity Dependent Grazing Rates of *Gammarus tigrinus* on Charophytes." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.15209202.v1.

Berthold, M., D. Zimmer, V. Reiff, and R. Schumann. 2018. "Phosphorus Contents Re-Visited after 40 Years in Muddy and Sandy Sediments of a Temperate Lagoon System." *Frontiers in Marine Science* 5: 1–14.

Berthold, M., D. Zimmer, and R. Schumann. 2015. "A Simplified Method for Total Phosphorus Digestion with Potassium Persulphate at Sub-Boiling Temperatures in Different Environmental Samples." *Rostocker Meeresbiologische Beiträge* 25: 7–25.

Björkman, S. O. 1947. "On the Distribution of *Chara tomentosa* L. Round the Baltic and some Remarks on Its Specific Epithet." *Botaniska Notiser* 1947: 157–70.

Blazencic, J., B. Stevanovic, Z. Blazencic, and V. Stevanovic. 2005. "Red Data List of Charophytes in the Balkans." *Biodiversity and Conservation* 15: 3445–57.

Blindow, I. 2000. "Distribution of Charophytes along the Swedish Coastin Relation to Salinity and Eutrophication." *International Review of Hydrobiology* 85: 707–17.

Blindow, I., S. Dahlke, A. Dewart, S. Flügge, M. Hendreschke, A. Kerkow, and J. Meyer. 2016. "Long-Term and Interannual Changes of Submerged Macrophytes and Their Associated Diaspore Reservoir in a Shallow Southern Baltic Sea Bay: Influence of Eutrophication and Climate." *Hydrobiologia* 778: 121–36.

Blindow, I., J. Dietrich, N. Möllmann, and H. Schubert. 2003. "Growth, Photosynthesis and Fertility of *Chara aspera* under

Different Light and Salinity Conditions." *Aquatic Botany* 76: 213–34.

Blindow, I., N. Möllmann, M. G. Boegle, and M. Schütte. 2009. "Reproductive Isolation in *Chara aspera* Populations." *Aquatic Botany* 91: 224–30.

Blindow, I., and M. Schütte. 2007. "Elongation and Mat Formation of *Chara aspera* under Different Light and Salinity Conditions." *Hydrobiologia* 584: 69–76.

Buchsbaum, R., I. Valiela, T. Swain, M. Dzierzeski, and S. Allen. 1991. "Available and Refractory Nitrogen in Detritus of Coastal Vascular Plants and Macroalgae." *Marine Ecology Progress Series* 72: 131–43.

Chambers, M. R. 1977. "The Population Ecology of *Gammarus tigrinus* (Sexton, 1939) in the Reed Beds of the Tjeukemeer." *Hydrobiologia* 53: 155–64.

Choudhury, M. I., P. Urrutia-Cordero, H. Zhang, M. K. Ekvall, L. R. Medeiros, and L.-A. A. Hansson. 2019. "Charophytes Collapse beyond a Critical Warming and Brownification Threshold in Shallow Lake Systems." *Science of the Total Environment* 661: 148–54.

Daunys, D., and M. L. Zettler. 2006. "Invasion of the North American Amphipod (*Gammarus tigrinus* Sexton, 1939) into the Curonian Lagoon, South-Eastern Baltic Sea." *Acta Zoologica Lituanica* 16: 20–6.

Dorgelo, J. 1973. "Comparative Ecophysiology of Gammarids (Crustacea: Amphipoda) from Marine, Brackish and Fresh-Water Habitats Exposed to the Influence of Salinity-Temperature Combinations. III. Oxygen Uptake." *Netherlands Journal of Sea Research* 7: 253–66.

Dorgelo, J. 1974. "Comparative Ecophysiology of Gammarids (Crustacea: Amphipoda) from Marine, Brackish and Fresh-Water Habitats, Exposed to the Influence of Salinity-Temperature Combinations – I. Effect on Survival." *Hydrobiological Bulletin* 8: 90–108.

Felten, V., G. Tixier, F. Guérold, V. De Crespin De Billy, and O. Dangles. 2008. "Quantification of Diet Variability in a Stream Amphipod: Implications for Ecosystem Functioning." *Fundamental and Applied Limnology* 170: 303–13.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*, 3rd ed. Thousand Oaks, CA: Sage.

Gärdenfors, U. 2010. *2010 Rödlistade arter I Sverige (The 2010 Red List of Swedish Species)*. Uppsala: ArtDatabanken.

Gessner, F. 1957. In *Meer und Strand*, 2nd ed., edited by F. Gessner. Berlin: VEB Deutscher Verlag der Wissenschaften.

Hasslow, O. J. 1931. Sveriges characéer. Botaniska Notiser: 63–136.

HELCOM. 2010. "Ecosystem Health of the Baltic Sea 2003-2007: HELCOM Initial Holistic Assessment." *Baltic Sea Environment Proceedings* 122: 68.

HELCOM. 2018. "Sources and Pathways of Nutrients to the Baltic Sea." *Baltic Sea Environmental Proceedings* 153: 48.

Herkül, K., V. Lauringson, and J. Kotta. 2016. "Specialization among Amphipods: The Invasive *Gammarus tigrinus* Has Narrower Niche Space Compared to Native Gammarids." *Ecosphere* 7: 1–16.

Janssen, F., T. Neumann, and M. Schmidt. 2004. "Inter-Annual Variability in Cyanobacteria Blooms in the Baltic Sea Controlled by Wintertime Hydrographic Conditions." *Marine Ecology Progress Series* 275: 59–68.

Karstens, S., U. Buczko, and S. Glatzel. 2015. "Phosphorus Storage and Mobilization in Coastal Phragmites Wetlands: Influence of Local-Scale Hydrodynamics." *Estuarine, Coastal and Shelf Science* 164: 124–33.

Karstens, S., U. Buczko, G. Jurasinski, R. Peticzka, and S. Glatzel. 2016. "Impact of Adjacent Land Use on Coastal Wetland Sediments." *Science of the Total Environment* 550: 337–48.

Kelley, A. L. 2014. "The Role Thermal Physiology Plays in Species Invasion." *Conservation Physiology* 2: 1–14.

Kelly, D. W., J. T. A. Dick, and W. I. Montgomery. 2002. "The Functional Role of *Gammarus* (Crustacea, Amphipoda): Shredders, Predators, or Both?" *Hydrobiologia* 485: 199–203.

Kelly, D. W., J. R. Muirhead, D. D. Heath, and H. J. Macisaac. 2006. "Contrasting Patterns Ingenetic Diversity Following Multiple Invasions of Fresh and Brackish Waters." *Molecular Ecology* 15: 3641–53.

Koop, J. H. E., and M. K. Grieshaber. 2000. "The Role of Ion Regulation in the Control of the Distribution of *Gammarus tigrinus* (Sexton, 1939) in Salt-Polluted Rivers." *Journal of Comparative Physiology – B Biochemical, Systemic, and Environmental Physiology* 170: 75–83.

Körner, S., and T. Dugdale. 2003. "Is Roach Herbivory Preventing Re-Colonization of Submerged Macrophytes in a Shallow Lake?" *Hydrobiologia* 506–509: 497–501.

Korpinen, S., and M. Westerbom. 2009. "Microhabitat Segregation of the Amphipod Genus *Gammarus* (Crustacea: Amphipoda) in the Northern Baltic Sea." *Marine Biology* 157: 361–70.

Kotta, J., H. Orav-Kotta, K. Herkül, and I. Kotta. 2011. "Habitat Choice of the Invasive *Gammarus tigrinus* and the Native *Gammarus salinus* Indicates Weak Interspecific Competition." *Boreal Environment Research* 16: 64–72.

Kraufvelin, P., S. Salovius, H. Christie, F. E. Moy, R. Karez, and M. F. Pedersen. 2006. "Eutrophication-Induced Changes in Benthic Algae Affect the Behaviour and Fitness of the Marine Amphipod *Gammarus locusta*." *Aquatic Botany* 84: 199–209.

Kufel, L., and I. Kufel. 2002. "*Chara* Beds Acting as Nutrient Sinks in Shallow Lakes—A Review." *Aquatic Botany* 72: 249–60.

Kuprijanov, I., J. Kotta, V. Lauringson, and K. Herkül. 2015. "Trophic Interactions between Native and Alien Palaemonid Prawns and an Alien Gammarid in a Brackish Water Ecosystem." *Proceedings of the Estonian Academy of Sciences* 64: 518–24.

Lenz, M., B. A. P. da Gama, N. V. Gerner, J. Gobin, F. Gröner, A. Harry, S. R. Jenkins, et al. 2011. "Non-Native Marine Invertebrates Are More Tolerant towards Environmental Stress Than Taxonomically Related Native Species: Results from a Globally Replicated Study." *Environmental Research* 111: 943–52.

Lindner, A. 1972. *Soziologisch-ökologische Untersuchungen an der submersen Vegetation in der Boddenkette südlich des Darß und Zingst*. Rostock: University of Rostock.

Melzer, A. 1999. "Aquatic Macrophytes as Tools for Lake Management." *Hydrobiologia* 395(396): 181–90.

Neumann, T., and R. Friedland. 2011. "Climate Change Impacts on the Baltic Sea." In *Global Change and Baltic Coastal Zones*, edited by G. Schernewski, J. Hofstede, and T. Neumann, 23–32. Dordrecht: Springer.

Normant, M., M. Feike, A. Szaniawska, and G. Graf. 2007. "Adaptation of *Gammarus tigrinus* (Sexton, 1939) to New Environments—Some Metabolic Investigations." *Thermochimica Acta* 458: 107–11.

Nowak, P., H. Schubert, A. Holzhausen, V. Sommer, and R. Schaible. 2018. "Morphological adaptations of Chara baltica

and Charaliljebladii (Characeae) under different light conditions." *Botany Letters* 165: 67–75.

Orav-Kotta, H., J. Kotta, K. Herkül, I. Kotta, and T. Paalme. 2009. "Seasonal Variability in the Grazing Potential of the Invasive Amphipod *Gammarus tigrinus* and the Native Amphipod *Gammarus salinus* (Amphipoda: Crustacea) in the Northern Baltic Sea." *Biological Invasions* 11: 597–608.

Östman, Ö., J. Eklöf, B. K. Eriksson, J. Olsson, P. O. Moksnes, and U. Bergström. 2016. "Top-Down Control As Important as Nutrient Enrichment for Eutrophication Effects in North Atlantic Coastal Ecosystems." *Journal of Applied Ecology* 53: 1138–47.

Paar, M., M. Berthold, R. Schumann, S. Dahlke, and I. Blindow. 2021. "Seasonal Variation in Biomass and Production of the Macrophytobenthos in Two Lagoons in the Southern Baltic Sea." *Frontiers in Earth Science* 8: 1–16.

Paiva, F., A. Barco, Y. Chen, A. Mirzajani, F. T. Chan, V. Lauringson, M. Baltazar-Soares, et al. 2018. "Is Salinity an Obstacle for Biological Invasions?" *Global Change Biology* 24: 2708–20.

Pellan, L., V. Médoc, D. Renault, T. Spataro, and C. Piscart. 2016. "Feeding Choice and Predation Pressure of Two Invasive Gammarids, *Gammarus tigrinus* and *Dikerogammarus villosus*, under Increasing Temperature." *Hydrobiologia* 781: 43–54.

Piepho, M. 2017. "Assessing Maximum Depth Distribution, Vegetated Area, and Production of Submerged Macrophytes in Shallow, Turbid Coastal Lagoons of the Southern Baltic Sea." *Hydrobiologia* 794: 303–16.

Pitkänen, H., M. Peuraniemi, M. Westerbom, M. Kilpi, and M. Von Numers. 2013. "Long-Term Changes in Distribution and Frequency of Aquatic Vascular Plants and Charophytes in an Estuary in the Baltic Sea." *Annales Botanici Fennici* 50: 1–54.

Pohl, P., M. K. Ohlhase, S. K. Rautwurst, and K. Laus-Kinnerk Baasch. 1987. "An Inexpensive Inorganic Medium for the Mass Cultivation of Freshwater Microalgae." *Phytochemistry* 26: 1657–9.

Puche, E., S. Sánchez-Carrillo, M. Álvarez-Cobelas, A. Pukacz, M. A. Rodrigo, and C. Rojo. 2018. "Effects of Overabundant Nitrate and Warmer Temperatures on Charophytes: The Roles of Plasticity and Local Adaptation." *Aquatic Botany* 146: 15–22.

Puntila, R. 2016. *Trophic Interactions and Impacts of Non-indigenous Species in Baltic Sea Coastal Ecosystems*. Helsinki: University of Helsinki.

R Core Team. 2013. *R: A Language and Environment for Statistical Computing*. Vienna: Austria.

Reusch, T. B. H., J. Dierking, H. C. Andersson, E. Bonsdorff, J. Carstensen, M. Casini, M. Czajkowski, et al. 2018. "The Baltic Sea as a Time Machine for the Future Coastal Ocean." *Science Advances* 4: eaar8195.

Rojo, C., M. Carramiñana, D. Cócera, G. P. Roberts, E. Puche, S. Calero, and M. A. Rodrigo. 2017. "Different Responses of Coexisting *Chara* Species to Foreseeable Mediterranean Temperature and Salinity Increases." *Aquatic Botany* 138: 53–63.

Sañudo-Wilhelmy, S. A., A. Tovar-Sanchez, F. X. Fu, D. G. Capone, E. J. Carpenter, and D. A. Hutchins. 2004. "The Impact of Surface-Adsorbed Phosphorus on Phytoplankton Redfield Stoichiometry." *Nature* 432: 897–901.

Schiewer, U. 2007. "Darß-Zingst Boddens, Northern Rügener Boddens and Schlei." In *Ecology of Baltic Coastal Waters*, 1st ed., edited by U. Schiewer, M. M. Caldwell, G. Heldmaier, R. B. Jackson, O. L. Lange, H. A. Mooney, E.-D. Schulze, and U. Sommer, 35–86. Berlin, Heidelberg: Springer.

Schubert, H., and I. Blindow, eds. 2003. *Charophytes of the Baltic Sea*. Ruggell: Gantner.

Schubert, H., I. Blindow, N. C. Bueno, M. T. Casanova, M. Pełechaty, and A. Pukacz. 2018. "Ecology of Charophytes – Permanent Pioneers and Ecosystem Engineers." *Perspectives in Phycology* 5: 61–74.

Schumann, R., H. Baudler, Ä. Glass, K. Dümcke, and U. Karsten. 2006. "Long-Term Observation on Salinity Dynamics in a Tideless Shallow Coastal Lagoon of the Southern Baltic Sea Coast and Their Biological Relevance." *Journal of Marine Systems* 60: 330–44.

Stewart, N. F., and J. M. Church. 1992. *Red Data Books of Britain and Ireland—Stoneworts*. Peterborough: Joint Nature Conservation Committee and Office of Public Works and Plantlife.

Torn, K., K. Herkül, A. Peterson, and Ü. Suursaar. 2020. "Predicting Potential Effects of Climate Change on Benthic Species: Current and Future Distribution of Native and Non-Native Charophytes and Amphipods." *WIT Transactions on Ecology and the Environment* 245: 85–95.

Torn, K., G. Martin, and R. Munsterhjelm. 2003. "*Chara tomentosa* L. 1753." In *Charophytes of the Baltic Sea*, edited by H. Schubert and I. Blindow, 131–41. Ruggell: Gantner.

Torn, K., G. Martin, and T. Paalme. 2006. "Seasonal Changes in Biomass, Elongation Growth and Primary Production Rate of *Chara tomentosa* in the NE Baltic Sea." *Annales Botanici Fennici* 43: 276–83.

Torn, K., A. Peterson, and K. Herkül. 2020. "Predicting the Impact of Climate Change on the Distribution of the Key Habitat-Forming Species in the NE Baltic Sea." *Journal of Coastal Research* 95: 177.

van der Linden, P., and J. F. B. Mitchell. 2009. In *ENSEMBLES: Climate Change and Its Impacts: Summary of Research and Results from the ENSEMBLES Project*, edited by P. van der Linden and J. F. B. Mitchell. Exeter: Met Office Hadley Centre.

Volkmann, C. 2016. *The Impact of Organic Material for Macrophytes in Coastal Waters of the Baltic Sea*. Rostock: University of Rostock.

Wood, S. N. 2011. "Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models." *Journal of the Royal Statistical Society (B)* 73: 3–36.

Wüstenberg, A., Y. Pörs, and R. Ehwald. 2011. "Culturing of Stoneworts and Submersed Angiosperms with Phosphate Uptake Exclusively from an Artificial Sediment." *Freshwater Biology* 56: 1531–9.

Zettler, M. L. 1995. "Erstnachweis von *Gammarus tigrinus* Sexton, 1939 (Crustacea: Amphipoda) in der Darss-Zingster-Boddenkette und seine derzeitige Verbreitung an der deutschen Ostsekueste." *Archiv der Freunde der Naturgeschichte in Mecklenburg* XXXIV: 137–41.

Zettler, M. L. 2001. "Some Malacostracan Crustacean Assemblages in the Southern and Western Baltic Sea." *Rostocker Meeresbiologische Beiträge* 9: 127–43.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Berthold, Maximilian, Christian Porsche, Antonia Hofmann, and Petra Nowak. 2022. "Increases in Temperature and Freshwater Inputs Will Shift Grazing Patterns of a Coastal Mesograzer on Foundation Species." *Ecosphere* 13(5): e4062. https://doi.org/10.1002/ecs2.4062