In Hot Water: How Non-native Shrimp Modify Baltic Sea Trophic Dynamics

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Author:
Stefanie Coxe

Supervisors:
Dr. Ulrika Candolin, University Lecturer
Tawfiqur Rahman, PhD Researcher
Linnea Kivelä, PhD Researcher

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Supervisor or supervisors: Ulrika Candolin, Tawfiqur Rahman, and Linnea Kivelä
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Abstract:

Climate change transforms ecosystems and creates disruptions to biological networks by altering abiotic factors like temperature and oxygen levels. Biological invasions weaken ecosystem stability by altering competitor or predatory pressures, altering trophic dynamics. The effects of these two factors can be amplified when acting together. The Baltic Sea is a unique marine environment due to its low salinity and slow water exchange and is experiencing rapid warming trends. One species that has taken advantage of this environment is *Palaemon elegans* due to its high tolerance for low salinity and warming. Although climate change and biological invasions are researched separately, few studies have looked at the effects of their interaction, especially in marine systems. Here, we investigate how the interaction of global warming and the non-native mesopredator *P. elegans* changes trophic dynamics in the Baltic Sea.

We manipulated temperature and shrimp presence using a 30-day 2×2 factorial mesocosm design. We found that the interaction of shrimp and warming increased algal biomass and some zooplankton body lengths, while the positive effect of shrimp on phytoplankton was mitigated by warming. In warm treatments, shrimp biomass decreased, and in the absence of shrimp, phytoplankton biomass and zooplankton densities increased. Shrimp presence in ambient temperature caused a reduction in amphipod biomass and some zooplankton densities, while increasing phytoplankton biomass. These outcomes reflect direct predation and structural changes in trophic dynamics, such as prey abundances, weakened top-down control, and shifts in energy flow. We provide insights for future ecological research by improving understanding of how warming and biological invasions interact in the Baltic Sea to reshape food web structure and functioning, causing trophic cascades. Incorporating these interactions into ecological planning and management strategies will be essential for protecting biodiversity and sustaining ecosystem services in marine systems.

Table of contents

1 Introduction

1.1 Environmental stressors

Two factors that disrupt ecological systems are climate change and invasive species. One of the effects of climate change is that it creates disruptions to biological networks by altering abiotic factors like temperature and oxygen levels (Doney et al., 2012). Climate change transforms ecosystems. For instance, coral bleaching is triggered by rising sea temperatures (Van Woesik et al., 2022). The response to increased temperature depends on a species' life history. Native species' efficiency may be constrained, while potentially invasive non-native species tend to have more success because they have broader thermal tolerances than native species (McKnight et al., 2021).

The other factor, biological invasions, may introduce novel parasites (Albins & Hixon, 2013) and weaken ecosystem stability by altering competitor or predatory pressures (Kotta et al., 2018). An example of a successful invasive species is the lionfish (*Pterois volitans*) in the western Atlantic. This species preys on native reef fish, reducing fish recruitment and destabilizing predator-prey dynamics (Albins & Hixon, 2013). These changes alter trophic dynamics, the interactions among organisms at different feeding levels that govern energy flow and nutrient cycling (Brown et al., 2004).

Climate change and biological invasions have individual effects, but the disturbances they cause to the ecosystem can be amplified when acting together (Mainka & Howard, 2010). Take, for example, the European green crab (*Carcinus maenas*), which has expanded its range along North American coasts due to warming (Yamada et al., 2021). This trend of warming waters has promoted the introduced crabs' survival and reproduction (Yamada et al., 2021), leading to habitat loss and declines in biodiversity.

In a stable ecosystem, species at higher trophic levels help regulate the populations of those below them through predation that scales with prey abundance (Schmitz et al., 2010). However, this control can weaken under environmental stress, such as rapid warming or the introduction of invasive predators. These imbalances can also occur from other than the highest trophic levels. For example, if primary producers proliferate due to increased nutrient inputs or warming and consumers cannot respond quickly enough then trophic imbalances can emerge (Doney et al., 2012; Kotta et al., 2018).

1.2 Ecological impact of non-native shrimp

The Baltic Sea is semi-enclosed and vulnerable to disruptions due to its unique conditions (Reckermann et al., 2022). Some of these conditions are low salinity (Kotta et al., 2018) and slow water exchange (Dutheil et al., 2022). Additionally, the Baltic Sea is said to have one of the fastest warming trends among any semi-enclosed sea (Dutheil et al., 2022), which alters trophic interactions by favoring some species while disadvantaging others.

One species that seems to have taken advantage of these changes is *Palaemon elegans* by rapidly expanding into the Gulf of Finland (Candolin et al., 2018) since its presence was first recorded in Tvärminne in 2003 (Lavikainen & Laine, 2004). Its capacity for low salinity and warming may have facilitated its spread (Janas et al., 2013). The species has a historic natural distribution that includes the North Sea, east coast of the Atlantic Ocean, the Mediterranean Sea, and the Black Sea (Lavikainen & Laine, 2004). As an opportunistic omnivore, it preys on a broad range of organisms, including benthic invertebrates, detritus, and macroalgae (Katajisto et al., 2013), leading to shifts in ecosystem structure (Doney et al., 2012).

As a non-native species in the Baltic Sea, *P. elegans* alters species interactions, triggering trophic cascades (Kotta et al., 2018). These trophic cascades cause system-wide shifts that spread through the food web (Figure 1) and affect ecosystem functions (Pace et al., 1999). The introduction or loss of predators shift herbivore and primary producer populations, destabilizing ecosystems (Schmitz et al., 2010). Mesopredators like *P. elegans,* acting as both predator and prey, can influence ecosystem dynamics, especially under climate-driven shifts (Elmhagen & Rushton, 2007).

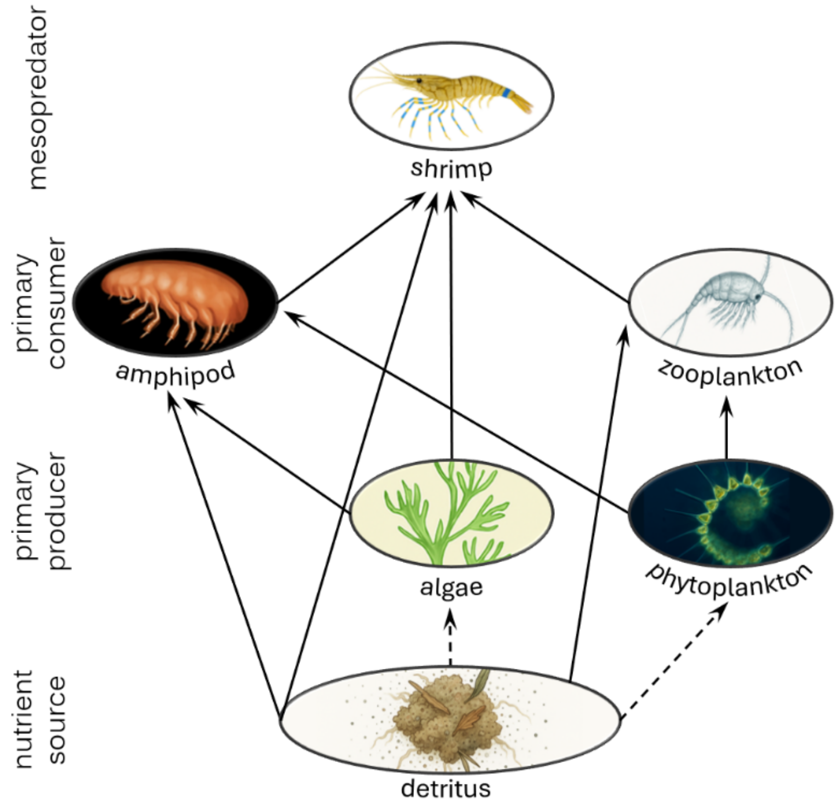

Figure 1. Simplified food web of mesocosm organisms. Solid lines signify direct energy transfer, while dashed lines depict indirect energy transfer. Figure created from images created by ChatGPT and adapted by the author.

1.3 Research gap

While studies such as Kindree et al. (2024) have explored how climate change and biological invasions interact in aquatic environments, there is a lack of region-specific research, such as in the Baltic Sea. Understanding the combined impacts of these stressors on trophic dynamics and ecosystem stability remains a critical knowledge gap. Trophic cascades in the Baltic Sea are caused by the presence of *P. elegans*, directly reducing grazer populations and indirectly increasing algal biomass (Liversage et al., 2021). However, knowing how and if climate warming amplifies these cascades and thereby intensifies predation pressure and the alteration of food webs remains underexplored.

According to the metabolic theory of ecology (MTE), organisms experience increased energetic requirements and activity as temperatures rise, which affects ecological interactions and energy flow across trophic levels (Brown et al., 2004). This may have implications for *P. elegans'* effect on trophic cascades, especially since Gómez et al. (2024) observed higher activity and feeding rates in *P. elegans* in the Baltic Sea when compared to the native shrimp *Palaemon adspersus*. Studies on non-native and invasive species in response to warming by McKnight et al. (2021) and Kindree et al. (2024) have shown increased feeding efficiency and reproductive success as a consequence of accelerated metabolic rates.

Since warming facilitates the spread of invasives and also amplifies their environmental effects, this could prompt cascading ecological impacts, diminishing species diversity and food web functions (Mainka & Howard, 2010). However, the extent to which these effects will be amplified remains understudied. To address these knowledge gaps, we investigated how the combined effects of warming and non-native species, specifically *P. elegans*, influence trophic dynamics in the Baltic Sea.

1.4 Hypotheses and expected contributions

Because the shrimp's preferred food items are invertebrates (Katajisto et al., 2013), we hypothesize that the presence of *P. elegans* reduces herbivore and zooplankton populations, weakening grazing pressure on primary producers. Additionally, since warmer conditions may increase metabolic rates, we predict amplified energy demands, thereby intensifying the effects of shrimp presence. Conversely, we hypothesize that in the absence of *P. elegans*, warming supports herbivore and zooplankton growth, strengthening grazing pressure and reducing phytoplankton and algal abundance. We conducted a mesocosm experiment to test these hypotheses by manipulating shrimp presence and temperature.

Our study provides insights for future ecological research by improving our understanding of how warming and invasive mesopredators interact in the Baltic Sea. Our findings contribute to broader research on species interactions under changing environmental conditions. These results may also inform future research or mitigation strategies regarding biological invasion impacts under warming scenarios.

2 Methods

2.1 Study site

We investigated warming and non-native shrimp effects on Baltic Sea trophic dynamics through a 30-day mesocosm experiment at Tvärminne Zoological Station (TZS) in Finland. The climate chambers at TZS provided controlled temperatures, while the greenhouse, which housed algae homogenization tanks and spare shrimp, was exposed to natural temperature fluctuations and photoperiods. Traps were set in a bay at Långskär (59°49'N 23°15'E), a nearby island in the westernmost part of the Gulf of Finland. This bay was chosen because *P. elegans* have been regularly observed in Långskär (Candolin et al., 2018). The experiment began on June 7, 2024, with only seawater added after the experiment began.

2.2 Species

2.2.1 Shrimp

Shrimp collection was conducted between June 2 and June 18, 2024. The traps, proven successful by Candolin et al. (2018), were transparent Plexiglas boxes (20 × 20 × 40 cm) equipped with wings designed to guide organisms toward the opening with a net attached to the back to prevent escape. Traps were placed at depths of 30 cm and 80 cm at three locations within the bay.

The trapped shrimp were identified to species level and the initial size was recorded, retaining those that met the minimum required length, while others were released. Only individuals with a total length (TL) of at least 40 mm were included in the study, as this threshold ensured the inclusion of adult shrimp. Bilgin et al. (2009) found that the maximum TL of female *P. elegans* in their study was 56 mm TL (38.44 ± 0.11 mm), while the largest male in their study was 55 mm TL (31.98 ± 0.16 mm). Our shrimp of undetermined sex and age ranged from 40 mm to 56 mm TL (mean 44.4 ± 3.08 mm) measured from the tip of the rostrum to the tip of the telson and had an initial mean body mass of 0.96 ± 0.26 g (N = 200).

The collected *P. elegans* were transported to TZS and placed in multiple glass holding tanks with flow-through until their transfer to experimental mesocosms. While in the holding tanks, shrimp were fed daily with thawed *Chironomus sp.* larvae. Ten shrimp per mesocosm were added to shrimp present treatments at the start of the experiment (Figure 2). Determining the precise natural density of *P. elegans* in the Baltic Sea is challenging due to a lack of systematic studies (Kotta & Kuprijanov, 2012), possible nocturnal behavior (Katajisto et al., 2013), and density variation observed between sites over several years (Candolin et al., 2018). However, the selected density was based on densities used in a similar study by Jakubavičiūtė et al. (2025). Once the experiment began, the shrimp's diet depended only on naturally occurring and regenerating food sources within each mesocosm.

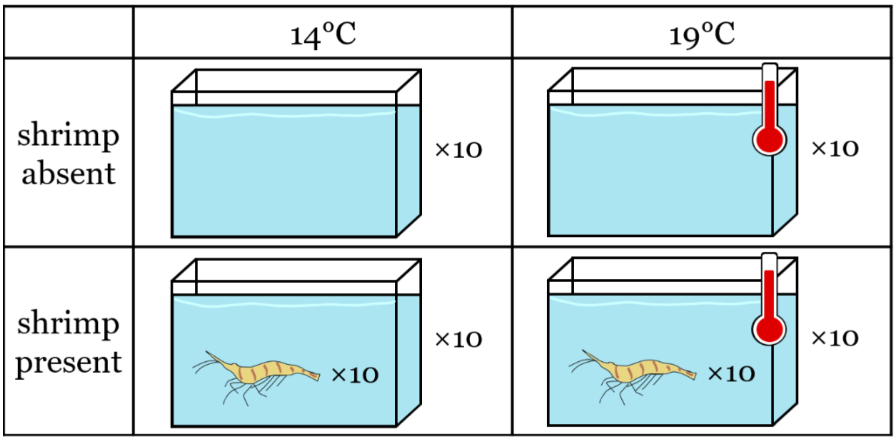

Figure 2. Experimental design of the 2×2 factorial mesocosm setup. Image created by the author.

To account for mortality during the experiment, extra shrimp were kept in the greenhouse holding tank and used as replacements when necessary. Over the experimental period, 12 shrimp died across the mesocosms and were replaced with individuals from the holding tank. Replacement shrimp were selected to match the deceased shrimp in length as closely as possible. The observed mortality rate was lower than the natural mortality rate of 97% within *P. elegans*' first-year (Vejan et al., 2022). This suggests that mortality patterns did not increase solely due to treatments.

2.2.2 Algae

The primary producer used in this study was *Cladophora glomerata*, a filamentous algal species. Algae were detached from rocky substrate by hand from shorelines at TZS between June 3 and June 4. To prepare the 40 algae mats, 150 g of wet-weight *C. glomerata* was attached to a (60 × 30 cm) 2 × 2 mm mesh vinyl-coated wire fence using green thread.

To ensure homogenization and equal distribution of the associated invertebrate fauna, the mats were placed into two glass aquaria with flow-through in the greenhouse. After three days, mats were transferred to the mesocosms. Additionally, a small stone was placed on top of the net to secure it.

2.2.3 Amphipod

Benthic macroinvertebrates, including gastropods, isopods, and amphipods (*Gammarus* sp.), naturally inhabited the algae and were incidentally collected along with the algae. Each mesocosm received 15 supplemental amphipods of consistent total biomass. They were gathered from nearshore TZS and homogenization tanks, where some had detached from the algae mats during processing. This was done to ensure a minimum amphipod density per treatment in case the algae net did not contain any amphipods. This emphasis on amphipod density was important because gammarids serve as the primary prey of *P. elegans* (Persson et al., 2008).

2.2.4 Zooplankton

Zooplankton taxa studied were rotifers, copepods, and cladocerans, which were associated with algae and continuously supplied through the inflow.

2.2.5 Phytoplankton

Phytoplankton was also naturally supplied through the inflow, ensuring relatively equal distribution across treatments.

2.3 Experimental design

Following a similar approach to Rahman et al. (2024), who examined temperature and mesopredator effects using threespine stickleback, we used a 2 × 2 factorial design. The four treatments included ambient temperature without shrimp, ambient temperature with shrimp, warm temperature without shrimp, and warm temperature with shrimp. Each treatment had 10 replicates, totaling 40 mesocosms. Half of the mesocosms were housed in each temperature treatment. To maintain 19°C, we used aquarium heaters (EHEIM thermocontrol 50W).

The setup included algae and benthic fauna to replicate natural Baltic Sea conditions. Water temperatures during the experiment were 13.91 ± 0.37°C for the 14°C treatment and 18.61 ± 1.05°C for the 19°C treatment. The 14°C treatment represents the June average (14.59 ± 0.66°C; 2019-2023; *North Sea/Baltic Sea - Sea Surface Temperature Analysis L3S.*) in Baltic Sea nearshore habitats where *P. elegans* occur. While the 19°C treatment represents regional high-temperature events in June (19.09 ± 2.6°C; 2019-2023; *North Sea/Baltic Sea - Sea Surface Temperature Analysis L3S.*) that may become more frequent as heatwaves occur more often due to climate change (Thompson et al., 2023).

Each mesocosm consisted of a 52 L plastic box with a continuous seawater inflow system. Water capacity was set at 30.5 L via an outflow hole, sealed with a cork, and fitted with 0.2 mm mesh to prevent shrimp and other organisms from escaping. Programmable LED lights (Aqua Medic Aquarius 120, 128W) were installed 52 cm above the water surface, following the natural photoperiod. Mesocosms ran for 24 hours to come to temperature before adding organisms.

2.4 Data collection

2.4.1 Mesocosm

We recorded dissolved oxygen (DO) concentration and temperature daily using a handheld meter (YSI ProSolo Optical Dissolved Oxygen Meter), adjusting inflow rate and heaters or climate chamber temperature as needed to maintain intended mesocosm temperature and oxygen levels. The mesocosms were also checked twice daily for shrimp mortality and any water flow issues. DO values were influenced by the flow applied to the system; therefore, we actively maintained DO levels (7.68 to 11.98 mg/L) within a range sufficient to support organism health (above the precautionary threshold of 6 mg/L; Piehl et al., 2023). We stopped the inflow after the 30-day experiment and collected ~500 mL of water per mesocosm for phytoplankton processing.

2.4.2 Shrimp

In addition to measuring the standard weight and TL of the shrimp before the experiment, we also took measurements afterward to observe growth trends under experimental conditions. All shrimp were released after the study.

2.4.3 Algae

At the end of the experiment, we removed algae from the mats and poured each mesocosm through a mesh sieve to collect all solid materials. We further separated flora from fauna and determined algal biomass by drying samples at 70°C for three days.

2.4.4 Amphipod

We assessed the abundance and biomass of amphipods. We recorded the total number of individuals for each mesocosm and determined biomass by drying the organisms at 60°C for two days before weighing. Gastropods and isopods were inconsistently present across mesocosms and therefore were excluded from further analysis.

2.4.5 Zooplankton

We collected zooplankton by filtering the entire remaining volume of each mesocosm through a 50 µm mesh net. We fixed the collected organisms in 4% formalin in brown-glass bottles to maintain their structural integrity (Nordeide, 2020) until microscopy. Although formalin may cause shrinkage (Nordeide, 2020), we assumed this effect would be uniform across all taxa. To prepare samples for microscopy, we used a plankton counting chamber consisting of a sedimentation chamber, base plate, and glass cover. At least two hours before microscopy, we prepared multiple base plate slides per bottle to allow the zooplankton to settle into the chamber. We counted, measured (in µm), and identified zooplankton taxa using an Olympus CKX41 Inverted Microscope with phase-contrast optics. We calculated zooplankton density by dividing the number of individuals of each taxon by the total water volume in each mesocosm (individuals per liter).

2.4.6 Phytoplankton

We measured chlorophyll-a concentration as a proxy for phytoplankton biomass since it is a key photosynthetic pigment found in all phytoplankton. To quantify chlorophyll-a, we vacuum-filtered 240-507 mL of water (mean 465 ± 55.78 mL) from each mesocosm through Whatman GF/F glass microfiber filters (25 mm diameter) and stored the filters at -20°C overnight to prevent pigment degradation before processing (Aminot & Rey, 2000). We then submerged filters in 10 mL of ethanol and allowed them to extract for 24 hours before measuring chlorophyll-a concentration (µg/L) using a Cary Eclipse fluorescence spectrophotometer with an excitation wavelength of 430 nm and an emission wavelength of 670 nm.

2.5 Data analysis

Statistical analyses were conducted using R v.4.4.2 (R Core Team, 2024) and RStudio v. 2024.12.1.563 (Posit team, 2025) to evaluate the influence of shrimp presence and warming, as well as the interaction between these two factors on amphipods, zooplankton, algae, and phytoplankton biomass and/or abundance. In addition, we analyzed the influence of temperature on shrimp biomass. Analyses were conducted separately for each response variable using packages dplyr (Wickham et al., 2023) and tidyr (Wickham et al., 2024) for data manipulation.

Prior to modeling, response variable distributions were assessed using Shapiro-Wilk tests, histograms, and Quantile-Quantile (Q-Q) plots to evaluate normality and determine the need for transformation. After model fitting, the four standard diagnostic plots (residuals vs. fitted, Q-Q plot, scale-location, and residuals vs. leverage) were used to assess model assumptions, including the normality and homoscedasticity of residuals. For linear models, residual histograms (R package ggplot2; Wickham, 2016) were used to assess normality, and the Breusch-Pagan test (R package lmtest; Zeileis & Hothorn, 2002) was used to assess homoscedasticity. For Poisson and Negative Binomial models (R package MASS; Venables & Ripley, 2002), dispersion statistics were calculated using Pearson residuals to assess model fit and detect potential overdispersion. Akaike Information Criterion (AIC) was used to select the best-fitting model with the lowest estimated information loss when models were directly comparable.

2.5.1 Shrimp

A linear model was used to compare net changes in shrimp body mass in response to temperature. Body mass was continuous and approximately normally distributed.

2.5.2 Algae

A linear model was used to assess algal biomass with shrimp, temperature, and their interaction as predictors. The data was continuous and normally distributed.

2.5.3 Amphipod

A negative binomial generalized linear model (GLM) was selected to model amphipod abundance (AIC = 318.4), with shrimp presence and temperature included as main effects after the interaction term was removed due to non-significance. This model was appropriate for positively skewed count data that included zeros and was chosen after diagnostic checks of an initial Poisson GLM showed overdispersion (dispersion ratio = 137.5 vs. 1.17) and a higher AIC (3934.7).

Amphipod biomass was assessed using a linear model with a cube root transformation. The response variable was continuous and positively skewed, and the transformation addressed zeros and stabilized variance. Interaction terms were excluded due to lack of significance, allowing for clearer interpretation of the main effects. Models not selected included a log-transformed linear model, whose diagnostic plots violated linear model assumptions, including normality and constant variance of residuals, and a Gamma GLM with a log link, which showed weaker alignment with model assumptions based on residual diagnostics.

2.5.4 Zooplankton

Zooplankton densities (individuals per liter), calculated as total count of each taxon divided by the measured mesocosm water volume, resulted in continuous, non-integer response variables with zeros and right-skewed distributions. These were analyzed using Gamma GLMs with a log link. For each taxon (rotifer, copepod, and cladoceran), models included only the main effects of shrimp presence and temperature, as interaction terms were removed after being found non-significant. A small constant (1×10^{-6}) was added to accommodate the log link function and address zero values. Alternatively, log-transformed linear models were evaluated but rejected due to departures from normality and large residual variance.

Linear models or Gamma GLMs with a log link were used to model zooplankton lengths since these variables were positive, continuous measurements. For copepod lengths (with interaction terms), the linear model was selected based on its lower AIC (7216) and reasonably well-behaved residual plots, while the Gamma GLM showed a higher AIC (7287.5) and its residual diagnostics suggested a poorer fit to the data. For rotifer lengths (with main effects only), a Gamma GLM was selected based on its lower AIC (3601.8) and more appropriate residual patterns compared to the linear model (AIC = 3608.4). For cladoceran lengths (with interaction terms), the Gamma GLM (AIC = 3185.3) was chosen for improved diagnostics over the linear model (AIC = 3236.9).

2.5.5 Phytoplankton

We used a linear model to analyze chlorophyll-a concentration with shrimp, temperature, and their interaction as predictors. The continuous variable was log-transformed to address positive skew and approximate normality.

3 Results

3.1 Shrimp

A linear model revealed a significant effect of temperature on shrimp body mass change ($F_{1,18} = 57.83$, $p = <0.001$). Raw means showed the net body mass change at 19°C was -0.157 ± 0.043 g, while those at 14°C experienced less change of -0.011 ± 0.044 g (model estimate = −0.147 ± 0.019 g, $t_{18} = -7.60$, $p < 0.001$; Figure 3).

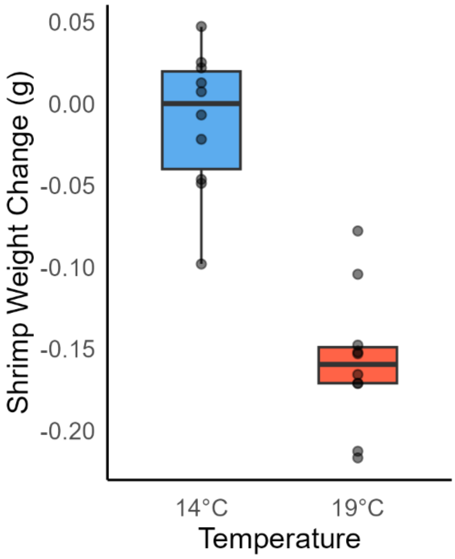

Figure 3. Boxplot illustrating the influence of temperature on shrimp net weight change. The horizontal line inside each box denotes the median, while the box spans the IQR. Whiskers extend to the smallest and largest values within 1.5 times the IQR. Individual data points correspond to the mean for each mesocosm, calculated from measurements of 10 shrimp per mesocosm (N = 20).

3.2 Algae

The linear model showed a positive significant interaction between shrimp presence and temperature on algal biomass ($F_{3,36} = 4.10$, $p = 0.013$; Table 1), revealing that the influence of shrimp is temperature-dependent, with stronger effects observed at higher temperatures (Figure 4).

Table 1. Summary of regression coefficients, standard errors, t-values, and p-values from the linear model (N = 40) examining the effects of shrimp presence and temperature on algal biomass.

Treatment	Estimate	SE	t	p
Algal Biomass				
Temperature	-0.189	0.196	-0.966	0.340
Shrimp	-0.028	0.196	-0.144	0.886
Temperature × Shrimp	0.681	0.277	2.457	0.019

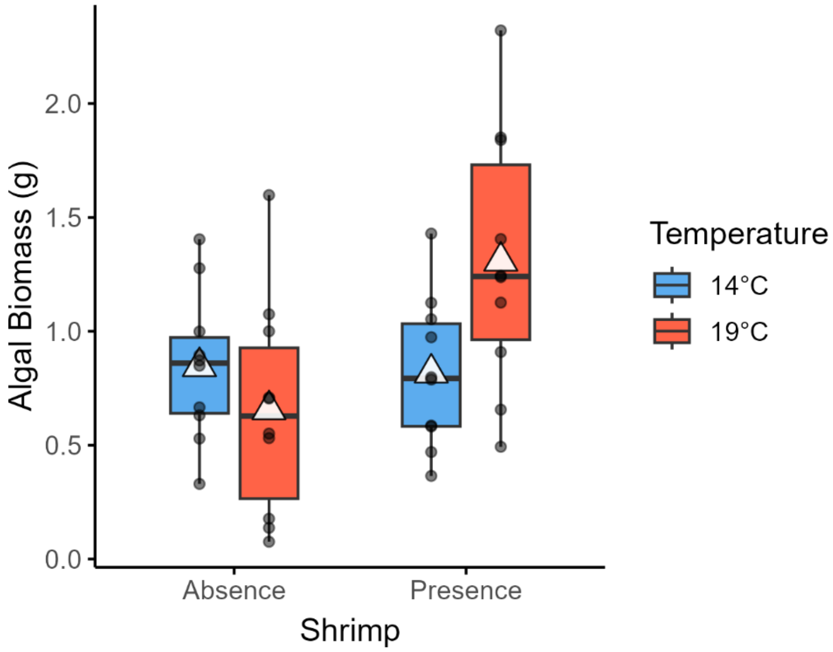

Figure 4. Boxplot illustrating the influence of shrimp presence and temperature on algal biomass. The horizontal line inside each box denotes the median, while the box represents the interquartile range (IQR, 25th to 75th percentile). Whiskers extend to the smallest and largest values within 1.5 times the IQR, highlighting variability within each treatment. The triangle represents the mean. Individual dots represent the total algal biomass recorded from each mesocosm.

3.3 Amphipod

The GLM revealed a significant effect of shrimp on amphipod abundance, with a 98.7% decrease in the presence of shrimp (based on raw means; Figure 5). Abundance declined from 192 ±293 at 14°C in shrimp-free mesocosms to 2.3 ±1.7 individuals when shrimp were present. A similar pattern was observed at 19°C, with abundance decreasing from 103 ±103 to 1.4 ±0.97. Temperature had no significant effect (Table 2).

The linear model used to analyze amphipod biomass also revealed a significant negative effect of shrimp presence ($F_{2,37} = 38.49$, $p < 0.001$; Figure 5). Temperature had no significant effect (Table 2).

Table 2. Summary of regression coefficients for the models examining amphipod abundance (N = 40) and biomass (N = 40).

Treatment	Estimate	SE	z	p
Amphipod Abundance				
Temperature	-0.579	0.323	-1.792	0.073
Shrimp	-4.365	0.334	-13.085	<0.001
	Estimate	SE	t	p
Amphipod Biomass				
Temperature	-0.029	0.049	-0.608	0.547
Shrimp	-0.425	0.049	-8.753	<0.001

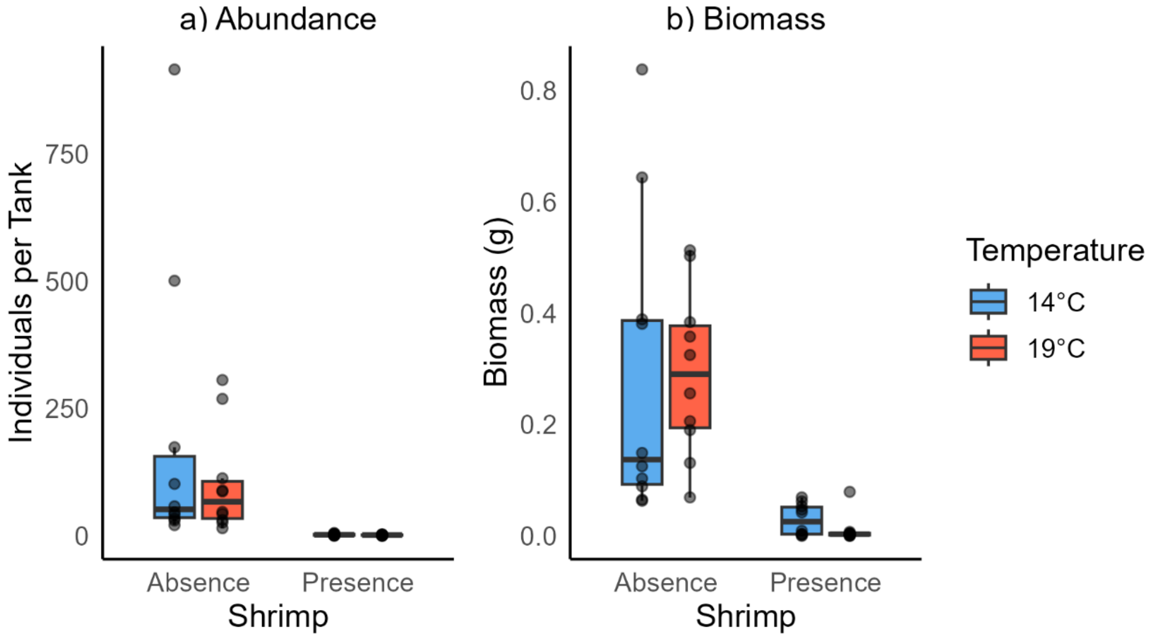

Figure 5. Boxplots illustrating the influence of shrimp presence and temperature on a) amphipod abundance and b) amphipod biomass. The horizontal line inside each box denotes the median, while the box spans the IQR. Whiskers extend to the smallest and largest values within 1.5 times the IQR. Each dot represents the abundance or biomass from each mesocosm.

3.4 Zooplankton

GLMs revealed consistent trends across zooplankton densities (Table 3). Temperature had a highly significant positive effect on all three taxa, with predicted densities at 19°C being approximately 2.8-3.6 times higher than at 14°C. Shrimp presence generally reduced zooplankton densities, with significant negative effects on rotifers and cladocerans and a non-significant negative trend for copepods (Figure 6).

Table 3. Summary of regression coefficients for Gamma GLMs with a log link examining zooplankton density (N = 40 mesocosms).

Treatment	Estimate	SE	t	p
Copepod				
Temperature	1.271	0.286	4.439	<0.001
Shrimp	-0.510	0.286	-1.780	0.083
Rotifer				
Temperature	1.032	0.208	4.964	<0.001
Shrimp	-0.602	0.208	-2.894	0.006
Cladoceran				
Temperature	1.101	0.282	3.912	<0.001
Shrimp	-0.784	0.282	-2.787	0.008

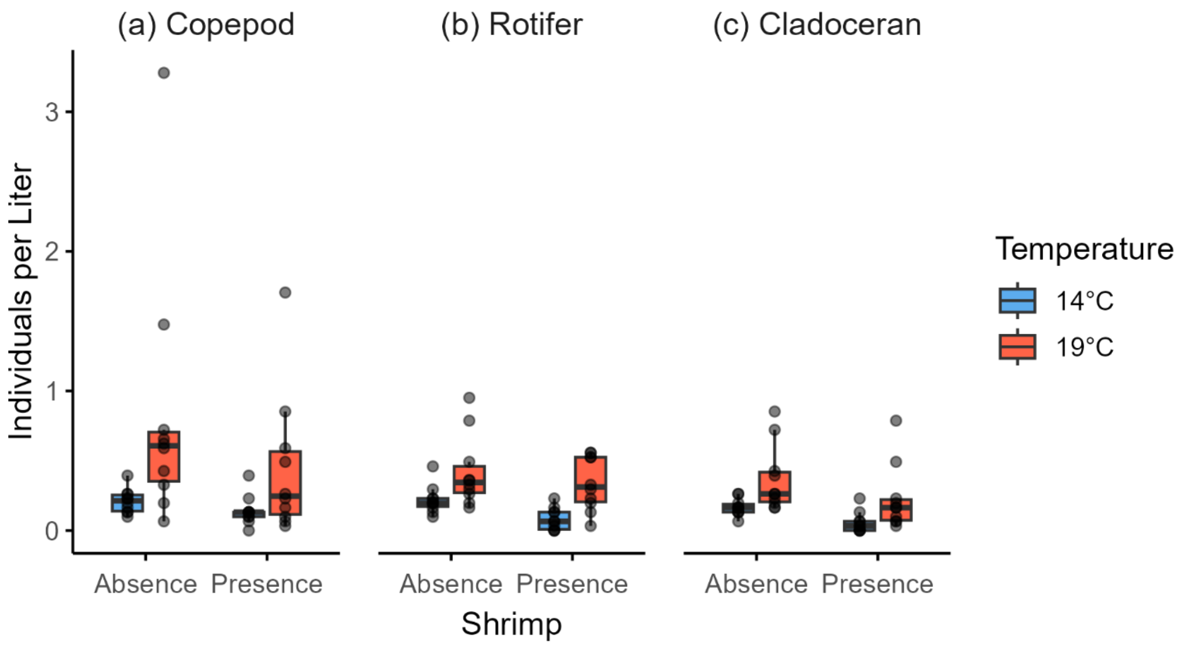

Figure 6. Boxplots illustrating the influence of shrimp presence and temperature on a) copepod density, b) rotifer density, and c) cladoceran density. The horizontal line inside each box denotes the median, while the box spans the IQR. Whiskers extend to the smallest and largest values within 1.5 times the IQR, and individual dots represent the zooplankton density counted in each mesocosm.

Body length responses to shrimp presence and temperature varied among the three zooplankton taxa, with significant interaction effects detected for copepods and cladocerans and significant independent main effects observed for rotifers (Table 4).

Copepod length, modeled with a linear model, revealed a significant interaction between shrimp presence and temperature ($F_{3,495} = 6.02$, $p < 0.001$) and a negative significant main interaction with temperature (Figure 7).

Rotifer length, modeled with a GLM, revealed significant positive effects of both shrimp and temperature. Higher temperatures and the presence of shrimp each independently led to increased body length.

Cladoceran length modeled with a GLM revealed a significant interaction between shrimp presence and temperature, as well as a significant main effect of temperature. At 19°C, body length was reduced compared to 14°C, but this trend was reversed when shrimp were present.

Table 4. Summary of regression coefficients for zooplankton length, based on a linear model for copepods and Gamma GLMs with a log link for rotifers and cladocerans. (N = 499, 323, and 250, respectively).

	Treatment	Estimate	SE	t	p
Copepod					
	Temperature	-180.45	46.43	-3.886	<0.001
	Shrimp	-87.71	65.49	-1.339	0.181
	Temperature × Shrimp	176.07	74.34	2.368	0.018
Rotifer					
	Temperature	0.079	0.034	2.309	0.022
	Shrimp	0.064	0.032	2.011	0.045
Cladoceran					
	Temperature	-0.139	0.065	-2.120	0.035
	Shrimp	-0.088	0.109	-0.814	0.417
	Temperature × Shrimp	0.266	0.124	2.152	0.032

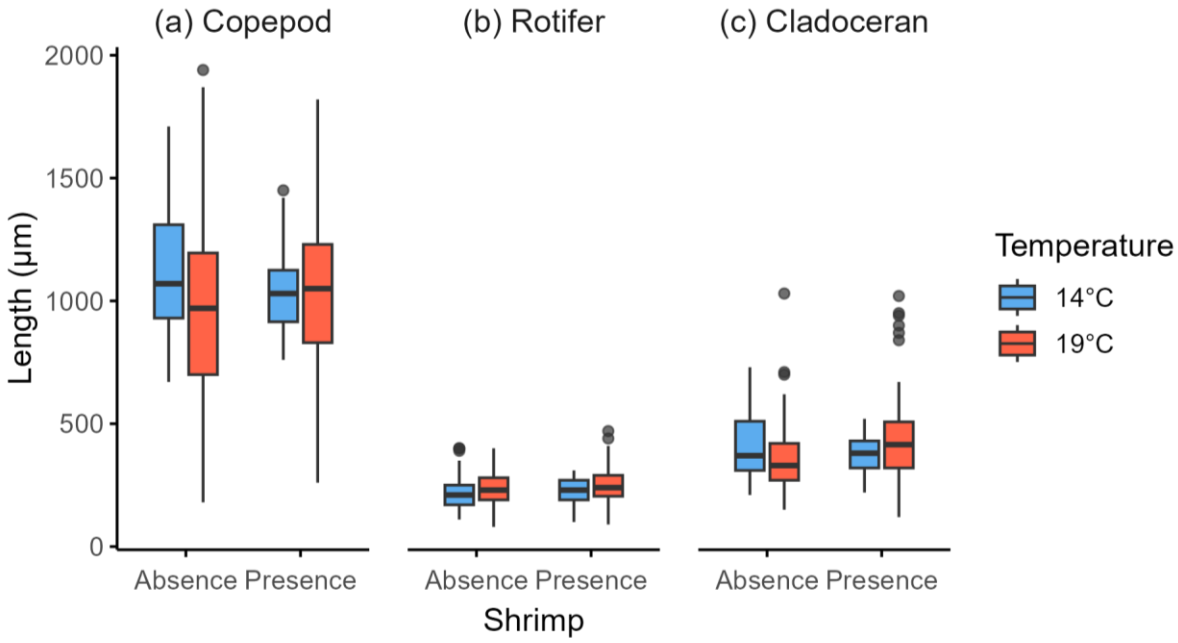

Figure 7. Boxplots illustrating the influence of shrimp presence and temperature on a) copepod length, b) rotifer length, and c) cladoceran length. The horizontal line inside each box denotes the median, while the box spans the IQR. Whiskers extend to the smallest and largest values within 1.5 times the IQR, and outliers are displayed as dots.

3.5 Phytoplankton

The linear model revealed a significant interaction effect between shrimp and temperature, along with significant main effects of both predictors on phytoplankton biomass (chlorophyll-a concentration; $F_{3,36} = 9.51$, $p < 0.001$; Table 5). Warming and shrimp presence each increased phytoplankton biomass independently, but the negative interaction estimate indicates that combined warming and shrimp presence increased the biomass less than expected, resulting in a mitigating effect (Figure 8). Warming increased biomass from 67.1 ± 12.4 to 149 ± 75.1 µg/L in the absence of shrimp, whereas in the presence of shrimp, the increase was more modest, from 102 ± 24.8 to 131 ± 43.6 µg/L.

Table 5. Summary of the regression coefficients from the linear model examining phytoplankton biomass (N = 40).

Treatment	Estimate	SE	t	p
Phytoplankton Biomass				
Temperature	0.710	0.146	4.878	<0.001
Shrimp	0.409	0.146	2.811	0.008
Temperature × Shrimp	-0.492	0.206	-2.393	0.022

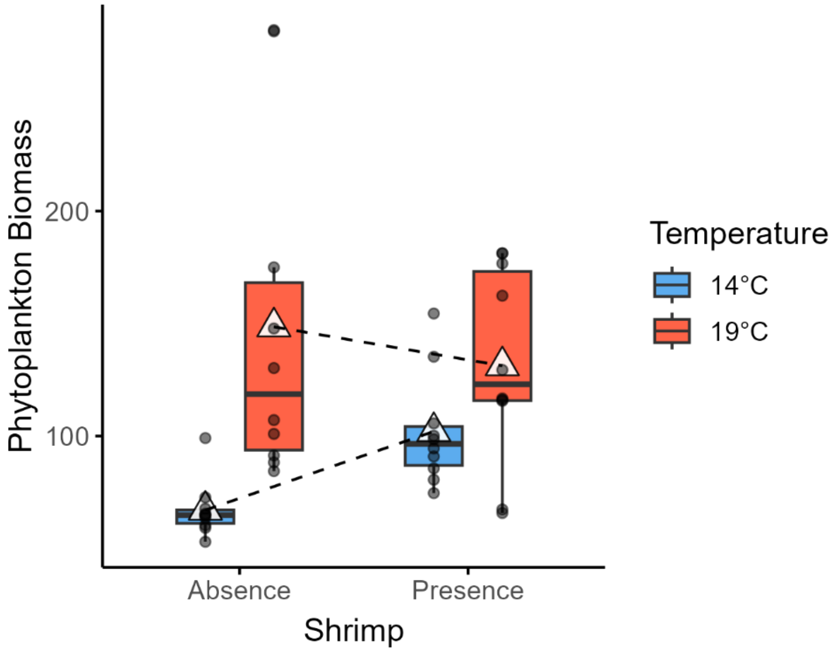

Figure 8. Boxplot illustrating the influence of shrimp presence and temperature on phytoplankton biomass. The horizontal line inside each box denotes the median, while the triangle represents the mean. The boxes span the IQR, with whiskers extending to the smallest and largest values within 1.5 times the IQR. Individual data points are displayed as dots and interaction effects as dashed trendlines.

4 Discussion

Our experiment investigated how the interaction of climate warming and the non-native mesopredator *P. elegans* changes trophic dynamics in the Baltic Sea. We performed a mesocosm experiment to manipulate temperature and shrimp presence to test whether warming intensifies mesopredator-driven top-down control. Our findings demonstrated that the magnitude of the trophic cascade depended on the interactions of species within each condition.

We found that the interaction of shrimp and warming increased algal biomass and copepod and cladoceran body lengths, while the positive effect of shrimp on phytoplankton was mitigated by warming. In warm treatments, shrimp biomass decreased and in warming and the absence of shrimp, phytoplankton biomass and zooplankton densities increased. Shrimp presence in ambient temperature caused a reduction in amphipod abundance and biomass and rotifer and cladoceran densities, while increasing phytoplankton biomass.

4.1 Shrimp physiological responses

The enhanced top-down control, a process in which predators suppress the abundance or activity of organisms at lower trophic levels (Pace et al., 1999), observed under warmer conditions may be partially explained by temperature-dependent physiological changes in *P. elegans*. At higher temperatures, shrimp lost more weight, indicating elevated metabolic demands consistent with the MTE. Similar findings have been reported in other decapod species. For instance, shrimp such as *Penaeus vannamei* exhibit elevated feeding rates at higher temperatures (Wyban et al., 1995). This is evidence that warming can increase predatory pressure on lower trophic levels. In our study, despite increased foraging by *P. elegans*, energy intake may not have corresponded with metabolic demands. Combined with potential stress induced by the artificial conditions of the mesocosm, this likely contributed to the observed net weight loss.

4.2 Algal responses and top-down control

Warmer conditions accelerate algal photosynthesis and reproduction (up to species-specific thermal optima; Claquin et al., 2008), which is evident in the tendency of *C.*

glomerata to form dense, ecologically disruptive blooms under warm, nutrient-rich conditions (Gubelit & Berezina, 2010). In warmer conditions, shrimp presence significantly increased algal biomass. This temperature-dependent increase mirrors findings by Rahman et al. (2024). In their study, mesopredator presence also increased algal biomass, particularly under warmer conditions (Rahman et al., 2024). Two mechanisms may cause this effect. First, a top-down effect, where shrimp reduced amphipod numbers, thereby decreasing grazing pressure on algae. Second, a bottom-up effect, where warmer temperatures boost algal productivity, possibly outpacing what shrimp alone can graze. In warm no-shrimp mesocosms, amphipods were abundant and likely exerted strong grazing pressure, reducing algal biomass despite the temperature-enhanced growth.

At ambient temperature (14°C), shrimp had no significant effect on algal biomass. This may suggest that since algae grow more slowly in cooler water, the reduction in grazing pressure from shrimp might not be enough to cause an increase in biomass. Even though we only tested a moderate temperature range (14°C to 19°C), the increase may have been enough to prompt temperature-sensitive processes. Our experiment demonstrated that temperature-regulated predator-prey interactions and trophic cascades occur in both top-down and bottom-up directions.

4.3 Predator-effects on amphipods

Similar to findings from Rahman et al., (2024), we found that the mesopredator, *P. elegans* in our case, created top-down control in all temperatures by diminishing amphipod populations. This finding aligns with studies documenting the shrimp’s high feeding rates in the Baltic Sea (Persson et al., 2008). Since amphipods contribute to detritus processing (Anderson & Sedell, 1979), their absence may reduce the breakdown of organic matter, which can cause nutrient imbalances or the accumulation of waste that would lead to trophic cascades.

4.4 Zooplankton under dual stressors

Warming increased the densities of rotifers, copepods, and cladocerans. A study on a marine copepod, *Acartia tonsa*, found development to be faster and reproduction rates to be earlier at 19°C compared to 13°C treatments (Garzke et al., 2020). This could explain why densities increased, and differing life histories between taxa could explain why responses differed in magnitude. For instance, although not statistically significant, copepod density in the presence of shrimp had the weakest decrease, which could be in part because of their fast response and acceleration rates considering their size (Waggett & Buskey, 2008), making them less vulnerable to predation. *P. elegans* suppressed the positive effect of warming, particularly for rotifer and cladoceran densities, highlighting its role in top-down control.

Besides density, warming and predation also affected zooplankton body length. Copepods and cladocerans experienced a decrease in size with increased temperature under shrimp-free conditions. These trends were reversed or weakened in the presence of shrimp combined with warming. This indicates that mesopredator interactions neutralized or suppressed temperature-driven size changes.

In contrast, rotifers increased in length under both stressors, suggesting plasticity in growth. Kauler & Enesco (2011) found a negative correlation between temperature and the survivorship of the rotifer *Brachionus calyciflorus*, with average lifespans of 4.1 days at 29°C, 6.4 days at 22°C, and 11.3 days at 16°C. It is possible that their rapid life cycles enable rotifers to quickly adjust body size in the face of environmental pressures such as warming or predation.

4.5 Phytoplankton under dual stressors

Phytoplankton biomass increased with both warming and shrimp presence, but their combined effect was buffered, meaning shrimp diminished the influence of warming. In the absence of shrimp, warming boosted phytoplankton biomass faster than grazing pressure could keep up. Despite the likely increase in grazer activity at higher temperatures, phytoplankton biomass more than doubled, suggesting that bottom-up effects outweighed top-down control under warming alone.

Although warming can stimulate phytoplankton growth by speeding up metabolism (Claquin et al., 2008), our results suggest that the indirect effects of shrimp were also important. In shrimp-present ambient temperature mesocosms, reduced grazer abundance likely lowered grazing pressure on phytoplankton, allowing their biomass to increase. Another possible contributor to their growth, although not measured in our experiment, could be increased nutrient input indirectly resulting from shrimp waste (Yang et al., 2020). However, when both stressors were present, the effect of warming was dampened, suggesting that shrimp reduced the effect that warming alone would have provided. It is also possible that phytoplankton growth reached an upper limit constrained by resource limitations such as nutrient availability.

4.6 Hypotheses in context

We observed that interactions between climate warming and non-native species combine to restructure coastal food webs with cascading trophic effects. Kratina et al. (2012) found that warming weakens trophic interactions and destabilizes grazer populations, which mirrors our findings. Our results demonstrate that the non-native *P. elegans* in the Baltic Sea can further amplify this ecological disruption. Due to its broad salinity tolerance, considerable osmoregulation capacity, and thermal resilience (Janas et al., 2013), this species may continue to increase its ecological footprint in the face of climate change.

The shrimp's top-down control occurred in most instances at both temperatures, inducing transformations in community composition and functionality. These patterns are broadly consistent with our initial hypothesis that *P. elegans* suppresses herbivores and zooplankton populations, thereby weakening grazing pressure on primary producers. However, this effect was not uniform across temperatures. For instance, shrimp presence did not increase algal biomass at 14°C.

Our second hypothesis, stating that warming would amplify the impact of *P. elegans* through increased metabolic demands, was partially supported. While shrimp lost more body mass at higher temperatures, and algal biomass increased under shrimp presence at 19°C, the interaction effect for phytoplankton was sub-additive, indicating that shrimp dampened the warming-driven increase in phytoplankton biomass. Moreover, zooplankton densities remained relatively high under combined warming and shrimp presence.

Contrary to our third hypothesis, warming in the absence of *P. elegans* did not reduce phytoplankton or algal biomass. Although zooplankton densities increased as predicted, these organisms did not apply enough top-down pressure to offset the strong bottom-up stimulation of primary producers, particularly phytoplankton. Amphipod responses to warming were negligible, and algal biomass remained unchanged.

4.7 Ecological significance and study limitations

These outcomes reflect not only direct predation, but also complex structural changes in trophic dynamics and energy flow. While we propose several speculations, such as increased nutrient input from shrimp waste, these theories likely vary across taxa and justify further investigation. Species-specific responses and unmeasured variables could influence these dynamics, and our interpretations should be viewed as theories to guide future work. For instance, future research could incorporate nutrient analysis to see how *P. elegans* influence nutrient cycling.

Despite prior research on the physiology and stress tolerance of *P. elegans* (Janas et al., 2013), few studies have examined its multi-trophic effects under warming conditions. Our findings help fill this research gap by demonstrating that *P. elegans* can interact with temperature to restructure community dynamics through both direct predation and indirect effects. As non-native mesopredators like *P. elegans* become increasingly widespread in coastal ecosystems, their presence must be integrated into ecological models to improve predictions of ecosystem responses to climate change. The ecological models or future experiments can also explore more temperature intervals and even increase the maximum temperature.

Although we were able to investigate effects of temperature and shrimp as planned in our mesocosm, the design faced limitations. We could not account for dynamics occurring in natural systems, such as spatial heterogeneity or behavioral complexity. In addition, the experiment duration may not have been long enough to manifest ecological processes like rebound of prey populations and predator satiation. Future research could extend the duration of the experiment to explore longer-term ecological responses. Moreover, real-world food webs often contain multiple interacting or competing predators, both native and non-native, whose combined effects may differ from the patterns we observed.

Our study provides insight into the dynamics of non-native species and warming. By addressing a regional research gap, we advance understanding of how climate change and biological invasions interact to reshape coastal food web structure and functioning. Incorporating these interactions into ecological planning and management strategies will be essential for protecting biodiversity and sustaining ecosystem services in vulnerable marine systems.

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Ethical statement: We minimized stress during animal handling to the fullest extent possible and organisms were protected from undue distress as much as possible. Permission was not needed to perform the research, as Finnish law on animal experimentation does not apply to invertebrates.

Declaration of AI tools: I used an artificial intelligence tool, ChatGPT 4, in compliance with the Guidelines for the use of AI in teaching at the University of Helsinki to create images. I received suggestions for grammar, punctuation, spelling, and clarity from Grammarly.

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