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The Role of Temperature in the Termination of Dormancy in Zooplankton

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ABSTRACT

Organisms in systems with seasonality require adaptations that enable them to endure harsh conditions and to emerge again at an optimal time to start a new period of production. One such adaptation is dormant eggs in zooplankton. While there is much information on the cues leading to the production of dormant eggs, less is known about the termination and hatching of these eggs, especially among marine zooplankton. Our results from a combined laboratory and field study at a coastal Baltic Sea site showed that hatching in some overwintering copepods was temperature-dependent, with a threshold-like initiation between 6°C and 9°C. In contrast, overwintering rotifers hatched in comparable abundances in all temperatures, once a similar amount of degree-days had been accumulated. The field study demonstrated that nauplii started to appear when temperatures increased above 6.8°C and were more abundant close to the sediment than in surface water in early spring, matching the hatching threshold found in the laboratory. Various rotifers increased in abundance at different times during the spring phenology, but without any differences in abundance between deep and surface waters. Hence, the hatching of zooplankton dormant eggs in this system is temperature-dependent, likely taxa-specific, and continued climate change is predicted to have implications for the plankton phenology, mismatches, and food web composition.

1 | Introduction

Temperature is highly influential in nearly all biological processes, from enzyme activities to population dynamics. Special demands are put on organisms to cope with the shifting environmental conditions in areas of large annual temperature fluctuations, such as temperate regions. This can drive the evolution of local adaptations, making organisms adapted to certain temperature regimes, for example, to avoid the adverse conditions during low productivity seasons and to match the life history cycles to favorable conditions (e.g., Belmonte and Rubino 2019; Varpe et al. 2007; Way and Montgomery 2015; Yamahira and Conover 2002).

One such strategy is behavioral avoidance in space, commonly manifested as migration between habitats (e.g., Alerstam 1990; Fryxell and Sinclair 1988). Another strategy is to escape the unfavorable conditions in time (Belmonte and Rubino 2019; Gilbert 2016, 2019; Gyllström and Hansson 2004; Holm et al. 2018; Schröder 2005). An example of the latter is dormancy, meaning a pause or delay in the life cycle allowing later development and reproduction. Dormancy is known from a range of environments and from several taxa/organisms (Belmonte and Rubino 2019; Dahms 1995; Fryer 1996; Gilbert 2016, 2019; Gyllström and Hansson 2004; Holm et al. 2018; Marcus and Boero 1998; Schröder 2005). Although initiation of dormancy is well described in zooplankton, less is known about the cues

to terminate dormancy and how to match emergence in response to overall environmental conditions and food resources (Belmonte and Pati 2007; Gilbert 2016, 2019; Gyllström and Hansson 2004; Holm et al. 2018; Marcus 1996; Marcus and Boero 1998; Schröder 2005). This knowledge gap is larger for marine zooplankton and Rotifera in general (both freshwater and marine), whereas Cladocera in freshwater systems have been more extensively studied (Fryer 1996; Gyllström and Hansson 2004).

Interestingly, resistant eggs in Copepoda can be of different types, including so-called resting eggs (quiescent subitaneous eggs as well as delayed-hatching) or so-called diapause eggs. A number of different ways exist in the literature to describe these phenomena, but here we use the word "dormancy" when we refer to the general period of delay in development, whereas the words "resting", "quiescence," and "diapause" refer to different types of eggs produced by zooplankton to endure a period of dormancy. These different types of eggs remain dormant and viable in the sediment for a variable amount of time ranging from days and months up to approximately 300 years (Hairston Jr. 1996). These dormancy eggs can be used for over-wintering or for longer-term storage, and the ratios of different types of eggs vary over the season, suggesting bet-hedging strategies to allow for at least some of the offspring to survive (Drillet et al. 2011; Engel 2005; Holm et al. 2018; Marcus and Boero 1998; Takayama and Toda 2019). For example, Takayama and Toda (2019) demonstrated that the ratio of diapause eggs increased sharply below a certain temperature and day length threshold. Even the same female can produce different types of eggs (Belmonte and Pati 2007; Takayama and Toda 2019).

It is important to depict factors regulating termination of dormancy, especially when environmental factors change, as has been predicted in recent climate change models. In temperate regions, the general seasonality is relatively predictable with low productivity during winter, but as spring arrives, production starts to increase again. In aquatic environments, there is typically a bloom of phytoplankton and an increasing abundance of zooplankton in spring (Sommer et al. 2012). Some zooplankton have been shown to overwinter in a later developmental stage, for example, as sub-adults (e.g., Cyclopoida and large arctic Calanoida, e.g. *Calanus* spp.) while others produce different types of resistant eggs, such as in Cladocera, Copepoda, and Rotifera (Belmonte and Pati 2007; Gyllström and Hansson 2004; Holm et al. 2018; Marcus and Boero 1998; Schröder 2005). Production of these resistant eggs in zooplankton is influenced by a variety of abiotic and biotic factors, including temperature, day length, food availability, and increasing population density (Avery 2005; Belmonte and Pati 2007; Drillet et al. 2011; Engel 2005; Gilbert 2016, 2019; Gyllström and Hansson 2004; Hirche 1996; Holm et al. 2018; Marcus and Boero 1998; Schröder 2005).

Sediments housing dormant eggs resemble the seed bank for terrestrial plants, but little is known as to what governs the timing of the emergence of zooplankton in spring, especially in temperate marine systems and among rotifers in general (Gilbert 2016, 2019; Holm et al. 2018; Marcus and Boero 1998; Schröder 2005). Early studies, corroborated by more recent studies, have found that dormant eggs from marine calanoid copepods hatch spontaneously under constant laboratory conditions after a certain amount of time (Ban 1992; Belmonte and Pati 2007; Boyer and Bonnet 2013; Grice and Gibson 1981; Johnson 1979; Marcus 1989). However, a quicker hatching can be induced in some cases by imposing the eggs to a period of harsh conditions (e.g., cooling) (Boyer and Bonnet 2013; Cooley 2003). Low temperature has been used to store marine Calanoida Copepoda subitaneous eggs in the laboratory before being hatched at room temperature (Drillet et al. 2006). These eggs were not resting, and this study demonstrates that temperature is an important factor for egg hatching, at least for subitaneous eggs. Other studies have suggested that a combination of temperature and photoperiod is of importance for the termination of dormancy in Calanoida resting eggs (Boyer and Bonnet 2013; Engel 2005; Hansen et al. 2009; Katajisto 2003; Katajisto et al. 1998; Landry 1975; Uye and Fleminger 1976; Uye et al. 1979; Viitasalo 1992). Also, Cladocera seem to rely on a combination of light and temperature, with a strong component of temperature dependence for hatching (Gyllström and Hansson 2004). Gilbert (2016) pointed out that the knowledge regarding the hatching of dormant eggs in Rotifera is limited. Suitable hatching conditions vary among species and generally require, or are associated with, sufficiently high temperatures and oxygen conditions, as well as suitable salinity and water turbulence associated with spring turnover (Gilbert 2016, 2019; Schröder 2005). For example, out of nine Rotifera species assessed, a majority hatched quicker at higher temperatures, but a few species had higher hatching rates at 5°C compared to 15°C (May 1987). This suggests species-specific temperature-dependent hatching (Gilbert 2019; May 1987; Schröder 2005). Hence, a major adaptation in pelagic marine zooplankton might be to enter dormancy during certain periods of the year and then emerge again from eggs stored in the sediment when suitable conditions occur.

Hence, here we use a combined field and laboratory approach and hypothesize that temperature influences the seasonal timing of hatching in dormant Rotifera and Copepoda eggs during the winter-spring-summer transition.

2 | Method

2.1 | Laboratory Incubations to Quantify Hatching of Zooplankton Eggs From Sediments at Different Temperatures

Sampling of Baltic Sea sediment was conducted in Southeastern Sweden (N56°65.9032′, E16°35.7659) the 8th of February 2017. Soft sediment was collected with an Ekman sampler (water depth of 4–5 m, sampled surface area 400 cm^2). The surface water had a temperature of 1.0°C and a dissolved oxygen (O_2) level of 12.4 $mg\,L^{-1}$ (in situ oxygen sensor, WTW Multiline). The sediment was stored cold (4°C, a typical winter-early spring temperature at the site) and in the dark directly after sampling, during transportation to the lab, and overnight until incubations started.

All the sampled sediment was mixed to account for potential patchy distribution of zooplankton eggs before sieving (mesh

size 2 mm) to remove potential macroinvertebrates. The sediment was partitioned based on wet weight into solid white plastic containers of 10 L (bottom surface area 531 cm^2). Each replicate container was supplied with 97.8 ± 2.5 g sediment and 5 L filtered Baltic Sea water (7 PSU, 0.1 μm mesh size). Four replicates were assigned to each temperature of 6.4°C ± 0.3°C, 9.0°C ± 0.1°C, 13.9°C ± 0.1°C, and 18.7°C ± 0.3°C (average ± standard deviation) to study the emergence of dormant zooplankton at a range of different temperatures. This is also the range of temperatures encountered during the spring to summer transition in this area.

All replicates were kept in the dark, with light aeration, and temperatures were increased gradually at 5°C per day^{-1} using temperature-controlled rooms until incubation temperatures were achieved. All treatments were incubated for 14 days at their respective incubation temperatures after the temperatures had stabilized.

2.2 | Sampling

Temperature and oxygen levels were monitored daily (same sensor as above). Oxygen concentration oscillated in the range of 6.1–8.3 mg L^{-1} during the experimental incubations. Samples for zooplankton and chlorophyll *a* were collected 3 times on days 4, 9, and 14. Sampling was conducted after gentle mixing of the water phase (1.2 L water per replicate). One liter was filtered through a 15 μm nylon mesh to collect and preserve (Lugol's Acid Solution) the emerged zooplankton to estimate the abundance per liter. The cumulative emergence of zooplankton per replicate was then calculated as the sum of zooplankton removed during the two initial samplings plus the estimated total amount of zooplankton present at the final sampling in the entire water volume. The cumulative emergence was normalized to the area of the bucket bottom. Furthermore, 100 mL was filtered for chlorophyll *a* (Whatman GF/C) analysis as a proxy for phytoplankton biomass. The filtered water was carefully poured back into the respective replicate after sampling to restore the initial volume and cause minimal turbulence and disturbance of the sediment.

2.3 | Field Time Series

Zooplankton abundances during spring were studied close to the sediment as well as in surface waters of the sampling location. Weekly samples (close to the sediment sampling location) were collected immediately after the winter ice began to disappear from the location (April 5th) until the beginning of summer (June 1st). Water depth at the location was approximately 5 m. Both the surface water (1 m below surface) and the bottom water (1 m above the bottom) were sampled with a 3 L Ruttner Sampler, collecting three replicates for each depth. In an effort to reduce vertical mixing of the water column, surface samples were collected before bottom samples. All samples throughout the season were collected between 10 and 12 a.m. In addition, we also measured temperature and O_2 concentration (mg L^{-1}) in the surface and the bottom water at the sampling occasion (using the same sensor as above).

Approximately 500 mL of the sampled water was filtered for chlorophyll *a* analysis (GF/C). Chl-*a* filters were stored at −20°C until later analysis. Approximately 1.5–2 L of water was then filtered onto a 15 μm nylon mesh and fixed with Lugol for zooplankton quantification.

Zooplankton community composition was quantified to the genus level when possible; otherwise, it was quantified to higher-level taxonomic grouping using morphological characteristics following the categorization: adult Copepoda (*Acartia* spp., *Eurytemora* sp., or Harpactacoida), Calanoida nauplii, Cladocera (*Podon* spp., or *Evadne* spp.), Rotifera (*Keratella* spp., *Synchaeta* spp., or *Trichocerca* spp.), and Unidentified. The annotation sp. and spp. follow the known occurrence of one or several species within the genus in the sampling area (Díaz- Gil et al. 2014).

2.4 | Sample Processing

Zooplankton were quantified using a dissecting microscope (OLYMPUS-SZX7; 40× magnification) and an inverted light microscope when better resolution was needed (OLYMPUS-CKX41). Chlorophyll *a* was extracted using 96% ethanol and determined fluorometrically (Turner Designs, Trilogy fluorometer; (Jespersen and Christoffersen 1987)). Triplicate subsamples of the sediment were dried at 60°C for a week to determine relationships between sediment dry weight, wet weight, and wet volume.

2.5 | Statistics

All statistical analyses were performed in R version 4.1.1 and 2021.09.0 (R Core Team 2018). Experimental data for rotifers and copepods were analyzed separately, and the effect of temperature on the hatching of zooplankton was analyzed using a one-way ANOVA, with the cumulative abundance of zooplankton (total sum emerging per replicate over the experimental period) set as the response variable. The effect of temperature, incubation time, and the interaction between the two on zooplankton abundances was assessed in a mixed model using generalized least square methods and the gls-package (Zuur et al. 2009). Temperature and time were included as fixed categorical effects, plus the addition of a compound symmetry correlation structure to account for potential autocorrelation.

The temperature treatment was also re-calculated to so-called degree-days by multiplying the number of incubation days with incubation temperature. The spring–summer seasonal pattern in zooplankton abundances was analyzed with generalized least square methods using the gls-package (Zuur et al. 2009). The relationship between zooplankton abundance, season (sampling date) and depth (surface/bottom) was analyzed separately for each taxon. There were no significant interactions between time and depth (surface vs. bottom samplings) and the final model only included time and depth as factors and a compound symmetry correlation structure to account for autocorrelation. Data was $\log_{10}$ or reciprocal transformed to meet the assumptions of the tests.

3 | Results

3.1 | Hatching Experiment Under Different Temperatures

Zooplankton emerged in all temperature treatments during the 14-day incubation. Calanoida nauplii were most abundant, but Rotifera also occurred (Figure 1a). The total cumulative amount of emerging nauplii varied between 283 to 5653 specimens per square meter (see methods on how cumulative amount is calculated). The temperature treatment lowered the hatching rate at 6°C compared to all higher temperatures (Table 1; Figure 1a). There was no significant difference between any of the higher temperatures, 9.0°C–18.7°C (Table 1). Hence, a temperature

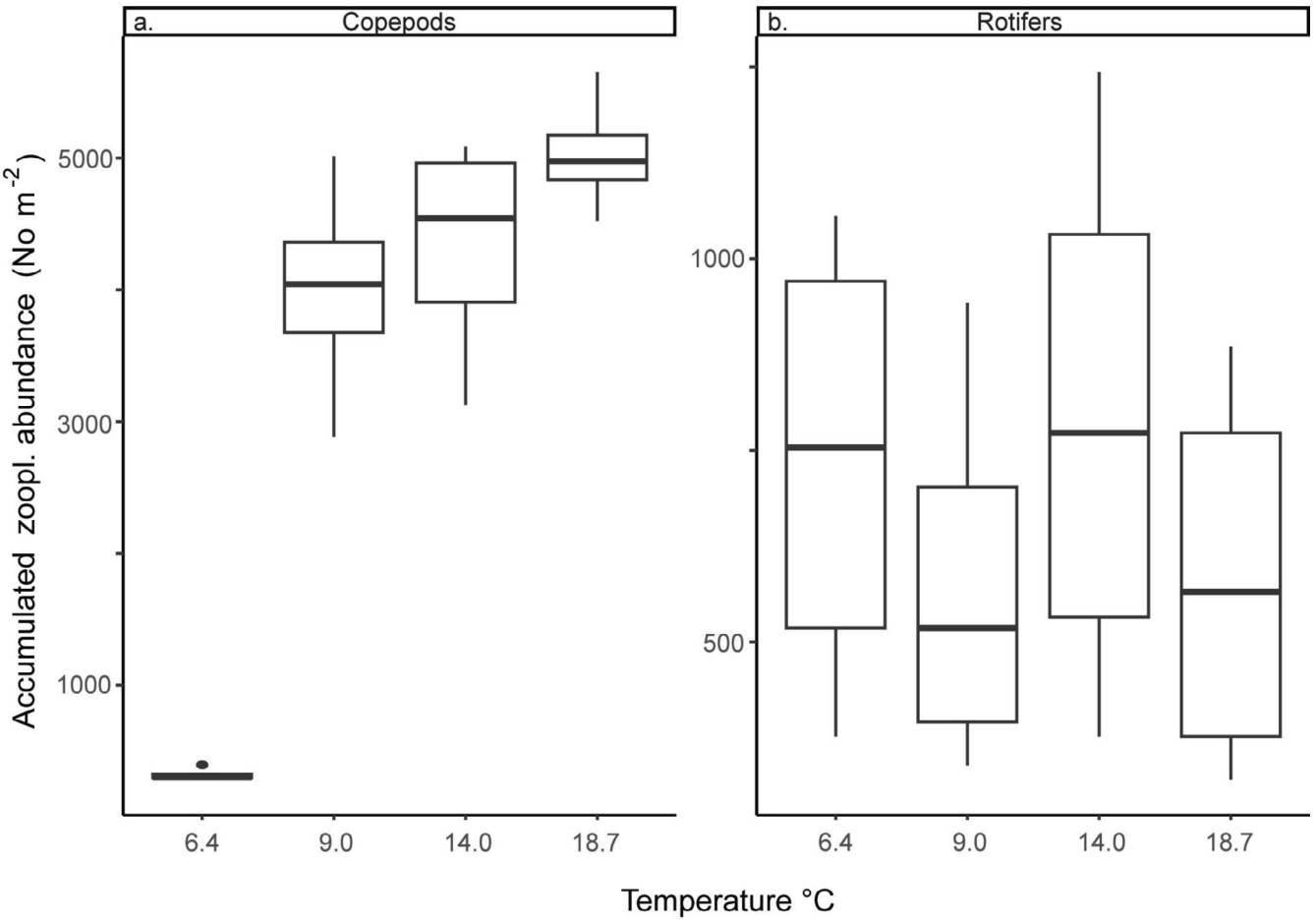

FIGURE 1 | Accumulated abundance of Calanoida (a) and Rotifera (b) per square meter and at different temperatures during the 14 day laboratory incubation. The boxplot illustrate the upper and lower quartiles and the bold lines represent the median.

TABLE 1 | Statistical tests of cumulative emergence of Copepoda (a) and Rotifera (b) in laboratory incubations ranging from 6.4°C–18.7°C.

(a) Total Copepoda emergence	Factor	*F*	d.f.	d.f. (residuals)	*p*
	Temperature	39.9	3	12	**<0.001**
Tukey HSD contrats	6.4–9.0				**<0.001**
	6.4–14.0				**<0.001**
	6.4–18.7				**<0.001**
	9.0–14.0				0.90
	9.0–18.7				0.18
	14.0–18.7				0.47
(b) Total Rotifera emergence	**Factor**	***F***	**d.f.**	**d.f. (residuals)**	***p***
	Temperature	0.4	3	12	0.41

Note: p-values in bold denote significant results.

threshold was identified between 6°C and 9°C where the hatching of Calanoida eggs was significantly upregulated from close to zero individuals emerging per square meter at 6.4°C to approximately 4000 at 9°C. The total cumulative abundance of emerging Rotifera hatchlings during the experimental time (14 days) ranged between 230 and 1244 Rotifera per square meter (Figure 1b) and there was no difference in the total cumulative number of emerged rotifers when comparing the different temperature treatments (Table 1). *Keratella* spp. and *Synchaeta* spp. showed similar emergence patterns as the total rotifer population (Figure S1).

3.2 | Hatching Over Time Under Different Temperatures

Calanoida egg hatching was different over time in the applied temperature treatments (Figure 2, top panel). There was a significant interaction effect between sampling date and temperature illustrated by no evident variation in nauplii abundance at 6.4°C but a gradual increase with time at 9°C (Figure 2, top panel; Table 2). In 14 and 18°C there was an increase in the abundance between the first and second sampling occasions followed by more stable abundances at the third occasion (Figure 2a). Regarding Rotifera, there was a gradual increase in abundance in all temperatures, with more rapid increases of the hatching rate at the warmest temperatures (14°C–18.7°C) indicated by significant interactions between sampling occasion and temperature treatment (Figure 2, middle panel; Table 2). The degree-days were calculated (see methods) for each replicate and sampling occasion as a proxy for the amount of thermal energy the zooplankton had accumulated up to a certain occasion. The abundance of both Calanoida nauplii and Rotifera emerging from the sediment increased as a function of degree-days (Figure 3). For Calanoida eggs, there was a difference in the response among treatments, with little to no hatching at 6.4°C at all degree-days, whereas hatching increased after a certain amount of degree-days in all other temperature treatments (Figure 3). However, Rotifera did not have this threshold-like pattern, and increases in abundances instead occurred in all temperatures after a certain number of degree-days.

Chlorophyll *a* concentrations were generally higher in the lower temperatures and at the first sampling (Figure 2, lower panel). This pattern was present except in the highest temperature treatment (18°C) where chlorophyll *a* concentration was similar throughout the experiment.

3.3 | Zooplankton Emergence in Field During the Winter–Spring–Summer Transition

The spring zooplankton community at this coastal Baltic Sea site mainly consisted of Calanoida (Figure 4a,b) and Rotifera (Figure 4c,d) with a few Harpactacoida, Ostracoda, Cirripedia nauplii, Cladocera, and unidentified taxa grouped as "Other zooplankton" (Figure 4e). In early April when the sampling was initiated, there was a low abundance of all zooplankton groups, both in surface and bottom waters (Figure 4a–e). As spring progressed, higher abundances of Calanoida nauplii were recorded. Abundances started to increase between samplings 3–4 when the water temperature increased above 6°C (Figure 4a, dashed line) and were higher in bottom waters compared to surface during samplings 5–6 (Figure 4a). There was a general difference in nauplii abundance comparing surface and bottom samplings (Table 3). A peak in nauplii abundance (~56 L^{-1}) was recorded on sampling 8 (May 24th)

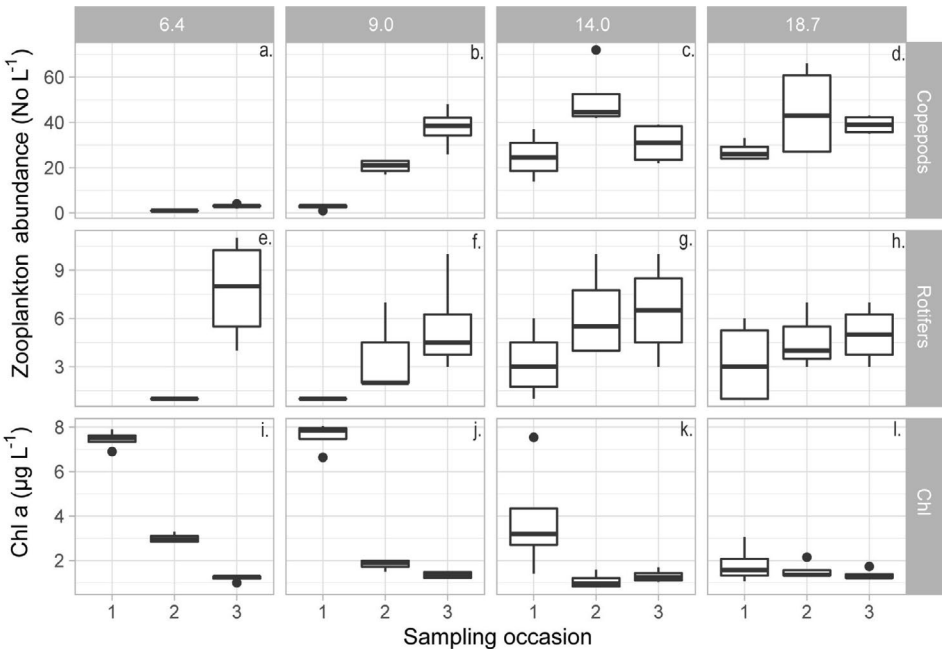

FIGURE 2 | The two top panels illustrate abundance of Calanoida (a–d) and Rotifera (e–h) at different temperature laboratory incubations (6.4, 9.0, 14.0, and 18–7C°) over the three sampling occasions (days 4, 9, and 14). No zooplankton were detected at sampling one at 6.4°C explaining the lack of a box in these sub-panels. The lower horizontal panel (i–l) illustrates chlorophyll *a* concentration at different temperature incubations and sampling occasions.

TABLE 2 | Statistical tests of emergence of Copepoda and Rotifera over three samplings (1–3) and in temperature treatments ranging from 6.4°C–18.7°C.

	Copepoda			Rotifera		
	F	***numDF***	***p***	***F***	***numDF***	***p***
Intercept	4230.3	1	**<0.001**	57.7	1	**<0.001**
Sampling occasion	65.2	1	**<0.001**	37.2	1	**<0.001**
Temperature treatment	291.5	3	**<0.001**	1.5	3	0.219
Sampling occasion × Temperature treatment	13.7	3	**<0.001**	3.1	3	**0.036**

Predictors	**Estimates**	**CI**	***p***	**Estimates**	**CI**	***p***
(Intercept)	−0.79	−1.36 to −0.22	**0.008**	−5.08	−8.63 to −1.54	**0.006**
Sampling occasion	0.72	0.45 to 1.00	**<0.001**	3.88	2.40 to 5.35	**<0.001**
Temp 9	1.08	0.27 to 1.89	**0.010**	3.00	−2.01 to 8.01	0.233
Temp 14	4.07	3.26 to 4.88	**<0.001**	7.17	2.16 to 12.18	**0.006**
Temp 18.7	4.02	3.21 to 4.83	**<0.001**	7.25	2.24 to 12.26	**0.006**
Sampling occasion × Temp 9	0.46	0.07 to 0.85	**0.021**	−1.37	−3.45 to 0.70	0.189
Sampling occasion × Temp 14	−0.61	−0.99 to −0.22	**0.003**	−2.25	−4.33 to −0.17	**0.035**
Sampling occasion × Temp 18.7	−0.54	−0.93 to −0.16	**0.007**	−3.00	−5.08 to −0.92	**0.006**
Observations		48			48	
R^2		0.943			0.494	

Note: p-values in bold denotes significant results.

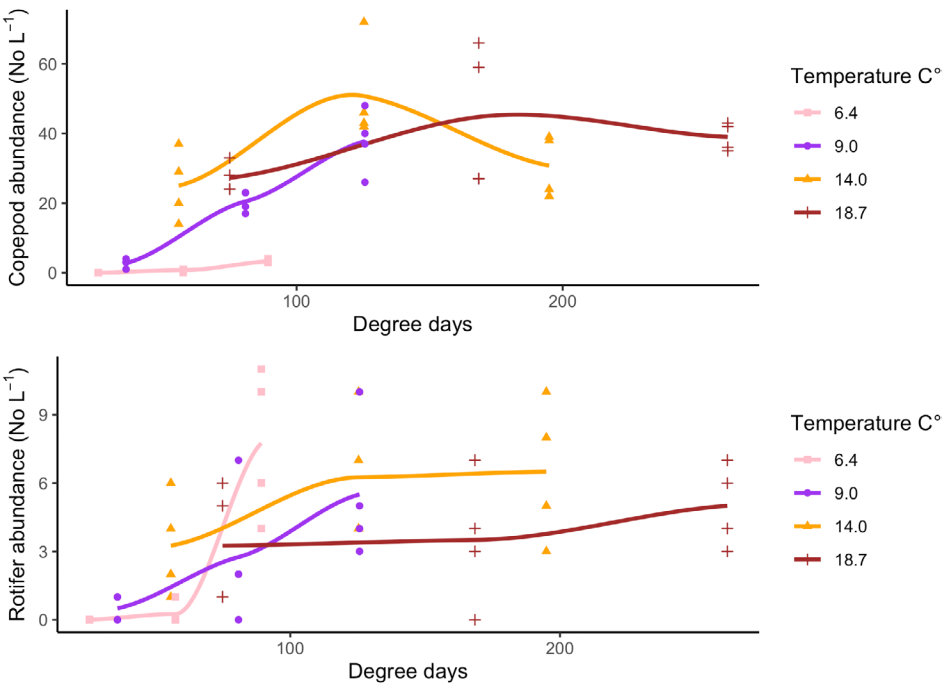

FIGURE 3 | Abundance of Calanoida copepods (top panel) and Rotifera (lower panel) emerging from the sediment during the laboratory experiment and as a function of degree-days. The different temperature treatments are indicated by different colors and lines represent locally weighted scatterplot smoothing curves.

approximately 1 month after the initial increase in abundance. Calanoida juveniles and adults were sparse in early spring and only became more abundant from sampling 7 and onwards when temperatures were above 16°C (i.e., 18 May; Figure 4b). The Calanoida adults and copepodites were generally more abundant in the bottom compared to surface waters

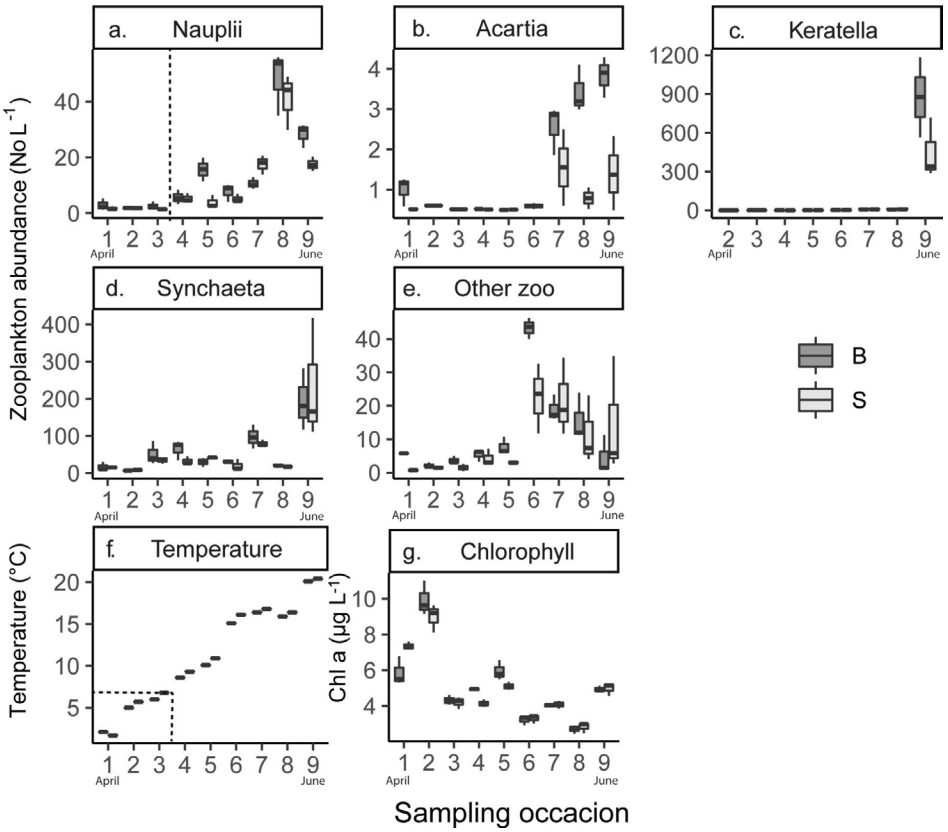

FIGURE 4 | Boxplot illustrating abundance of different zooplankton taxa (a–e; number per liter) over time during field samplings in surface (S) and bottom (B) waters. Sampling occasions were approximately once per week and started April 5 and ended June 1. Temperature and chlorophyll *a* concentrations during samplings are in subpanels f and g. Dashed line in subpanel a and f illustrates the timing when field temperatures reached more than 6.4°C (compare with Figure 1).

TABLE 3 | Statistical tests of zooplankton abundance and chlorophyll *a* concentrations in bottom versus surface samplings in the winter–spring–summer interface.

Variable	Factor	*t*	d.f. (residual)	d.f. (total)	*p*
Nauplii	Bottom versus surface	2.6	50	53	**<0.05**
	Time	12.6	50	53	**<0.001**
Acartia	Bottom versus surface	2.1	26	29	**<0.05**
	Time	4.5	26	29	**<0.001**
Keratella	Bottom versus surface	0.2	35	38	0.85
	Time	9.6	35	38	**<0.001**
Synchaeta	Bottom versus surface	1.1	51	54	0.26
	Time	5.4	51	54	**<0.001**
Other zooplankton	Bottom versus surface	2.4	50	53	**<0.05**
	Time	4.5	50	53	**<0.001**
Chlorophyll	Bottom versus surface	0.7	51	54	0.50
	Time	5.6	51	54	**<0.001**

Note: p-values in bold denote significant results.

(Figure 4b; Table 3). *Acartia* spp. dominated > 95% of the copepod community, but there were also a few *Eurytemora* sp. and Harpacticoida copepodids.

The rotifer community at this coastal Baltic Sea site mainly consisted of *Keratella* spp. and *Synchaeta* spp. (Figure 4c,d). The abundance of *Synchaeta* spp. was fluctuating, and *Keratella*

spp. was present only in low numbers throughout the course of sampling in spring. A rapid increase occurred in late May, and maximum abundances of both groups were recorded at the final sampling occasion (i.e., 1 June; Table 3; Figure 4c,d). There were no significant differences for Rotifera when comparing surface and bottom samplings. Chlorophyll *a* fluctuated but generally decreased over time (Figure 4g). A distinct spring bloom was recorded during the second sampling occasion (April 12th) with water temperatures still being < 6°C. There were no significant interactions detected between time and surface/bottom variables in the data set underlying Figure 4.

4 | Discussion

Here we demonstrated that dormant eggs in Calanoida copepods hatch under high temperature with little to no hatching below 6.4°C but full hatching at 9°C. On the other hand, Rotifera emergence was more similar among temperatures, suggesting other cues, apart from temperature, to be of importance. Field samplings throughout the spring–summer demonstrated that Calanoida nauplii started to emerge at the same temperature threshold found in the laboratory incubations, especially in samplings close to the sediment (i.e., sampling 1 m above sediment surface and total water depth ~ 5 m). On the other hand, Rotifera had taxa-specific patterns where some taxa emerged during spring, whereas other taxa only appeared when summer temperatures were reached. This could indicate that other cues, apart from temperature, are of importance for Rotifera. Alternatively, there could be species-specific temperature adaptations leading to the observed patterns.

4.1 | Abundance of Dormant Eggs

In the order of 300–5700 Calanoida dormant eggs per square meter sediment hatched in the laboratory study during the 14-day incubation. We cannot distinguish between different types of dormant eggs, that is, quiescence eggs or diapause eggs, but the abundance of hatchlings was higher or in the same range as the abundances of nauplii found in the field samples throughout the spring phenology. Katajisto et al. (1998) argued that the benthic-pelagic coupling is important for Calanoida copepods in the Baltic Sea and that subitaneous eggs produced in surface waters sink down to the sediment and go into dormancy as quiescent eggs. Hence, these eggs could be important for the initiation of the spring production of copepods. However, some caution is merited in the comparison between field abundances and laboratory estimates since laboratory-based hatching studies might overestimate hatching. For example, in the field situation there are deposit-feeding macroinvertebrates that can consume eggs, reducing the overall hatching (Viitasalo et al. 2007) and our laboratory incubation did spread out the sediment over a slightly larger area than the sampled area, exposing more sediment to favorable hatching conditions. Many other studies have likewise found variable abundances of dormant eggs in sediments (Gyllström and Hansson 2004; Holm et al. 2018; Marcus 1996) but it is not likely that all of these eggs readily hatch (Rubino and Belmonte 2021). Nevertheless, these benthic eggs could be a major adaptation in pelagic Calanoida copepods in temperate marine systems, as in this coastal Baltic system, to avoid winter and then emerge again in spring from eggs stored in the sediment, as also suggested by Katajisto et al. (1998) and Hansen et al. (2009). Rotifera egg hatching from the sediment in the experimental study was modest, and abundances of active stages in the water were lower compared to the field samplings. Dormant eggs of Rotifera in sediments are likely an important adaptation to avoid harsh conditions (Gilbert 1974, 2016, 2019; Schröder 2005) but this study suggests that additional cues apart from temperature might be necessary to induce rapid hatching. Additionally, some studies suggest that population increase via dormant eggs in Rotifera may be of less importance compared to pelagic production and also less in comparison to Cladocera and Calanoida (Mnatsakanova and Polishchuk 1996).

4.2 | Cues for Termination of Dormancy

The reason for dormancy to evolve has long intrigued researchers. It has been argued that it is a bet-hedging strategy to avoid harsh abiotic or biotic conditions and to allow some of the offspring to survive (Dahms 1995; Gyllström and Hansson 2004; Holm et al. 2018; Marcus and Boero 1998). Interestingly, even the same female copepod can produce different types of dormant eggs, which could be an important adaptation in variable environments (Takayama and Toda 2019), such as the one studied here. Recent syntheses show that seasonality is a key factor affecting the occurrence of dormancy in Calanoida (Belmonte and Pati 2007; Holm et al. 2018). Interestingly, some species avoid cold winters whereas other species avoid warm periods (Holm et al. 2018). These periods in between production and hatching, often having unsuitable conditions like chill temperatures, have been observed in both field and laboratory studies (Belmonte and Pati 2007; Boyer and Bonnet 2013; Castellani 2003; Cooley 2003; Grice and Gibson 1981; Johnson 1979; Uye et al. 1979; Viitasalo 1992). The incubations here were performed in darkness and without phytoplankton additions, suggesting that temperature alone is enough to trigger copepod dormancy termination. Likewise, other studies have suggested temperature dependence in copepod dormancy termination (Boyer and Bonnet 2013; Hansen et al. 2009; Katajisto 2003; Katajisto et al. 1998; Landry 1975; Uye and Fleminger 1976; Uye et al. 1979; Viitasalo 1992). Katajisto et al. (1998) demonstrated that eggs found in top sediments hatch at all temperatures, albeit at a slower rate in 3°C, compared with 13°C–18°C. Furthermore, when bottom water temperature increases above 3°C–6°C, there was an increase in the hatching rate of the sediment eggs (Katajisto et al. 1998). Hence, this would suggest that eggs deposited in shallow well-mixed areas (i.e., water mixing), as in the present coastal Baltic study system, would hatch earlier in spring than eggs deposited in deeper, less mixed areas. However, other factors apart from temperature have to be optimal for dormancy to terminate. For example, low oxygen levels reduce hatching of both Calanoida and Rotifera resting eggs (Broman et al. 2015; Invidia et al. 2004; Uye et al. 1979). Likewise, the light regime has also been suggested to be of importance for the termination of dormancy, with lower hatching in darkness in some taxa (Boyer and Bonnet 2013; Landry 1975; Uye et al. 1979). However, this environmental cue could be less reliable since dormant eggs may sink down below the light penetration level and would need turbulence to be mixed up to water depths where light is available. Here, we did observe hatching

in darkness, suggesting that temperature is the main cue for the studied copepod taxa. Furthermore, other studies have also proposed that environmental conditions experienced by the female copepods, and not the eggs, could influence the rest duration and subsequent hatching (Ban 1992; Belmonte and Pati 2007).

Dormant eggs from Rotifera showed little evidence of temperature dependence compared to Calanoida. Hence, this suggests that Rotifera might need other cues, apart from temperature, for their termination of dormancy, but single-species studies are needed to further understand cues triggering Rotifera emergence in response to temperature. Our results are also in contrast to early studies from freshwater systems where temperature generally is regarded as the main cue for termination of Rotifera dormancy (Birky and Gilbert 1971; Gilbert 1974), whereas more recent reviews acknowledge that both temperature, light, and salinity affect the process in a species-specific way (Gilbert 2019). For all zooplankton including Cladocera, Rotifera, and Copepoda, there is a general notion in the literature that abiotic cues are the main explanatory variables for the termination of dormancy, although there are few studies actually quantifying potential biotic drivers such as food availability or cues from predators (Gyllström and Hansson 2004). As pointed out by Gilbert (2016, 2019) we know relatively little regarding the termination of rotifer dormancy in the field (Gilbert 2016, 2019). Different taxa seem to have specific temperature niches (May 1987; Schröder 2005) and this is supported by our field samplings where some taxa emerged in early spring whereas other taxa were only present when summer temperatures were reached. This is in line with previous studies demonstrating various emergence patterns in spring in terms of rotifer populations developing before or after copepods and cladocerans throughout spring phenology (Gilbert 2016; Jones and Gilbert 2016; Winder and Schindler 2004).

4.3 | Sediment as a Storage of Eggs for Spring Initiation

It is a fundamental concept that the fitness of an organism depends on its temporal and spatial synchrony with the availability of its food items (Cushing 1990). The timing of zooplankton emergence from benthic dormant stages in freshwater systems has been shown to be important for the initiation and population growth during spring (Brendonck and De Meester 2003) but this has not been extensively studied in marine systems. Katajisto et al. (1998) and Hansen et al. (2009) suggested such a mechanism in marine systems, and here we demonstrate that abundances of newly emerged zooplankton are higher close to the bottom sediment compared to surface samples during spring, especially at temperatures of approximately 10°C–11°C (sampling 5). We cannot be certain that these nauplii originate from the sediment, but the laboratory-derived threshold for hatching between 6°C–9°C and significantly higher abundances of nauplii close to the bottom compared to surface samples suggest that they indeed emerged from the sediments. Although pelagic egg production is low at temperatures below 6°C, some of this egg production does contribute significantly to the total spring increase of the copepod population in spring–summer (Durbin et al. 2003; Kiørboe and Nielsen 1994), suggesting both pelagic and benthic source populations for spring initiation.

5 | Conclusions

Recent studies demonstrate that sediments harbor a diverse community of zooplankton resting stages, and their complex interactions with the environment call for more efforts to understand their importance for the pelagic populations (Rubino and Belmonte 2021). The degree of phenological change and its subsequent effects on consumer-resource match-mismatch dynamics depend on the environmental variables used as cues for the event (Forrest and Miller-Rushing 2010; Visser and Gienapp 2019). Here, our results highlight temperature-dependent hatching of Calanoida dormant eggs, which points towards an earlier spring–summer emergence of zooplankton with ongoing climate changes. Future studies should focus on the coupling of phytoplankton and zooplankton emergence in spring to determine the risk of decoupling between producers and consumers during climate change. Such decoupling could severely affect the overall production of aquatic ecosystems.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Raw data can be provided upon request via e-mail.

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