Life-history traits of lake plankton species may govern their phenological response to climate warming

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Abstract

A prominent response of temperate aquatic ecosystems to climate warming is changes in phenology – advancements or delays in annually reoccurring events in an organism's life cycle. The exact seasonal timing of warming, in conjunction with species-specific life-history events such as emergence from resting stages, timing of spawning, generation times, or stage-specific prey requirements, may determine the nature of a species' response. We demonstrate that recent climate-induced shifts in the phenology of lake phytoplankton and zooplankton species in a temperate eutrophic lake (Müggelsee, Germany) differed according to differences in their characteristic life cycles. Fast-growing plankton in spring (diatoms, *Daphnia*) showed significant and synchronous forward movements by about 1 month, induced by concurrent earlier ice break-up dates (diatoms) and higher spring water temperature (*Daphnia*). No such synchrony was observed for slow-growing summer zooplankton species with longer and more complex life cycles (copepods, larvae of the mussel *Dreissena polymorpha*). Although coexisting, the summer plankton responded species specifically to seasonal warming trends, depending on whether the timing of warming matched their individual thermal requirements at decisive developmental stages such as emergence from diapause (copepods), or spawning (*Dreissena*). Others did not change their phenology significantly, but nevertheless, increased in abundances. We show that the detailed seasonal pattern of warming influences the response of phyto- and zooplankton species to climate change, and point to the diverse nature of responses for species exhibiting complex life-history traits.

Key words: algae, cyclopoid copepods, *Daphnia*, *Dreissena polymorpha*, lake ecosystems, life-history traits, phenology, seasonal warming

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Introduction

A prominent response of temperate aquatic (Weyhenmeyer *et al.*, 1999; Gerten & Adrian, 2002; Edwards & Richardson, 2004) and terrestrial ecosystems (Walther *et al.*, 2002) to climate warming is changes in phenology (i.e. annually reoccurring phenomena especially in relation to climate such as the timing of first occurrence, or the timing when population maxima are reached; for a review, see Gerten & Adrian, 2002; Straile *et al.*, 2003). Some coexisting species may respond to climate change at similar rates and thus maintain synchrony, whereas for other coexisting species, loss of synchrony may lead to a decoupling of tightly coupled interactions

(Cushing, 1990; Stenseth & Mysterud, 2002; Winder & Schindler, 2004). Besides winter warming, spring and summer are now also subject to warming in Central Europe (Houghton *et al.*, 2001).

The detailed seasonal timing of warming can determine the nature of a species' response, depending on whether species-specific life-history events such as emergence from resting stages, spawning, or generation times, are matched by the time window during which the warming occurs. Plankton communities in temperate lakes are characterized in spring by a dominance of fast-growing species, which are adapted to the prevailing steep temporal gradients in temperature and light conditions (Reynolds, 1984; Sommer *et al.*, 1986), resulting in immediate and likely synchronous phenology shifts to climate warming (Weyhenmeyer *et al.*, 1999; Gerten & Adrian, 2000; Straile & Adrian, 2000 – but see

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Winder & Schindler, 2004). During summer, by contrast, temporal gradients of temperature and light are small. Slow-growing zooplankton species predominate (e.g. copepods), whose complex life cycles span several months. Such plankton are thus prone to warming events across seasons (Gerten & Adrian, 2002), that do not necessarily coincide. For example, changes in day-length-specific temperatures during spring along with a concurrent warming during winter and spring may significantly influence the emergence of resting stages, and cause mismatches between species later in the year.

Our hypothesis is that climate-induced phenology shifts of slow-growing summer plankton species are less synchronized than phenology shifts of fast-growing spring species, as the longer life cycles of summer species may prevent from synchronous changes in response to climate warming. To test this hypothesis, we investigated the interactive effects of warming on the performance of fast (algae, *Daphnia*) vs. slow growing (cyclopoid copepods, larvae of the mussel *Dreissena polymorpha*) lake plankton species, using multidecadal time series (24 years) from a shallow eutrophic lake in Germany (Müggelsee). The rationale behind our choice of taxa was to compare species, which differ substantially in their life-history traits and their life span – processes that are all subject to season-specific changes in water temperature (WT). In addition, all taxa are common in Europe (Næss *et al.*, 1993; Maier, 1994).

Parthenogenetically reproducing *Daphnia* are able to respond rapidly to environmental changes, exhibiting exponential growth over a period of several weeks in spring. Temperature and photoperiod are important cues for the emergence of *Daphnia* resting eggs (Cáceres, 1998). Cyclopoid copepods, on the other hand, undergo a complex life cycle that encompasses many preadult stages (six nauplii stages and five copepodid stages before they moult into the adult stage), spanning a period of several weeks to months (Maier, 1994). Each larval stage has distinct prey requirements: nauplii are strictly herbivorous (Hansen & Santer, 1995), while late copepodids and adults are omnivorous (Brandl & Fernando, 1978; Adrian & Frost, 1993). Most of the copepod species studied here undergo diapause in the sediment in a late copepodid stage during winter (Maier, 1994), which is most likely also the case in Müggelsee, as adults are absent from the pelagic zone during winter and early spring. Photoperiod is the main cue stimulating diapause and emergence of copepodids, although this effect may be modified, in particular, by WT (Næss *et al.*, 1993; Hairston, 1998). Moreover, egg development, clutch size and growth rate at each life-history stage are positively related to ambient temperature (Vijverberg, 1980; Maier, 1989).

D. polymorpha is the only freshwater mussel to reproduce via pelagic larvae (Borcherding, 1991), whereas this strategy is commonly found in marine systems. A free-swimming planktonic larva hatches from the egg and remains suspended in the water column for about 8–10 days before settling to the substratum. *D. polymorpha* mussels have a life span of 5–6 years (McMahon, 1991). An individual mussel participates in three to four annual spawning events, with the first spawning event known to be determined by WT (Borcherding, 1991).

We show that the detailed seasonal pattern of warming is crucial for the individual response of various phyto- and zooplankton species to climate change, and relate this evidence to the fact that the species exhibit different life-history traits. For species with complex and long life-history traits, it seems important whether the seasonal timing of warming matches their individual thermal requirements at decisive developmental stages.

Materials and methods

Phenology events were determined from long-term high-resolution records (1979–2003) of ice break-up dates (daily), WT in 0.5 m depth (daily), and phyto- and zooplankton abundances (mostly weekly) in Müggelsee, a small (7.3 km^2), shallow (maximum depth 8 m), eutrophic, polymictic lake in Berlin, Germany (52°26′N, 13°39′E). A detailed description of the sampling methodologies is given in Gerten & Adrian (2000). Air temperature records (1967–2002) were provided by the German Weather Service for the nearby station of Berlin–Schönefeld.

Given the weekly sampling intervals of the plankton, phenology events are expressed as week of the year for the following events in the seasonal plankton succession: the timing of first appearance (*Daphnia*; adult cyclopoid copepods *Thermocyclops oithonoides*, *Diacyclops bicuspidatus*, *Mesocyclops leuckarti*, *Acanthocyclops robustus*; larvae of *D. polymorpha*) and last appearance in the pelagic zone (copepods), the timing of peak abundance in spring (phytoplankton, *Daphnia*) and summer (copepods), and the magnitude of the peak abundance of the copepod species. As the overall abundances of *Dreissena* larvae result from multiple spawning events during summer (McMahon, 1991), we calculated the sum of the abundances derived from each sampling date as an estimate of the total number of larvae being released in the course of one summer. The timing of appearance and disappearance of species was determined as follows. The first appearance represents the date when a species was observed for the first time followed by a lasting presence of that species in the pelagic zone, while the disappearance represents the

last observation of a species after a continuous presence. To determine the potentially combined effects of changes in WT and light conditions (relevant for the emergence of zooplankton resting stages), we extracted the dates when WT in spring first reached 5°, 8°, and 12 °C, respectively (WT$_{5,8,12}$), which are biologically relevant temperature thresholds (Reynolds, 1984; Peters & De Bernardi, 1987; Borcherding, 1995), along with the corresponding day lengths (in hours (h); DL$_{5,8,12}$).

The nonparametric Mann–Kendall trend was used to detect significant monotonous trends over time (Helsel & Hirsch, 1992). As this test was applied for each monthly time series separately (i.e. one value per year, $n = 19$–25), autocorrelation was negligible. Only for time series with trends, we plotted their cumulative z-scores (i.e. the deviations from the long-term mean of the series divided by its standard deviation; Lozan & Kausch, 1998). The cumulative z-score plots indicate the transient behaviour, and specifically help to distinguish periods with predominantly positive anomalies from periods with predominantly negative anomalies (years that distinguish these periods are herein referred to as 'years of change'). As the z-scores are standardized values, the plots enable direct comparison of the years of change for different variables, irrespective of their absolute values. Differences between the subperiods as identified by the cumulative z-score plots were tested for significance using the nonparametric Mann–Whitney test.

To analyse whether the phenology changes actually were related to concurrent warming, we calculated their Spearman's ρ correlation coefficients with mean WT of the respective preceding months, WT$_{5,8,12}$, DL$_{5,8,12}$, the ice break-up date, and the above-mentioned cardinal phenology events. Abundances were log-transformed (ln individuals L^{-1}) before correlation analysis.

Food conditions for the summer species – i.e. total algal mass, phytoflagellate mass – the main food source for nauplii, which are the bottleneck in copepod development, and total rotifer abundances (prey for late copepodid stages and adult copepods) – were examined for the growing season of these species (April–September). All computations were performed using SAS® 8.02 and SPSS 9.0.

Results and discussion

Warming trends

During the investigation period (1979–2003), the study lake (Müggelsee) experienced significant warming of surface WT in different seasons (trends: winter, $+1.02$ K; spring, $+2.40$ K, summer, $+2.31$ K). These warming trends were not identical, but commenced

successively (Figs 1 and 2a, c and e; Table 1); the years of change lay in 1988 (winter), 1989 (spring), and 1994 (summer), respectively. Biologically relevant threshold WTs of 5°, 8°, and 12 °C (WT$_{5,8,12}$) were reached up to 2 weeks earlier in spring in the latter years, which corresponds to lower light availability on these days (i.e. their day lengths DL$_{5,8,12}$ were shortened by up to 1.6 h; Table 1). The upward trends in WT followed the trends in concurrent air temperature (except for winter temperatures), which were also evident in a longer time period (air temperature 1967–2002: winter $+2.39$ K, spring $+1.97$ K, summer $+0.84$ K). The winter/spring warming was accompanied by shorter periods with ice cover (43 days) and earlier ice break-up dates (3.5 weeks) (Table 1, Fig. 3).

Changes in phenology during spring

Phytoplankton and zooplankton phenology advanced significantly in spring, largely synchronously with the
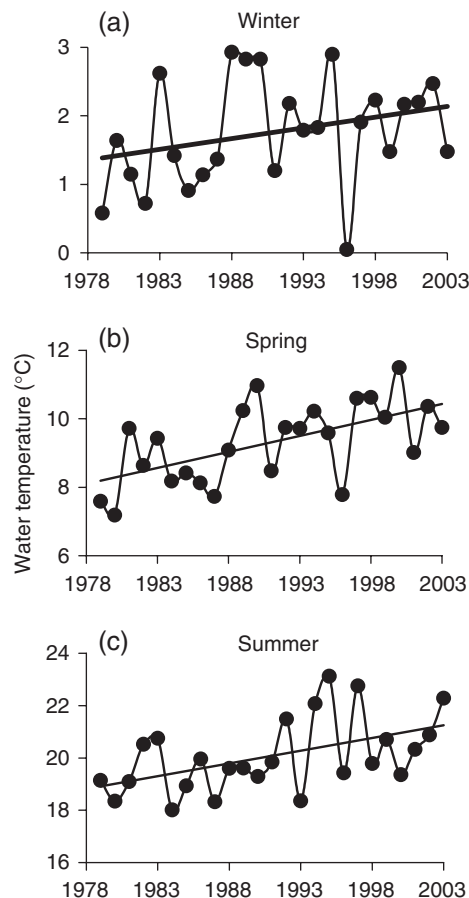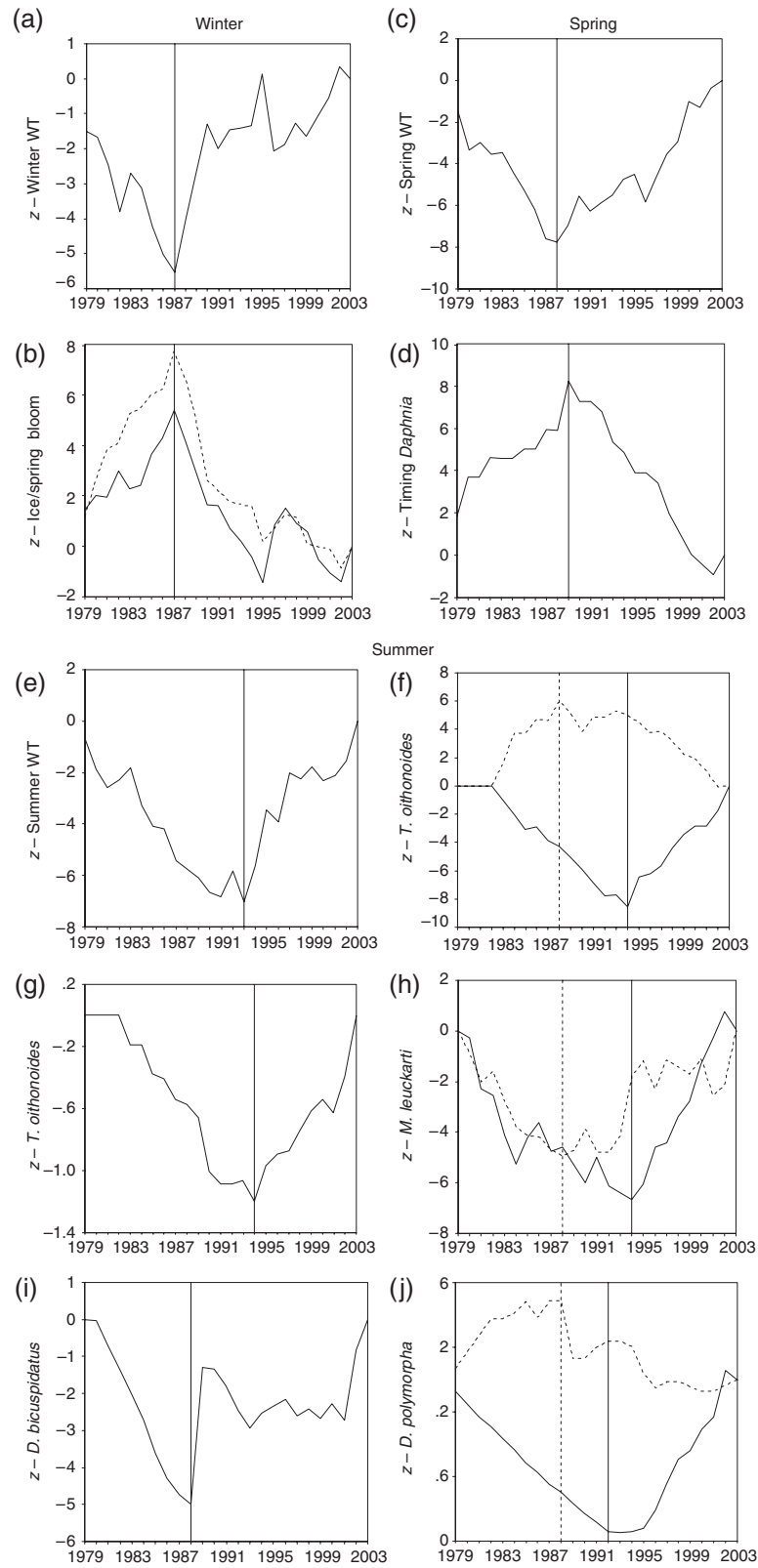

Fig. 1 Mean near-surface water temperature (°C) of Müggelsee derived from daily measurements in (a) winter (December–February); (b) spring (March–May); and (c) summer (June–August), 1979–2003. The straight lines indicate the linear trends over time based on the Kendall–Theill robust line.

sequential winter (phytoplankton) and spring warming (zooplankton). The phytoplankton bloom, of which diatoms comprised >80%, occurred around 4.5 weeks earlier from the year 1988 as compared with the preceding decade (Table 1). Evidently, this advancement was related to the shorter period with ice cover (Fig. 3) and associated improvements in turbulence and light conditions (Weyhenmeyer *et al.*, 1999; Gerten & Adrian, 2000). The relationship between ice conditions and the timing of the bloom is signalled by the synchronicity of the year of change of both events, 1988 (Figs 2 and 3, Table 1), and their strong correlation ($P < 0.001$).

Peak abundances of the *Daphnia* populations, which typically predominate after the breakdown of the phytoplankton bloom, also advanced by about 2 weeks (Fig. 3; Table 1). The same pattern of change was also found for single *Daphnia* and *Bosmina* species (data not shown), i.e. these plankton species responded synchronously to the spring warming. In contrast to the phytoplankton, the earlier timing of the peak abundances of *Daphnia* was largely decoupled from the winter situation and a direct response to elevated WT in spring and particularly in May ($P < 0.001$), which is also indicated by the synchronicity of the year of change in the *Daphnia* and the spring WT time series (1989/1990; Fig. 2c and d). The first appearance of adult *Daphnia* in spring was closely related to WT_5 and DL_5 ($P < 0.01$); the day length that corresponds to WT_5 was reduced by 1.6 h during the study period (DL_5 in Table 1). Although photoperiod is an important cue for the emergence of *Daphnia* resting eggs (Cáceres, 1998), this reduction in DL obviously was not critical for their emergence: if DL (i.e. light availability) would have prevented the emergence in a sufficient number of years, the correlation between timing of first appearance and DL_5 would be lower than the correlation with WT_5, which is not the case. An interesting question is, however, whether the reduction in DL influences such features as *Daphnia* clone selection of emerging resting eggs.

This study documents an observed synchronous forward movement, of 2–4 weeks, for spring phenology events of fast-growing lake plankton species in response to a significant warming in winter and spring (Fig. 2a–d). This synchrony indicates that they all responded rapidly to warmer conditions, although these changes were not causally linked. The observed earlier occurrence of fast-growing phyto- and zooplankton in spring is not restricted to the lake under examination here, as it has also been reported for other, distant lakes (Weyhenmeyer *et al.*, 1999; Straile, 2000; Winder & Schindler, 2004). The timing of ice break-up is a major driver of spring phytoplankton phenology in ice-covered lakes of the temperate zone (Adrian *et al.*, 1999; Weyhenmeyer *et al.*, 1999). Underlying mechanisms driving the spring phytoplankton developments are, however, different in large lakes or marine systems, which lack the development of ice (Straile, 2000; Edwards & Richardson, 2004). In these ecosystems, phytoplankton phenology remained relatively fixed in time, despite analogous warming in winter and early spring.

Changes in phenology during summer

In summer the phenological shifts in the predominating zooplankton were clearly species-specific (Table 1) and not synchronized (Fig. 2e–j) as were the changes in winter/spring. *T. oithonoides* – the most thermophilic of the four copepod species studied – appeared much earlier in spring (9.5 weeks) and also ended its pelagic phase notably later in autumn (3.5 weeks) in more recent years (Table 1, Fig. 4). The earlier start of the pelagic phase was synchronized with the timing of winter/spring warming (Table 1, Fig. 2). Furthermore, annual peak abundances of *T. oithonoides* significantly increased during the study period ($P < 0.001$, Table 1, Fig. 4), which, however, coincided with summer warming (Table 1, Fig. 2). Phenologies of *D. bicuspidatus* and *M. leuckarti* exhibited no systematic change, but both populations demonstrated increased peak abundances (Table 1, Fig. 4). *A. robustus*, a species adapted to a broad temperature range (Maier, 1989), extended its pelagic phase into autumn but the magnitude of its peak abundance remained unchanged (Table 1, Fig. 4). *M. leuckarti* reached its abundance peaks 3 weeks later in more recent years (Table 1).

Fig. 2 Cumulative *z*-score plots of (a) mean winter (December–February) surface water temperature (WT) of Müggelsee; (b) ice duration (solid line) and timing of the spring phytoplankton bloom (dashed line); (c) mean spring (March–May) surface WT; (d) timing of *Daphnia* spring maximum; (e) mean summer surface WT (June–August); (f) start of the pelagic phase of *Thermocyclops oithonoides* (dashed line) and magnitude of the *T. oithonoides* summer abundance maximum (solid line); (g) end of the pelagic phase of *T. oithonoides*; (h) magnitude of the *Mesocyclops leuckarti* summer abundance maximum (dashed line) and timing of the *M. leuckarti* summer abundance maximum; (i) magnitude of the *Diacyclops bicuspidatus* summer abundance maximum, (j) start of the pelagic phase of *Dreissena polymorpha* larvae (dashed line) and cumulative sum of the summer abundances of *D. polymorpha* larvae (solid line). Note the synchronicity in the timing of change between WT in winter (1987) and spring (1988) and phenology events in the spring plankton in opposition to the asynchronous responses of the summer species.

Table 1 Significance levels (P) according to the Mann–Kendall trend test for phenology events and peak abundances in spring and summer in Müggelsee, 1979–2003 (copepods, 1980–2003)

	$P<$	Subperiods	Medians of subperiods
Air temperature			
Winter (December–February)	ns		
Spring (March–May)	0.05	1979–1988/1989–2002	8.3 °C/9.5 °C
Summer (June–August)	0.05	1979–1990/1991–2002	17.3 °C/18.5 °C
Water temperature			
Winter (December–February)	0.1	1979–1987/1988–2003	1.2 °C/2.2 °C
Spring (March–May)	0.01	1979–1988/1989–2003	8.3 °C/10.1 °C
Summer (June–August)	0.01	1979–1993/1994–2003	19.3 °C/20.8 °C
WT_5 (mid-March: 12 ± 2.5 w)	0.05	1979–1988/1989–2003	14.0 w/10.0 w
WT_8 (begin April 14 ± 1.4 w)	ns		
WT_{12} (begin May: 18 ± 1.2 w)	0.01	1979–1991/1992–2003	18.0 w/17.0 w
Day length at specific WT			
DL_5	0.05	1979–1988/1989–2003	12.8 h/11.2 h
DL_8	ns		
DL_{12}	0.001	1979–1991/1992–2003	15.1 h/14.3 h
Ice break-up date	0.02	1979–1987/1988–2003	12.0 w/8.5 w
Spring species			
Timing phytoplankton spring bloom (mid-April: 15 ± 3.2 w)	0.01	1979–1987/1988–2003	20.0 w/15.5 w
Timing *Daphnia* peak (mid-May: 22 ± 2.1 w)	0.01	1979–1989/1990–2003	23.0 w/21 w
Summer species			
Copepods (from 1980 only)			
Start pelagic phase			
Thermocyclops oithonoides (mid-May: 21 ± 5.3 w)	0.01	1980–1987/1988–2003	27.5 w/18.0 w
Mesocyclops leuckarti (begin April: 14 ± 3.6 w)	ns		
Diacyclops bicuspidatus (mid-April: 16 ± 7.9 w)	ns		
Acanthocyclops robustus (end May: 22 ± 6.3 w)	ns		
End pelagic phase			
Thermocyclops oithonoides (begin October: 41 ± 3.3)	0.001	1980–1993/1994–2003	39.0 w/42.5 w
Mesocyclops leuckarti (begin October: 41 ± 3.0 w)	ns		
Diacyclops bicuspidatus (mid-September: 38 ± 5.7 w)	ns		
Acanthocyclops robustus (end September: 40 ± 3.5 w)	0.05	1980–1985/1986–2003	36 w/41 w
Timing summer peak			
Thermocyclops oithonoides (begin August: 32 ± 3.3 w)	ns		
Mesocyclops leuckarti (begin August: 33 ± 2.3 w)	0.01	1980–1994/1995–2003	32 w/35 w
Diacyclops bicuspidatus (end July: 29 ± 4.5 w)	ns		
Acanthocyclops robustus (begin August: 32 ± 4.0 w)	ns		
Magnitude summer peak			
Thermocyclops oithonoides	0.001	1980–1994/1995–2003	1.6 Ind. L^{-1}/16.0 Ind. L^{-1}
Mesocyclops leuckarti	0.05	1980–1988/1989–2003	17.1 Ind. L^{-1}/30.0 Ind. L^{-1}
Diacyclops bicuspidatus	0.001	1980–1993/1994–2003	1.5 Ind. L^{-1}/5.0 Ind. L^{-1}
A. robustus	ns		
Dreissena polymorpha larvae			
Start pelagic phase (begin May: 19 ± 3.0 w)	0.05	1979–1988/1989–2003	21.0 w/19.0 w
Magnitude summer peak	0.001	1979–1992/1993–2003	344 Ind. L^{-1}/2769 Ind. L^{-1}

The respective two periods were determined from cumulative z-score plots (see 'Materials and methods') and tested with the Mann–Whitney test; they all differed significantly from each other. WT_5, WT_8, and WT_{12} refer to the week when water temperature first reached 5, 8, and 12 °C, respectively; DL_5, DL_8, and DL_{12} refer to the corresponding day lengths. The average week $\pm$ standard deviation of the phenology events is given in brackets.

Importantly, the start of the pelagic phase of adult *T. oithonoides* was correlated with WT_5 ($P<0.05$), WT_8 ($P<0.05$), and DL_8 ($P<0.01$). This suggests that WT of around 5–8 °C and DL of around 13.3 h (average DL between 1979 and 2003), which are usually surpassed in March/April, are key requirements for the emergence
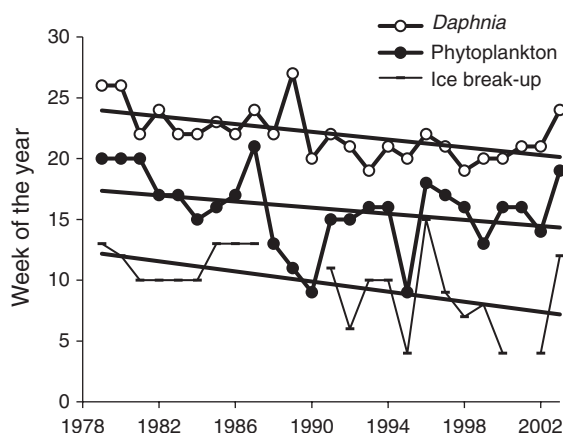
Fig. 3 Annual timing of key phenology events in spring in Müggelsee, 1979–2003: ice break-up, spring phytoplankton bloom, and peak abundance of *Daphnia* in spring. Significant phenology shifts of these events lay in the order of 1 month (Table 1). The straight lines indicate the linear trends over time based on the Kendall–Theill robust line. Gaps in the ice break-up dates indicate years without ice (1988, 1989, 1990), or with rare ice formation.

of this species from diapause. Other factors were probably also important for the emergence of these species (especially as WT_8 and DL_8 did not change significantly over the study period, see Table 1). Light availability is known to be important for the emergence of cyclopoid copepods in both limnetic (Watson & Smallman, 1971) and marine ecosystems (Teasdale *et al.*, 2004). The earlier emergence could also have been a consequence of the extension of the pelagic phase in autumn, since the later in the season diapause is initiated in some cyclopoid copepods, the shorter it lasts (Teasdale *et al.*, 2004). Furthermore, the first appearance of adult copepods is only a proxy for the emergence of larval stages, which unfortunately have not been classified to species level in Müggelsee.

The magnitudes of the peak abundance of three out of the four copepod species were correlated with WT in May and/or June only ($P < 0.05$). This suggests that the early appearance in the pelagic zone by more than 1 month allows the development of an extra generation, which may have contributed to the enhanced peak abundances during summer (Table 1; Gerten & Adrian, 2002). For *T. oithonoides* it has been shown that higher WTs do indeed allow the completion of a further generation (Næss *et al.*, 1993), if food is not limiting. Although Müggelsee has undergone a reduction in total algal mass in the past years as a consequence of reduced inflow and nutrient load (Köhler *et al.*, 2005), concentrations of (e.g. phytoflagellates) – a key resource for nauplii, the bottleneck in copepod development – remained at or above known limitation levels for cyclo-
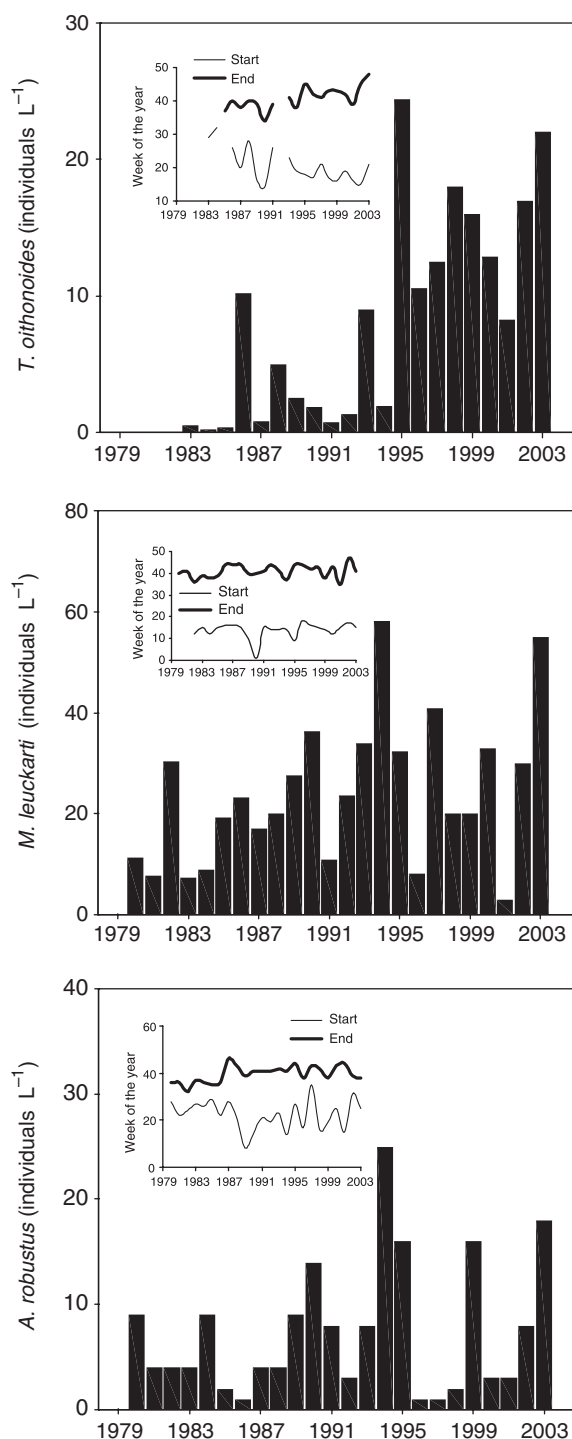
Fig. 4 Magnitude of annual peak abundances of adult *Thermocyclops oithonoides, Mesocyclops leuckarti* and *Acanthocyclops robustus* in summer in Müggelsee, 1980–2003. The inner plots shows the week of the year when adults were first detected in the pelagic zone (start) and their disappearance in fall (end).

poids, $0.2–0.3\,mg\,C\,L^{-1}$ for *M. leuckarti* and *Cyclops vicinus* nauplii (Hansen & Santer, 1995). From June till August, the critical period of nauplii development for
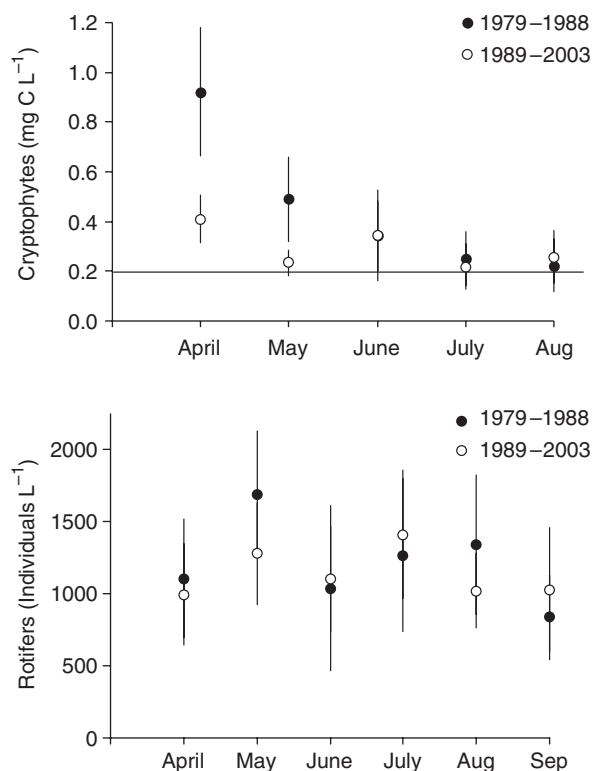
Fig. 5 Monthly means of phytoflagellates mass (cryptophytes), total alagal mass and rotifer abundances in Müggelsee from April to August/September for the periods 1979–1988 and 1988–2003. Each data point represents monthly means ± 95% confidence level. The horizontal line in the upper graph indicates the food threshold concentration of copepod nauplii for phytoflagellates (0.2 mg C L^{-1}, see text).

Fig. 6 Sum of the abundances of pelagic *Dreissena polymorpha* larvae (Ind. L^{-1}) in summer in Müggelsee, 1979–2003. The inner plot shows the week of the year when larvae were first detected in the pelagic zone (Start) and the timing of WT$_{12}$ – the temperature threshold when *Dreissena* mussels starts to spawn.

prey are therefore not a major driver of the observed changes in phenology, especially since most summer species increased in their abundances, which is not to be expected when food resources become limiting.

Changes in the population development of *D. polymorpha* larvae were probably a consequence of the warming events in both winter/spring and in summer. Their pelagic phase started on average 2 weeks early (year of change 1989, concurrent with spring warming, Figs. 2j and 6; Table 1), and they reached significantly higher peak abundances from 1993 onwards, concurrent with summer warming (Fig. 2j). The start of their pelagic phase was correlated with WT in May ($P < 0.05$) and specifically with WT$_{12}$ ($P < 0.01$), which was usually surpassed in May. It is well known that adult *Dreissena* start to spawn when ambient WTs reach 12 °C (Borcherding, 1995). The findings of the present study clearly indicate that a spring warming in this temperature range induces early spawning of *Dreissena* mussels in lakes where algal prey is not limiting. As fecundity in terms of gonad size or number of oocytes per female is determined by winter/spring temperature and prey conditions (Borcherding, 1991, 1995), the increase in the summer abundance appears to be already initiated by winter/spring conditions (S. Wilhelm & R. Adrian, unpublished data).

Consequences of summer warming have rarely been examined so far in lakes (but see Gerten & Adrian, 2002), thus, underlying mechanisms of change are not fully understood. During summer, responses seem to be more complex and more species specific, as this study demonstrates. Furthermore, responses in summer will likely be of a more indirect nature. For example, warm-

summer cyclopoid species, phytoflagellate mass did not differ between the two subperiods 1979–1988 and 1989–2003 (Fig. 5). These subperiods were chosen in analogy to the change in the start of the pelagic phase in spring of the most responsive summer copepod species, *T. oithonoides*; the same pattern was found e.g. for the subperiods 1979–1992 vs. 1993–2003, which are more representative for the observed changes in other summer species. Average total algal mass was generally lower in the latter years and more often below known threshold concentrations (6.6 mg C L^{-1} for adult *Tropocyclops*; Adrian & Frost, 1992). However, during June–August – the main growing season of the studied copepods – differences in total algal mass were not significant (Fig. 5; see overlap in 95% confidence intervals). The total number of rotifers – an important prey for late copepodid stages and adult cyclopoid copepods – did not change significantly in the course of the investigation period (Fig. 5). The same was true for nauplii, which also belong to the prey spectrum of adults (data not shown). The decreases in total algal
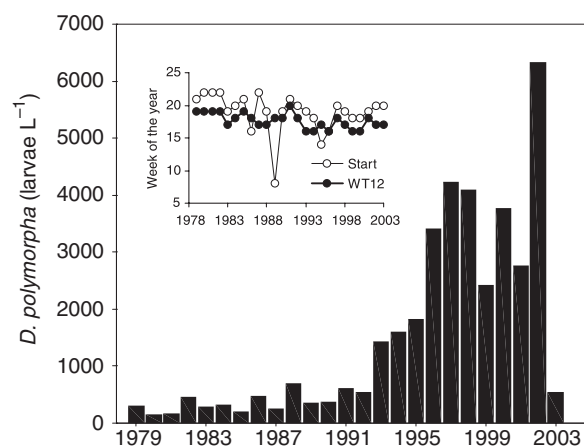
ing should affect the intensity and duration of thermal stratification of lakes (Schindler *et al.*, 1990), with repercussions on turbulence and nutrient conditions, finally affecting phytoplankton development. The early spawning of *Dreissena*, however, can be directly attributed to the early attainment of the 12 °C threshold temperature. Stage-specific food requirements of summer species may add to the complexity in their response to environmental changes such as global warming and/or reduction in eutrophication. Moreover, as we have shown, summer species can be already influenced by previous winter/spring warming, such that warming events earlier in the season may propagate in time and, thus, confound processes in summer. To what extent the increase in abundances on the one hand and the extension of the pelagic phase on the other hand of some summer species affect food web interactions will be discussed elsewhere (R. Adrian, in preparation).

Conclusions

The detailed seasonal pattern of warming influences the response of floral and faunal species to climate change. We show that fast- vs. slow-growing lake plankton species differed with respect to the synchrony of change in response to higher WT. Populations of fast-growing species, adapted to spring-specific steep gradients in temperature and light conditions, are able to directly respond to warming trends (Fig. 2b and d, Fig. 3). This is likely also a reason why the rate of change in spring plankton phenology is somewhat higher than mean advancements in the spring phenology phases for plant and animal species of terrestrial ecosystems (5.1 days per decade; for review see Badeck *et al.*, 2004).

By contrast, slow-growing species with longer and more complex life cycles are potentially affected by multiple warming events in the course of a year, which do not necessarily lead to changes in their phenologies. Warming may be required over the entire growing period or at least during decisive development stages. Larvae, for example, often represent the bottleneck in a species' life cycle with respect to population development or dispersal, such that warming during sensitive developmental stages – such as emergence from diapause or spawning – is of particular importance for aquatic and terrestrial ecosystems. Moreover, individual effects of multiple warming events within a year may propagate throughout the growing season and perhaps into the next year. The asynchronous timing of the seasonal warming trends (spring warming started around 1989, summer warming started around 1994), may have contributed to the diverse nature of observed changes in the copepod and *Dreissena* phenologies on the one hand and changes in peak abundances

on the other hand, which were not *per se* interrelated (Fig. 2f–j).

Our findings imply that intra and interannual differences in the timing of warming, along with differences in species' life history strategies, potentially cause disruptions of established species interactions in freshwater ecosystems. But, as our results also suggest, these mismatches are more likely to occur during summer, when species with long and complex life cycles dominate.

One challenge is to estimate thresholds of further changes in the phenology of species under future climate change scenarios, that predict further warming (Räisänen *et al.*, 2004). Apparently, the extent to which plankton phenology can advance in spring is limited. The presence or absence of ice, and the WT at specific day lengths, appear to be important variables setting these thresholds as they are important drivers of phytoplankton development (Reynolds, 1984), but they are also important cues for the emergence of zooplankton resting stages (Cáceres, 1998; Vandekerkhove *et al.*, 2005). During summer, changes in the strength of thermal stratification, or in the case of polymictic lakes, changes in the frequency of stratified periods, may set some of the boundaries of the responses of the summer species.

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