Influence of oligotrophication and climate variability on a copepod community: The roles of seasonality, life cycle strategy, and stage-structured interactions

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General Introduction

Species are exposed to a broad variety of external forces, which at least partly drive their inter- and intraannual population dynamics (Turchin 2003). Although much effort was done in ecological research to understand the influences of external forces on populations dynamics (Bjørnstad and Grenfell 2001), it is still challenging to elucidate the underlying mechanisms and observed fluctuations in communities and populations often remained unexplained. The understanding of these relationships has become even more important during the last decades since many abiotic parameters changed dramatically, e.g., temperature, CO$_2$ (IPCC 2007), and nutrient concentrations (Smith et al. 1999), with far-reaching consequences for community and ecosystem processes (Carpenter et al. 1998; Stenseth et al. 2002; Riebesell et al. 2007). It is therefore of crucial importance to understand the mechanisms driving population dynamics particularly in the view of future environmental changes.

The strength of environmental forcing is usually not constant through time and species’ ontogeny. Thus, in analyzing the influence of environmental change on population dynamics, ecologists have to deal with three major difficulties: (1) the seasonality of the environmental force, (2) the seasonal niche of species, i.e., their life cycle strategies, and (3) the demography of the population. Most environmental changes exhibit a strong seasonality, e.g., climate change affected species population dynamics in winter more strongly than during summer (Stenseth et al. 2002), which may have sustaining effects on performance of cohorts throughout their life time (Lindström 1999). For example, cohorts of ungulates born after harsh winter conditions showed reduced fecundity and longevity until adulthood (Post et al. 1997; Lindström 1999; Forchhammer et al. 2001). On the other hand, the seasonal niche of a species, i.e., its life cycle strategy, determines whether an external driver influences that species at all since many species avoid harsh conditions by migrating to more favourable sites, e.g., birds, or entering dormant stages, e.g., diapause in insects and crustaceans. Compared to non-migratory and non-diapausing species, this strategy, however, may reduce the potential to respond accordingly to environmental changes at the breeding
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For instance, climate warming was shown to alter the outcome of competition between migrating and non-migrating birds (Ahola et al. 2007). In stage- (or age-) structured populations the topic gets even more complicated since offspring is usually more sensitive to environmental forcing than adults and hence the response of a population is mainly determined by the response of offspring (Gaillard et al. 2000). In many species offspring is only present during a certain period of the year and consequently the regulators of population dynamics could differ among breeding and non-breeding seasons (Sæther 1997). Taking together, a population will experience varying selective pressures depending on the interaction of environmental seasonality, the population's life cycle, and contribution of sensitive stages to the population (Coulson et al. 2001). To understand the influence of environmental change on population dynamics it is therefore increasingly recognized that the whole life cycle of a species embedded in its environment must be considered (Adahl et al. 2006). However, research on this topic mainly focused on single species populations. This thesis provides an attempt to investigate community responses to environmental changes. This was done while analysing a long-term data set of a copepod community in Lake Constance (Germany/Switzerland/Austria) and its responses to decreasing nutrient concentration (oligotrophication) and climate variability.

Copepods are well suited to analyze the roles of seasonality, life cycle strategies, and stage-structured interactions in the response to environmental change. They are strongly affected by environmental forcing (e.g., Huntley and Lopez 1992; Rusak et al. 1999; Beaugrand et al. 2002), exhibit a variety of different life cycle strategies (Santer 1998), and their populations have a complex demography with 12 developmental stages (Einsle 1993). Copepods are among the most abundant animals on Earth and conservative estimations revealed that they likely outnumber the abundance of insects (Boxshall 1998; Schminke 2007), representing one of the biggest sources of animal protein in the world. Copepods play a central role in freshwater and marine food webs and are established in almost all aquatic ecosystems world-wide (Boxshall and Defaye 2008). As primary or secondary consumers they transfer the energy of primary production to higher trophic levels, may control or at least influence phytoplankton dynamics and provide an important food source for a broad variety of predators (Fryer 1998). However, despite of their importance in aquatic ecosystem functioning, the factors shaping copepod communities are not well understood and the observed population fluctuations frequently remained unexplained (Fryer 1998).
This incomplete understanding of population dynamics of copepods is not due to a lack of effort since copepodology has a long-lasting tradition spanning more than 100 years (Schminke 2007) and numerous studies focused on copepods, e.g., searching for ‘copepod’ in ISI Web of KnowledgeSM revealed more than 19,000 matches. It is rather a consequence of the complexity and diversity of copepod life cycles and their ecological requirements. The life cycles of non-parasitic copepods comprises 6 naupliar stages, 5 copepodid stages, and an adult stage (Einsle 1993), including a major metamorphosis from the last naupliar to the first copepodid stage. As a consequence, ontogenetic development encompasses a large range of body sizes and concomitant changes in diets and predator vulnerability (Santer 1994). Offspring, i.e., nauplii, often face the highest mortality rates (e.g., Eiane et al. 2002) and are considered as a bottleneck in population dynamics of copepods (Santer and Lampert 1995). Mortality rates of offspring can vary substantially, i.e., more than an order of magnitude, within a season (e.g., Braner and Hairston 1989; Ohman and Wood 1996; Hirst et al. 2007) indicating a strong seasonality of environmental forcing. Hence, vulnerability of copepods to environmental forcing varies with season as well as with ontogenetic development. The analysis of copepod population dynamics is further hampered by the diversity of their life cycle strategies. Many species enter a dormant stage or produce resting eggs to avoid seasonal harsh conditions (Dahms 1995), whereas the duration, timing, and intensity of diapause varies among species (Hairston and Bohonak 1998). Diapause performance, however, also varies among populations of the same species (Santer 1998). For instance, *Cyclops abyssorum* reproduces throughout the year in some lakes but in other lakes the copepod may perform a diapause either in summer or in winter (Santer 1998). *Mesocyclops leuckarti*, on the other hand, is able to enter encysted resting stages in the sediments (Smyly 1961) or remains pelagic in a state of active diapause (sensu Elgmork 1980). This variability in diapause strategies has been observed in a variety of species (Santer 1998) and is suggested to be induced by environmental conditions, e.g., predation (Hairston 1987) or food availability (Santer and Lampert 1995). Hence, the decision whether or not to diapause is at least partially plastic and thus specific to food web conditions. Although this complexity and diversity of copepod life cycles strongly hampers a comprehensive analysis, it also offers the opportunity to investigate the role of life cycle strategies and demography in the response to environmental changes.

During the last decades, many lakes experienced changes in their trophic status, i.e., eutrophication and oligotrophication (Carpenter et al. 1998; Jeppesen et al. 2005b).
The influence on copepod population dynamics was analysed from the 60ies onwards (Gliwicz 1969) until present (Anneville et al. 2007). Many studies suggest that species of the subfamily Cyclopoida tended to increase stronger with eutrophication than species of Calanoida (Gliwicz 1969; Patalas 1972; Straile and Geller 1998a; Anneville et al. 2007). However, this pattern might not be consistent among lakes since Jeppesen et al. (2005a) reported reduced numbers of cyclopoids under eutrophic conditions in eight Danish lakes. On a species level, the relationship to lake trophy was also diverse as the cyclopoid *Mesocyclops leuckarti* declined with eutrophication while *Cyclops vicinus* increased (Einsle 1983). Maier (1996) also found species-specific responses of cyclopoids in a study of 22 lakes in southern Germany: *C. vicinus* increased with lake trophy, whereas *M. leuckarti* decreased and *Cyclops abyssorum* remained constant. These examples highlight that the response of copepods to environmental changes should not be analysed on the level of the genus or the family as done in many other studies. One recent study investigated long-term dynamics of a copepod community during a phase of declining lake trophy in the context of whole food web responses (Anneville et al. 2007). Although the authors were able to provide a huge amount of data of almost all relevant trophic levels over a long period, the mechanisms shaping the response of copepods were difficult to elucidate. This stresses the complexity of ecological processes following oligotrophication and raises the need of further research on this topic.

In recent years, an increasing body of studies highlighted the impact of climate variability on copepods. Particularly in marine ecosystems, climate variability was shown to alter abundances and community composition of copepods (e.g., Fromentin and Planque 1996; Rebstock 2002; Beaugrand et al. 2002; Chiba et al. 2006). In freshwater ecosystems, studies on climatic influences on copepods are rare (but see Rusak et al. 1999; Gerten and Adrian 2002; Adrian et al. 2006). However, despite clearly demonstrating the influence of climate variability on the copepods, the studies in marine and freshwater ecosystems often were unable to provide a convincing mechanistic explanation for the observed changes. Most studies focused on concomitant changes of abundances and temperature while changes in the phenology, i.e., timing of biological events, of copepods were even less studied up to now. The few published studies showed that start and end of pelagic phases as well as peak timing of populations shifted with temperature (Adrian et al. 2006), which in one case probably resulted in varying numbers of generations per year (Gerten and Adrian 2002). Molinero et al. (2005) even reported contrasting shifts in phenology due to climate variability in two marine species, which was suggested to be caused by biotic
interactions. However, the low number of studies analysing copepod responses to climate variability in detail again stressed the need of further research on this topic.

Lake Constance seemed to be well suited for such an analysis since the lake is well studied and regularly monitored with high sampling frequency since 1961. In this thesis, I mainly focus on the period from 1970 to 1995 since during this period zooplankton was sampled with a high ontogenetic, temporal, and spatial resolution offering a unique possibility to investigate accurately the influence of oligotrophication and climate variability on copepod population dynamics. In a first step, I analysed the responses in a copepod species with a comparatively ‘simple’ life cycle, i.e., without a diapause or resting eggs (chapter I). In a second chapter, a species with a complex life cycle, i.e., exhibiting a seasonal diapause in summer/autumn, tightly coupled to environmental conditions was analysed in detail. In a third step, the responses of the copepod community to oligotrophication was analysed with an emphasis on interspecific interactions (chapter III). Finally, I investigated whether the observed interannual variations were consistent with spatial variations along presumed gradients of productivity and temperature within the lake (chapter IV).

Chapter I comprises a detailed study of a single species response to both environmental parameters. The species under investigation was *Eudiaptomus gracilis*, which is a typical representative of central European oligotrophic lakes. The copepod reproduces continuously throughout the year and does not produce any dormant stages or resting eggs (Einsle 1993). Thus, the demography of the population did not change substantially during the year, i.e., all developmental stages were present in all seasons. Hence, *E. gracilis* provided a good model organism with a comparatively ‘simple’ life cycle and low seasonal demographical variation. This enabled a close examination of stage-specific responses to climate variability and oligotrophication. Moreover, this chapter aimed at analysing seasonal variation of copepod responses and potential interactions of both environmental changes.

On the other hand, species with more complex life cycles, i.e., including a seasonal diapause, could be affected by the same parameter in different ways. These species experience environmental changes only during a certain season while they diapause during the rest of the year. The consequences of changes in that season are therefore essential for the whole population. For instance, climate warming is known to affect winter and spring weather conditions stronger than summer conditions (Stenseth et al. 2002) and species, which were active during summer, were probably less affected by
rising temperatures than spring species. Furthermore, the life cycle of diapausing species is often tightly coupled to environmental conditions to determine the optimal initiation and termination of diapause (Alekseev et al. 2007). The onset of diapause in crustaceans is usually triggered by a set of environmental factors such as photoperiod, crowding, etc. (Alekseev et al. 2007), which could modify the effects of oligotrophication and climate variability. One of these species with a complex life cycle is *C. vicinus*, reproducing in April/May and diapasing during summer and autumn. In chapter II the life cycle of this copepod is analysed in detail and the stage-specific adaptations to environmental triggers were elucidated by comparing the variability of its life cycle among years but also among sites within the lake. The role of these adaptations in modifying the responses to oligotrophication and climate variability is then analysed in detail.

In former studies, the impact of oligotrophication on copepod population dynamics was found to be an indirect effect mediated by the copepod’s food, competitors, or predators (e.g. Anneville et al. 2007). This could be confirmed in chapters I and II as observed long-term trends in abundances were suggested to be mainly caused by inter- and intraspecific interactions of crustaceans. To capture potential effects of these biological interactions on the copepod community structure, the responses to oligotrophication of all copepod species in Lake Constance were analysed together (chapter III). The four species mainly differed in their presence and timing of diapause (summer diapause, winter diapause, or no diapause), which enabled a detailed investigation of the role of life cycles in the response to environmental forcing by comparing responses of diapausing vs. non-diapausing and summer- vs. winter-diapausing species.

The first three chapters of this thesis focus on the long-term influences of changes in productivity and water temperature by comparing interannual variations, i.e., comparing high and low TP-years or warm and cold years. However, in Lake Constance productivity presumably varies along a spatial gradient as well. Chapter IV thus focused on the variation of copepod and cladocerans abundances along this spatial gradient. The purpose of this chapter was twofold: (1) Spatial gradients within a lake are usually weak and superimposed by water currents. I therefore wanted to test whether spatial variations in zooplankton abundances among sampling stations were persistent over time, reflecting local environmental conditions, or due to spatial processes such as water currents and dispersal of zooplankton. Since samples at the five locations were taken over a period of 14 years in parallel, intraannual variability of
spatial heterogeneity could be verified with a high number of replicates. (2) The variation of zooplankton abundances along the spatial gradients could be compared with the temporal gradients investigated in previous chapters. This allows for the assessment whether variations in zooplankton abundances were consistent in space and time along variations of the same parameter. Furthermore, it could be tested whether it is appropriate to substitute the temporal gradient with the spatial gradient of the same parameter, i.e., to perform a space-for-time substitution within the lake.

Former studies highlighted that the response of copepods to environmental changes might depend on a variety of factors and complex interactions. To gain more insights in the mechanisms shaping their responses, it is thus imperative to investigate environmental conditions and their influences on copepod population dynamics in detail considering variations among seasons, species, and developmental stages. This thesis is considered as an attempt to apply this on a more or less closed ecosystem, i.e., a lake. The high amount of data covering most trophic levels from algae to fish and the high resolution of copepod ontogeny offered a rather unique possibility to have a closer look on the mechanistic relationships between species and its environment. This thesis provides novel insights particularly in (1) the single and interacting influences of environmental parameters, (2) the interactions of environmental seasonality and species’ seasonal niche, (3) stage-structured interactions, (4) and spatio-temporal dynamics of copepods within a lake.
Population dynamics of a freshwater calanoid copepod: Complex responses to changes in trophic status and climate variability

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Abstract

The long-term dynamics of the calanoid copepod *Eudiaptomus gracilis* were analyzed in Lake Constance, a deep lake that has been influenced strongly by changes in trophic status and climate variability during the last few decades. Although copepod abundances remained rather stable throughout the study period (1970-1995), the seasonal pattern changed strongly, including a seasonal shift in the timing of peak abundance from spring to late summer with increasing oligotrophication. This shift in seasonality resulted from seasonally opposing long-term trends in abundances (a reduction in abundances in spring and an increase in summer) possibly due to seasonally opposing long-term trends in naupliar mortality (an increase in late winter mortality and a decrease in early summer mortality). The changes in seasonality were most pronounced within the early copepodid stages, whereas the long duration of the adult stage seemed to buffer the adult dynamics against seasonal environmental
variability. The effects of climate variability on population dynamics were more subtle and consisted of faster development in spring in years with faster vernal warming. Furthermore, the accelerated development in spring resulted in earlier occurrence of the population minimum in summer, and subsequently in an earlier abundance increase in late summer/autumn. Hence, abundances in summer/autumn were still related to spring climate variability, which shows that spring environmental variability can be transferred further into the season by the cohort dynamics of continuously reproducing populations.

Introduction

Most, if not all, aquatic ecosystems are exposed to multiple external factors that influence population dynamics and food web interactions. Two of the most important factors are nutrient loading and climate variability (Stenseth et al. 2002; Straile et al. 2003b; Jeppesen et al. 2005b). Zooplankton populations in aquatic ecosystems will be directly and indirectly influenced by these two forcing factors (Straile and Geller 1998b). However, studies analyzing in detail the joint effects of multiple environmental factors on zooplankton populations are still rare.

Copepods are dominant members of zooplankton communities in lakes, and even more so in the oceans. Eutrophication and climate variability have been shown to alter both the abundances and the community structure of copepods (Beaugrand et al. 2002; Jeppesen et al. 2005b; Adrian et al. 2006). The influence of climate variability on copepod populations and communities has been especially highlighted in marine systems (e.g. Rebstock 2002; Beaugrand et al. 2002; Molinero et al. 2005), whereas few studies up to now have documented climate effects on freshwater copepods (but see Rusak et al. 1999; Gerten and Adrian 2002; Adrian et al. 2006). Copepods have a complex life cycle with six naupliar and five copepodid stages, an adult stage, and a major metamorphosis from the last naupliar to the first copepodid stage (Einsle 1993). As a consequence, ontogenetic development encompasses a large range of body sizes and concomitant changes in diet and predator vulnerability (Santer 1994). Unfortunately, most long-term studies do not distinguish between developmental stages, which makes it very difficult to obtain a good mechanistic understanding of the relationships between copepod population dynamics and environmental stressors.
The freshwater calanoid copepod *Eudiaptomus gracilis* is the most widely distributed calanoid copepod in lakes of Central Europe (Einsle 1993). It is known to be able to develop at low food concentrations (Muck and Lampert 1984) and hence often dominates the crustacean zooplankton in oligotrophic lakes (Straile and Geller 1998a). Due to its low food threshold for reproduction, *Eudiaptomus* is able to reproduce throughout the year, i.e., also during winter, and neither a diapause stage nor resting eggs are part of its life cycle (Einsle 1993).

Here, we analyze a long-term data set of *Eudiaptomus gracilis* population dynamics for evidence of the response of this species to environmental changes. In addition to the long time span covered by the data set (1970-1995), it has also a high temporal resolution (2 samples per month) and ontogenetic resolution (copepodid stages are distinguished). As far as we know, this combination of temporal and ontogenetic resolution is unique for either freshwater or marine copepod time series. Hence, it enables close examination of the effects of environmental conditions on different developmental stages, and enables the responses to environmental conditions in the course of ontogenetic development to be traced. Using this data set, we analyze (1) the relative importance of changes in trophic status and climate variability for *Eudiaptomus* population dynamics, and (2) the vulnerability of different ontogenetic stages of the copepod to both environmental stressors.

**Methods**

Study site and sampling methodology
Lake Constance is a large (472 km$^2$), deep ($z_{\text{max}} = 254$ m), warm-monomictic lake located in southwestern Germany. The lake has been studied intensively during the last few decades, especially its response to anthropogenic changes in trophic status, eutrophication, and oligotrophication (Güde et al. 1998; Bäuerle and Gaedke 1998). However, recent studies have recognized that in addition to changes in nutrient loading, climate variability has influenced the interannual variability of many components of the pelagic ecosystem (Straile 2000; Straile et al. 2003a).

Plankton samples were taken fortnightly from 1970 to 1995 in the centre of Upper Lake Constance. There is only one major gap in the data, as no sampling was conducted during 6 months in 1987. Generation times of *Eudiaptomus* vary between
I Single species response

approximately 120 days (17 days egg development + 36 days naupliar development + 67 days copepodid development) at 5°C and approximately 23 days (2 + 9 + 12 days) at 20°C (Munro 1974). Hence, our sampling interval is shorter than one generation even at high temperatures. However, during summer, copepods may develop through the copepodid stages within one sampling interval. In contrast, average adult life expectancy is large relative to our sampling interval and can exceed one moth (Berger and Maier 2001). Up to 1985, the water column was sampled between 0 and 100 m depth by taking an integrated sample; thereafter, consecutive depth layers (0-5 m, 5-10 m, 10-20 m, 20-30 m 30-40 m, 40-50 m, 50-60 m, 60-100 m) were sampled. For each depth, 3-4 net hauls were combined to enhance the reliability of the abundance estimates. Up until 1985, a Nansen closing net (mesh size 105 µm) was used; however, this was found to strongly underestimate zooplankton numbers. All subsequent samples were collected using a new, improved net (Hydrobios, mesh size 100 µm). Comparative hauls with both types of net revealed a difference in zooplankton abundance by a factor of three. All abundance data prior to 1986 were therefore multiplied by three. Counting categories consisted of all five copepodid stages, males, females, and ovigerous females of *Eudiaptomus gracilis*. Subsamples were analyzed under a binocular microscope at 20x magnification until at least 20 individuals of each category were encountered. Clutch sizes (on average \( n = 46 \) per sampling date) were determined from 1976 to 1981 at roughly monthly sampling intervals.

Total phosphorous concentrations were measured monthly (Güde et al. 1998). We used the maximum total phosphorus concentration (\( TP_{MIX} \)) during the winter mixing period (February, March) as a proxy variable for the trophic status of the lake in a given year (Fig. 1). Interannual climate variability was represented by the water temperatures in April (\( T_A \)). During the study period, \( T_A \) did not increase significantly (\( r = 0.19, \) df = 26, \( p = 0.36 \)) but showed considerable interannual variability (Fig. 1). Water temperature was measured

![Fig. 1 The development of \( TP_{MIX} \) (maximum total phosphorus concentration during winter mixing (February, March)) and April water temperatures (\( T_A \)) during the study period.](image)
monthly during the sampling period at distinct depths. As *Eudiaptomus* is found at depths from 0 to 40 m during spring, we used the average $T_A$ from 0 to 40 m. Covariation of $T_A$ with $T_{\text{P MIX}}$ was weak ($r = -0.11$, df = 26, $p = 0.58$, Fig. 1).

**Data Analysis**

All analyses were based on log-transformed *Eudiaptomus* abundance data. To highlight the changes in *Eudiaptomus* seasonal dynamics during the study period, we estimated the trend component and the seasonal component of the copepod time series using the “Seasonal Trend Decomposition Procedure Based on LOESS” (STL) (Cleveland et al. 1990) for each developmental stage. STL decomposes a time series into trend, seasonal, and residual components using locally weighted robust regressions (LOESS). In order to calculate the STL, the 1987 data gap was filled by linear interpolation of biweekly values between years (e.g., abundances in late May 1987 were estimated using late May abundances from 1986 and 1988). STL consists of an inner loop nested inside an outer loop. In the inner loop, the trend component and the seasonal component are calculated by LOESS smoothing. First, a trend is fitted to the total time series. Second, the residuals are split up into seasonal subcycles (in our case, into 24 subcycles that represent the sampling regime of two samples per month; i.e., the first subcycle consisted of all values in early January, the second subcycle of all values in late January, and so on). To calculate the seasonal component, LOESS is applied to each subcycle. The various fits are then combined to yield the complete seasonal component for the whole time series. Within the outer loop, robustness weights are computed that are used during the next run of the inner loop to reduce the influence of outliers. We followed the recommendations and diagnostic graphical methods given by Cleveland et al. (1990) in setting the smoothing parameters (bandwidths) for the trend component ($n_{(t)} = 41$), the low-pass filter ($n_{(l)} = 25$), and the seasonal component ($n_{(s)} = 15$). To determine the contributions of the trend and seasonal components to the explanatory power of the STL fit, we calculated $R^2$ values for the trend component and for the trend component plus the seasonal component. The latter was calculated instead of the $R^2$ value of the seasonal component alone because the seasonal component is centered around the mean.

The relationships between log-transformed *Eudiaptomus* abundances and environmental factors were analyzed for every two-week period separately. This allows for seasonal changes in the relationship between environmental variables and *Eudiaptomus*. Although covariation between $T_{\text{P MIX}}$ and $T_A$ was low, we removed the effects of one variable from the abundance time series by subtracting a LOESS fit in
order to analyze the effects of the other variable. The smoothing parameter of the LOESS fit was chosen based on Akaike’s information criterion. We choose this nonlinear method to control for the effects of environmental variables instead of a simple linear least-square fit as we wanted to avoid potential pitfalls that might arise because of nonlinearity in the relationships between the abundances and the environmental variables. After removing the effect of either $TP_{\text{MIX}}$ or $TA$, the influence of the other variable on copepod abundances was analyzed using Pearson correlation coefficients. For a better understanding of the variable’s influence on population dynamics, we plotted the average population dynamics - corrected for the influence of $TP_{\text{MIX}}$ and $TA$, respectively - for the years corresponding to the upper quartile of the respective parameter against the years corresponding to its lower quartile. Data analysis was performed using SAS (SAS Institute Inc. 2004) and R (R Development Core Team 2007).

Results

Seasonal cycle of *Eudiaptomus gracilis* from 1976 to 1981

The seasonal cycle of *Eudiaptomus* (Fig. 2) is shown for the years 1976 to 1981, as these are the only years for which clutch sizes are available. During these years, $TP_{\text{MIX}}$ was at its maximum, whereas $TA$ was rather intermediate (Fig. 1). *Eudiaptomus* reproduced throughout the year. Abundance and percentage of ovigerous females were lowest in November and December, and increased slightly until April (Fig. 2a, b). The abundances of ovigerous females were elevated until June and declined towards the end of the year, whereas the percentage of ovigerous females remained rather high until October. Clutch size was low during January/February, with a first peak in May (Fig. 2c). As a consequence of low numbers of ovigerous females and low clutch size during winter, total egg abundance was low during this time of the year (Fig. 2d). Despite this, first copepodid (C I) abundance (Fig. 2e) was at its maximum in April and declined thereafter to low values from June to August. Hence, at least during these years, reproduction and survival seemed to be decoupled, with low winter reproduction resulting in high C I abundances in April and higher summer reproduction resulting in low C I abundances.
Long-term dynamics

Exemplary, STL decomposition of the time series (1970-1995) into trend component, seasonal component, and residuals was carried out for CI and adults (Fig. 3). Overall, the population remained remarkably constant during the study period (Fig. 3a, e). However, this stability resulted from two opposing trends in abundance in different seasons (Fig. 3b, c, and f, g). Abundances declined in spring but increased in summer, resulting in a switch of maximum abundance from spring during the early years of the study period towards summer during the later years (Fig. 3b, f). These seasonal differences in population development were strongly supported by STL decomposition (Fig. 3c, g). Adults showed a similar pattern, with a lag of approximately one month with respect to the CI (Fig 3). However, STL suggests that with oligotrophication adults increased in abundance during summer less than CI and that seasonal variability was lower for adults than for CI. This is supported by the statistical analysis of log-transformed abundance data: The ratio of CI to adult Eudiaptomus during the second half of the year increased during the study period \(r = 0.70, \text{df} = 25, p < 0.0001\), and the seasonal variability, expressed as the coefficient of variation for each study year, was less pronounced in adults than in CI \(t = 6.2, \text{df} = 44, p < 0.001\).

Due to the opposing trends of the Eudiaptomus abundances during April and August, the abundances of CI in April and August differed in their relationship to TP\(_{\text{MIX}}\) (Fig. 4a): In April, the abundances were positively related to TP\(_{\text{MIX}}\), whereas from July to October they were negatively related to TP\(_{\text{MIX}}\). Significant correlations were found not only for CI but also for other stages. However, with increasing ontogenetic stage,
I Single species response

**Fig. 3** STL decomposition of the time series of C I (left panels) and adults (right panels) into (a, e) trend component (dashed line), (c, g) seasonal component, and (d, h) residuals. The abundances of C I and adults are shown twice (solid lines in a, e and b, f) in order to compare the population development with the STL trend (a, e) and to highlight the population development in specific months (b, f). Open circles highlight the long-term dynamics during the second halves of April (C I) and May (adults), while open squares indicate the long-term dynamics in the second halves of August (C I) and September (adults). The trend component explained 13% and 19% of the variability for C I and adults, respectively, whereas $R^2$ for the trend component plus the seasonal component was 0.47 for C I and 0.49 for adults.

Significant correlations appeared increasingly later in the season. The abundance of ovigerous females, as well as the percentage of ovigerous females, were positively related to $TP_{MIX}$ in January (Fig. 4a).

After removing the influence of $TP_{MIX}$, the biweekly time series of *Eudiaptomus* showed no temporal trends. Detrended abundances showed a complex pattern of relationships with $T_A$ (Fig. 4b). $T_A$ was positively related to copepod abundances in May and again in July/August. In addition, $T_A$ was negatively related to the abundances of C I and C II (second copepodids) in June (Fig. 4b). In contrast to the effects of $TP_{MIX}$, $T_A$ did not influence the maximum abundances achieved by different ontogenetic stages from April to June or from July to September.
Fig. 5 allows the phenology and the magnitude of the effects of oligotrophication and high spring temperatures on *Eudiaptomus* population dynamics to be compared. In April, the abundances of almost all developmental stages were higher during high TP<sub>MIX</sub> years than during low TP<sub>MIX</sub> years. In contrast, from July to September abundances were strongly elevated in more oligotrophic years. Oligotrophication thus coincided with strong changes in the abundance of both the spring and the summer cohort of *Eudiaptomus*. Differences in the abundance of specific stages between high and low T<sub>A</sub> years are generally comparable to those observed between high and low TP<sub>MIX</sub> years. However, these differences are short-term differences that probably result from a temporal shift in population dynamics. Thus, the overall abundances of the spring and summer cohorts of *Eudiaptomus* seem not to be influenced by differences in T<sub>A</sub>.

**Discussion**

During the study period, the Lake Constance ecosystem was strongly influenced by at least two major factors: anthropogenic changes in nutrient loading to the lake, and climatic variation. Both these factors may influence the population dynamics of *Eudiaptomus* in Lake Constance in many ways by altering the abiotic and biotic environment. For example, climate variability associated with the North Atlantic Oscillation has been shown to influence water temperatures, nutrient availability (Straile et al. 2003a), the abundance of *Daphnia* (Straile 2000), and the year-class
Fig. 5 Left panel: Comparisons of the mean seasonality (with one standard error of the mean) of copepod abundances in the different ontogenetic stages for those years within the upper quartile (n = 6) of TP<sub>MIX</sub> (maximum total phosphorus concentration during winter mixing (February, March)) (dashed line) with those years within the lower quartile of TP<sub>MIX</sub> (solid lines). The influence of T<sub>A</sub> (April water temperature) within the individual biweeks was removed by subtracting LOESS fits. To restore the typical seasonal dynamics the grand mean of the copepod abundances in the individual biweeks were then added to the residuals. Right panel: As for the left panel, but comparing the population dynamics between high and low T<sub>A</sub> years after removing the effects of TP<sub>MIX</sub>. F<sub>ovg</sub> = number of ovigerous females.

strength of whitefish (Straile et al. 2007) in the lake. Hence, copepods will very likely be influenced by climate variability via temperature effects on copepod developmental rates, but probably at least to some extent also via its influence on the copepods’ food, competitors, or predators. The potential influence of the lake’s trophic changes on the copepods is equally complex. For example, algal concentrations and community
composition (Gaedke 1998) and ontogenetic growth and community composition of fish (Eckmann and Rösch 1998) have been shown to respond to the lake’s oligotrophication. Hence, any significant results obtained by correlation analysis between the copepods’ abundances and either $TP_{\text{mix}}$ or water temperatures might be due to a large number of potential mechanisms.

It is however a difficult task to identify whether the change in abundances of *Eudiaptomus* with, for example, oligotrophication, is due to bottom-up or top-down regulation of *Eudiaptomus* abundances because fish and phytoplankton are known to respond to oligotrophication (Eckmann and Rösch 1998; Gaedke 1998), which might result in covariation between the time-series. Additionally, *Eudiaptomus* showed contrasting population developments in spring and summer, suggesting that different mechanisms are responsible for the respective population trajectories (see below). On the other hand, it seems likely that the changes in *Eudiaptomus* population development associated with $TP_{\text{mix}}$ are indeed ultimately linked to changes in trophic status, because Lake Constance is a well-studied ecosystem and we are not aware of any other environmental factor, which underwent continuous change during the observation period.

In analyzing the effects of environmental factors, we computed a large number of correlations (2 environmental parameters $\cdot$ 7 development stages/categories $\cdot$ 24 biweeks $= 336$ correlations). Hence, we expect roughly 17 correlations to be significant at the $\alpha = 0.05$ level by chance alone. Although the number of significant correlations (44) considerably exceeds this number, interpreting these results should be nevertheless done with great care. Especially, correlations specific to individual combinations of development stage and sampling period should not be considered, but only patterns in correlations across development stages and sampling periods. For example, confidence in the ecological significance of the statistical relationships is high when significant relationships occur not only in one developmental stage but also, with a delay, in older developmental stages. This delay is apparent, for instance, in the negative relationships between the abundances and $TP_{\text{mix}}$ from July to October (Fig. 4a): The significant correlation first appears within CI in July and continues through the ontogenetic sequence until the adult stage in October.

In fact, the responses of *Eudiaptomus* to changes in both trophic status and water temperature were first observed at the CI stage, which suggests that environmental influences on this or earlier ontogenetic stages (i.e., nauplii) determined the overall
response of the population. This supports earlier work that suggests that mortality is highest during the naupliar stages (Eiane and Ohman 2004) and that nauplii can be considered as a bottleneck in copepod population dynamics (Santer and Lampert 1995). However, not all changes in C I abundances between years were also observed for the more advanced ontogenetic stages, which suggests that density-dependent factors operate during development. For example, the increasing ratio between the summer abundances of C I and adults during oligotrophication suggests that the increase in C I abundances was accompanied by increased mortality in more advanced stages. Consequently, the abundance of adults increased less than the abundance of C I.

The seasonal cycle, at least during the years 1976-1981, shows that periods with high fecundity do not coincide with periods of high offspring survival (Fig. 2): Low fecundity in February/March resulted in relatively high copepodid numbers in April, whereas higher fecundity during May to July produced less copepodids. Hence, seasonal differences in nauplii survival seem to decouple fecundity and offspring numbers. This interpretation is supported by an estimation of nauplii mortality rates using Wood’s population surface method (Wood 1994) for the years 1977-1979: Overall mortality during the naupliar stages in June/July was estimated to be 5-10 times higher than naupliar mortality during March/April, despite the fact that higher summer temperatures allowed faster development through this critical life cycle stage (Seebens unpubl. data).

The control of *Eudiaptomus* population dynamics has been suggested to be primarily top-down (Einsle 1993; Maier 1996), and nauplii are very vulnerable to predation and an important prey for many invertebrate predators (e.g., Kawabata 1991; Van den Bosch and Santer 1993). For example, the decline of *Eudiaptomus* in Müggelsee has been attributed to the predatory cyclopoid copepod *Cyclops vicinus* (Adrian 1997).

The strong potential for top-down control of *Eudiaptomus* also suggests that the changes in seasonal dynamics of *Eudiaptomus* during oligotrophication were primarily due to changes in mortality rates. While the year-class strength of the dominant planktivorous fish species, *Coregonus lavaretus*, did not show any relationship to abundances of *Eudiaptomus*, abundances of the carnivorous stages (C V and adults) of the cyclopoid copepod *Mesocyclops leuckarti* during spring did increase with oligotrophication, which resulted in a significantly negative relationship between the abundances of the C I of *Eudiaptomus* with *Mesocyclops* \( r = -0.49, \text{df} = 25, p < 0.05 \). *Mesocyclops spp.* have been shown to be efficient predators of both calanoid nauplii and of early copepodids in a number of experiments (Jamieson 1980; Kawabata 1991).
Alternatively, the decline in abundances of *Eudiaptomus* in April might be due to reduced food availability. The clutch size of *Eudiaptomus* has been found to be related to the trophic status of lakes (Elster 1954; Einsle 1983; Maier 1996), and the clutch size of *Eudiaptomus* in Lake Constance during the mixing period in 1976-1981 was almost twice the clutch size in the 1930s, i.e., before eutrophication (Elster 1954). However, *Eudiaptomus* clutch size during the 2005-2006 mixing period was $8.9 \pm 2.4$ (Straile unpubl. data), i.e., not lower than in 1976-1981 despite the fact that oligotrophication has continued up to the present. This suggests that the decline in abundances of *Eudiaptomus* during spring is not caused by bottom-up control, but is due to increased predation pressure on *Eudiaptomus* nauplii, probably as a result of an increased abundance of predatory *Mesocyclops*.

The mechanism(s) behind the increase in abundances of *Eudiaptomus* during July – September are less clear. Bottom-up forcing is unlikely to be the reason for the increase, as phytoplankton biovolume during summer declined with oligotrophication (Gaedke 1998). Also, there is no evidence of an increase in other potential prey taxa, e.g., ciliates, as ciliate biomass is usually tightly coupled to the biomass of algae. In addition, changes in phytoplankton species composition do not suggest a strong change in *Eudiaptomus* food quality; e.g., blue-green algae were never a dominant part of the phytoplankton community in Lake Constance (Kümmerlin and Bürgi 1989). This suggests that the increase is not due to food effects on fecundity or nauplii survival but rather to decreasing predatory losses of nauplii. Indeed, the increase with oligotrophication during July/August coincided with a reduction of summer abundances of invertebrate predators (*Bythotrephes longimanus*, *Leptodora kindtii*) in Lake Constance during the study period (Einsle unpubl. data). However, as the relationships between the abundances of invertebrate predators and the abundances of *Eudiaptomus* were not significant, we are not yet able to provide a convincing explanation of the mechanism that results in the population increase in summer.

The contrasting trends revealed for April/May and August/September also imply that our results were not affected by methodological changes (e.g., by the change in sampling nets in 1986). Also, a second data set on *Eudiaptomus* (which, however, distinguished only between size classes but not ontogenetic stages) that was sampled in the Überlinger See, a fjordlike appendix of Upper Lake Constance, shows similar contrasting trends during the season (Straile unpubl. data). In fact, decreasing abundances in spring and increasing abundances in summer suggest that with further oligotrophication the population dynamics of *Eudiaptomus* will approach the dynamics...
I Single species response

observed in oligotrophic Lake Constance during 1932-1935, i.e., highest abundances of CI during September/October (Elster 1954). Hence, the comparison between the years 1932-1935 and 1976-1981 suggests that under more oligotrophic conditions, the spring cohort of *Eudiaptomus* will further decrease in abundance relative to the summer cohort. The development of *Eudiaptomus* seasonal dynamics with oligotrophication towards a seasonality observed during the oligotrophic conditions that prevailed prior to eutrophication also suggests that the changes associated with T*P*<sub>MIX</sub> in our data set are indeed causally linked to the trophic status of the lake.

In addition to the observed changes in the trophic status of the lake, climate variability also influenced *Eudiaptomus* population dynamics. Correlation analyses with T<sub>A</sub> showed significantly positive correlations during May and again during July/August (Fig. 4b). Spring water temperatures at various depths have been shown to be closely related to the North Atlantic Oscillation (NAO) in Lake Constance (Straile et al. 2003a). Results obtained with respect to climatic influences on *Eudiaptomus* are robust with regard to which temperatures are used as a climate proxy, i.e., water temperature from March, or May, or temperature averages of these months yielded results similar to those obtained using T<sub>A</sub>. Correlations of *Eudiaptomus* abundances with Hurrell’s index of the NAO (Hurrell 1995) were somewhat weaker than correlations with spring water temperatures but nevertheless showed similar tendencies.

Higher water temperatures should definitely speed up ontogenetic development, which would explain the higher abundances of the individual stages found during April/May in high T<sub>A</sub> years (Fig. 4b, 5). Subsequently, faster development in April/May results in an earlier occurrence of the population minimum in June/July (Fig. 5) (resulting in significantly negative correlations with April temperatures, Fig. 4b) and consequently in an earlier increase of abundance towards the second maximum in August/September (resulting in positive correlations with April temperatures). Hence, the differences in population dynamics between high and low T<sub>A</sub> years suggest that the correlation patterns reflect to a large extent the result of a temporal shift in population dynamics (Fig. 5). Moreover, this shift shows that environmental variation in spring can be transferred further into the season by the cohort dynamics of reproducing populations. That is, high abundances of late copepodids and adults in August and September in some years most probably resulted from elevated April temperatures in those years. Cohort dynamics thus complement other mechanisms such as food web interactions (Straile 2000; Molinero et al. 2005) and hydrodynamical processes (Straile et al. 2003a; Straile et al. 2007), transferring the effects of spring meteorological forcing further into
the season. However, increased water temperatures in some years did not allow *Eudiaptomus* to build an additional generation, as has been suggested for copepods in other lakes (Gerten and Adrian 2002). Also, the temporal shift in population dynamics of *Eudiaptomus* did not result in any change in absolute abundances; i.e., an earlier peak in warmer springs was neither considerably higher nor lower than the somewhat later peak during colder springs. Hence, there is no evidence for a mismatch of *Eudiaptomus* population dynamics with environmental conditions due to climate warming. Faster development through the highly vulnerable naupliar stage might additionally reduce mortality. However, this effect of warmer temperatures seemed not to be very strong, as overall spring maxima of, for instance, C I were not related to water temperatures.

*Eudiaptomus* abundances during specific months of the year were influenced by both oligotrophication and warm spring temperatures (Fig. 5). However, it depended on the season, whether the two factors had additive or subtractive effects on abundances. In July, for example, both oligotrophication and high spring temperatures resulted in increased abundances of C I, whereas in April the effects of these two factors were opposite. In our case study, trophic changes were not strongly related to changes in climate. During most of the study period, nutrient concentrations declined monotonically, whereas our climate proxy showed no trend but considerable interannual variability. This allowed us to disentangle statistically the effects of trophic and climate changes. This will be much more difficult in systems in which trophic and climate changes show a higher degree of covariation. In such systems it is possible that no effects might be detected, as trophic and climate-related changes might compensate for each other, or it will be more difficult to disentangle the effects of both stressors due to their additive nature.

The overall influence of the changes in *Eudiaptomus* abundance on its phytoplankton prey is difficult to predict. *Eudiaptomus* is known as a selective feeder (Demott 1988) consuming large phytoplankton but also ciliates (Sommer et al. 2003). Predation on large phytoplankton species, which are resistant to grazing by e.g. *Daphnia*, may influence phytoplankton succession. Feeding on ciliates can have cascading effects on small phytoplankton species thereby releasing small algae from predation pressure (Sommer et al. 2003). Hence, the changes in *Eudiaptomus* seasonality in response to environmental stressors as observed in this study may have had a distinct impact on the seasonality of phytoplankton size structure with further consequences on e.g. food web energetics. A recent study suggests that copepods indeed influence the population
dynamics of large phytoplankton species in Lake Constance (Huber and Gaedke 2006). However this study did not distinguish between different copepod species and detailed analysis of the influence of *Eudiaptomus* on phytoplankton succession and size structure remains to be done.

To conclude, this analysis has shown that the calanoid copepod *Eudiaptomus gracilis* revealed a complex response to changes in trophic status and climate variability. The high ontogenetic resolution of the data set enabled us to follow environmental effects through the different developmental stages and showed that the changes in the seasonal dynamics of *Eudiaptomus* mostly originated from changes in the survival patterns of its early ontogenetic stages. The effects of climate variability and of changes in trophic status on abundances of *Eudiaptomus* differed strongly. While changes in trophic status modified environmental conditions during both winter and summer, thereby strongly changing abundances in these two seasons, climate variability resulted in a temporal shift in the seasonal dynamics of *Eudiaptomus* without strongly affecting overall abundances. However, due to the cohort dynamics of *Eudiaptomus*, the effects of spring climate variability were transferred far into the season.

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Copepod life cycle adaptations and success in response to phytoplankton spring bloom phenology

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Abstract

In a seasonal environment, the timing of reproduction is usually scheduled to maximize survival of offspring. Within deep water bodies the phytoplankton spring bloom provides a short time window of high food quantity and quality for herbivores. The onset of algal bloom development, however, varies strongly from year to year due to interannual variability in meteorological conditions. Furthermore, the onset is predicted to change with global warming. Here, we use a long-term data set to study a) how a cyclopoid copepod, Cyclops vicinus, copes with the large variability in phytoplankton bloom phenology, and b) if bloom phenology has an influence on offspring numbers. C. vicinus performed a two-phase diapause, i.e., the actual diapause of fourth copepodid stages at the lake bottom is followed by a delay in maturation within the fifth copepodid stage until the start of the spring bloom. This strategy seems to guarantee a high temporal match of the food requirements for successful offspring development, especially through the highly vulnerable naupliar stages, with the phytoplankton spring bloom. However, despite this match with food availability in all study years, offspring numbers, i.e., offspring survival rates, were higher in years with an early start of the phytoplankton bloom. In addition, the phenology of copepod development suggested
that also within study years, early offspring seems to have lower mortality rates than late produced offspring. We suggest that this is due to a longer predator-free time period and/or reduced time stress for development. Hence, within the present climate variability the copepod benefited from warmer spring temperatures resulting in an earlier phytoplankton spring bloom. Time will show if the copepod’s strategy is flexible enough to cope with future warming.

Introduction

The life cycle of many species incorporates either a dormancy or a migration period to cope with seasonally harsh conditions (Tauber et al. 1986; Alekseev et al. 2007). Such taxa are thought to be especially vulnerable to climate change (Durant et al. 2007) as possible changes in the cues used for breaking diapause or back-migration from overwintering habitats may differ from the phenological changes in the breeding season and habitat. For example, a long-distance migratory passerine, the pied flycatcher *Ficedula hypoleuca*, experienced population declines during the last decades presumably because it was not able to adjust its breeding phenology and arrival from winter grounds, respectively, to an earlier appearance of its food (Both et al. 2006). A mismatch might also occur if a temperature change in the overwintering habitat results in too early remigration into the breeding habitat (Inouye et al. 2000). Likewise, advanced emergence of the marmot *Marmosa flaviventris* from dormancy due to warmer temperatures results in a mismatch because the timing of snow melting has not advanced accordingly (Inouye et al. 2000).

A dormancy period is also widespread within zooplankton (Alekseev et al. 2007). Many species among the cladocerans, copepods, rotifers, and ciliates are known to bridge seasonally unfavourable conditions with a dormancy or diapause period. Zooplankton use a variety of environmental cues such as temperature (Marcus 1982), photoperiod (Hairston and Kearns 1995), density (Kleiven et al. 1992), predator kairomones (Slusarczyk 1995), and food quality (Koch et al, submitted) to optimize the timing of diapause initiation and/or termination. In addition, also maternal effects might be important for the production of diapausing stages (LaMontagne and McCauley 2001).

Copepods have a complex life cycle with six naupliar (N I – N VI), five copepodid stages (C I – C V), and an adult stage with a major metamorphosis from the naupliar
towards the copepodid stages. Diapause in copepods can occur through the production of resting eggs or due to an interruption of development usually within an advanced copepodid stage (C IV or C V) (Santer 1998). Despite the global importance of copepods (Humes 1994), there are no studies, which address the consequences of diapause for copepod fitness in the context of climatic warming or climatic variability.

The freshwater cyclopoid copepod *Cyclops vicinus* is an important member of the zooplankton community in many European lakes (Einsle 1993). In most of these lakes, the copepod disrupts ontogenetic development within C IV in early summer to perform a diapause. Summer diapause of *C. vicinus* has been suggested to be ultimately due to the dependency of herbivorous nauplii on a high food availability, which is only warranted during the phytoplankton spring bloom, but not during the summer season (Santer and Lampert 1995). However, high predation pressure during summer has also been discussed as the ultimate cause for the summer diapause of *C. vicinus* (Maier 1989). Diapause initiation has been suggested to be controlled by photoperiod (Einsle 1964b; Spindler 1971; George 1973) and diapause is carried out in the sediment at the bottom of the lake. The strategy to avoid unfavourable conditions thus is a combination of diapause and migration. Especially in deep lakes this is not without problems as environmental conditions on the bottom of the lake do not provide reliable cues about the conditions at the surface (Straile et al. 2007), i.e., on when it is best to terminate diapause. Facing this challenge, individuals of C IV re-emerge from diapause during winter and complete their development.

In many lakes, the timing of the phytoplankton spring bloom is highly variable and may differ interannually up to two months depending on meteorological forcing (Adrian et al. 1999; Peeters et al. 2007a). Given the dependency of successful naupliar development on the algal spring bloom (Santer and Lampert 1995), this variability poses two major problems for the copepod: 1) Diapause termination needs to be well in advance to the onset of the phytoplankton bloom in order to allow for a timely maturation and reproduction to finally ensure that naupliar hatching matches with the phytoplankton bloom. 2) As diapause induction is controlled by photoperiod, high variability in phytoplankton bloom timing results into a high variability in the time window available for the copepod to develop towards the diapausing stage (C IV). Especially, during years with a late phytoplankton bloom, the shortened time span might result into time stress.
II Modification of single species responses

Here, we use a long-term data set to study the life cycle strategy of *C. vicinus* in a deep Central European lake with a high variability in phytoplankton bloom phenology (Peeters et al. 2007b). We study the phenology of diapause re-emergence and reproduction of this copepod in response to algal bloom timing. In addition, we analyse the influence of the phenology of reproduction on reproductive success, i.e., offspring survival of *C. vicinus*.

**Methods**

Study site and sampling

The study was done in deep (\(z_{\text{max}}=254\)m), large (472 km\(^2\)), and warm-monomictic Upper Lake Constance located in southwestern Germany. During the last decades the lake was influenced by anthropogenic changes in trophic status, i.e., a period of eutrophication until late 1970ies and a period of oligotrophication until today (Güde et al. 1998; Bäuerle and Gaedke 1998), as well as climate variability (Straile et al. 2003a). Both forcing factors were shown to influence zooplankton of Lake Constance (Straile and Geller 1998a; Straile 2000).

Zooplankton and phytoplankton were sampled fortnightly from 1970 to 1995 in the centre of Upper Lake Constance (main station, depth = 250 m). We excluded three years (1970, 1987, and 1995) from further statistical analysis since these years contained large gaps of more than one month. The sampling methodology for zooplankton is described in more detail in Seebens et al. (2007). All five copepodid stages, males, females, and ovigerous females of *C. vicinus* were distinguished. Unfortunately, abundances of *C. vicinus* nauplii were not determined. Zooplankton was also sampled during 14 years (1972 – 1985) with the same temporal and ontogenetic resolution within the Bay of Bregenz, at a shallow part of Upper Lake Constance (\(z_{\text{max}} \approx 60\)m). Phytoplankton was counted from integrated samples of the upper 20 m of the water column (Kümmerlin 1998), but only at the main station. The trophic status of the lake in a specific year was represented by the maximum total phosphorous concentration during winter (February, March) mixing (TP). Water temperatures were measured monthly at distinct depths (0 m, 5 m, 10 m, 15 m, 20 m, 30 m, 50 m, 100 m, 200 m, 250 m) during the whole study period. As *C. vicinus* was found at depths from 0 to 20 m during spring we used the average temperature of the upper 20 m. In order to determine the start of stratification, Schmidt’s stability index (Schmidt 1928) was
calculated for all temperature profiles. This index is a measure for the amount of mechanical work, which is necessary to homogenise the water column ($g \ cm \ cm^{-2}$). The index value increases with stratification from a minimum value of zero at isothermal conditions. The onset of stratification in spring was defined at the arbitrary threshold of 200 $g \ cm \ cm^{-2}$, which was exceeded on average in early April. The choice of this threshold did not significantly influence the overall results, e.g., timing of exceeding the threshold of 200 and 100 $g \ cm \ cm^{-2}$ were highly correlated ($r = 0.83$, df = 25, $p < 0.0001$).

Statistical analysis

Except for the determination of abundance maxima, all abundances were log-transformed for further statistical analyses. The annual peak timing of *C. vicinus* stages and phytoplankton biomass were captured by fitting Weibull-distributions to the abundance and biomass curves, respectively, to generate distinct single peaks (Fig. 1). Using Weibull fits revealed similar peak timings as compared to simply choosing the timing of maximum abundance without a fit ($r = 0.93$, df = 138, $p < 0.0001$). However, Weibull fits integrate over sampling intervals and therefore produce more realistic peak timings (Fig. 1). The onset of phytoplankton growth was approximated by using the first 20 % quantil of the Weibull fit on phytoplankton biomass. The Weibull fits were applied to phytoplankton biovolume from February until June to include all relevant phases of the spring bloom, i.e., onset, growth, maximum, and decline. The Weibull-fitting procedure is easily applicable to single maximum curves but fails when more then one peak must be fitted within the same year. This was the case only for C IV of *C. vicinus* since two cohorts appear and may even overlap somewhat in specific years. Here, we separated both cohorts (in the following C IV$_1$ and C IV$_2$) at the time between their two peaks when abundance was lowest.

The interrelationships between developmental stages and the copepod’s response to environmental factors were analysed with Pearson correlations and Pearson partial correlations. We checked variables for non-normality and collinearity, i.e., near-linear dependences among variables, using Shapiro-Wilks test and variance inflation factor, respectively (Belsley et al. 1980). A comprehensive model predicting the timing of the copepod’s egg-production and abundance of offspring was tested with path analysis. Path analysis allows to investigate complex multivariate causal models based on path diagrams and tests whether a specific model, represented by this path diagram, is an acceptable description of the underlying causal mechanisms (Grace 2006). Performing this method, we were able to test a comprehensive model, which could formerly only
assessed for each dependent variable separately. Based on a covariance-variance matrix including all parameters path analysis calculates path coefficients, which are the same as standardized partial regression coefficients from multiple regression.

The goodness-of-fit of path models was measured by using different tests and indices, in particular $\chi^2$ test, Comparative Fit Index (CFI), root mean square error of approximation (RMSEA), and Hoelter’s Critical N (Belsley et al. 1980; Bollen 1989). The latter represents the sample size, which results in a significant $\chi^2$ test. Note that a non-significant $\chi^2$ test indicates a good fit. Additionally, the total $R^2$ for each model is shown. The model, which fulfills $\chi^2$ test (non-significant), a CFI above 0.95, and RMSEA less 0.06, is regarded as a good description of the data (Hu and Bentler 1999). Data analysis was performed using SAS/STAT software (SAS Institute Inc. 2004).

Results

The life cycle of *C. vicinus* is exemplary shown for one year (1976) in Fig. 1. In Lake Constance, individuals of the diapausing stage (C IV), reappeared in the pelagic zone mainly during winter and reached the adult stage in April shortly after the start of the phytoplankton bloom. The reproduction took place during the spring bloom in April/May and offspring developed quickly to C IV, which entered diapause again in late May/early June. On average, the maximum abundance of re-

![Fig. 1 Phyttoplankton development and life cycle of C. vicinus in 1976 (December 1975 to July 1976). Dots represent abundance of phytoplankton biovolume and copepodid stages (C IV, and C V), adults, ovigerous females (OFM), and offspring copepodid stages (C I, C II, C III, and C IV). Dashed line represent Weibull fits. The arrow shows the 20 % quantil of phytoplankton spring development. Note the different y-axes.](image-url)
emerging C IV₁ was on the 14th of February (Fig. 2), soon followed by the maximum abundance of C V (4th of March). However, the average timing of the maximum abundance of adults and ovigerous females was more than two months delayed (3rd of May and 13th of May, respectively). Maximum abundances of next generation copepodids occurred on average from mid May onwards with successive ontogenetic stages closely following each other: C I: 25th of May, C II: 26th of May, C III: 28th of May, and C IV₂: 31st of May. The interannual variability of peak timing decreased with ongoing ontogenetic stage as indicated by the declining trend of coefficients of variation (cv) from the peak of C IV₁ in winter (cv = 36) until the peak of C IV₂ in May/June (cv = 4) (Fig. 2, r = -0.85, df = 7, p < 0.01). The late winter peak of C IV₁ and C V exhibited a variability of peak timing 3.6 and 2.5 times, respectively, higher as observed for the adult stage and this in turn was twice as variable as offspring. Thus, within the ontogenetic development there seemed to be two major declines in variability of peak timing: from C V towards adults, and from ovigerous females towards C I (Fig. 2).

Assuming a straightforward ontogenetic development we would expect that more advanced individual stages follow its precursor stages within a regular time schedule, e.g., an early occurrence of C IV₁ in a specific year will also result in an early occurrence of C V, while a late C IV₁ occurrence will also result in a late C V occurrence. That is, there should be a high covariation between the phenologies of different developmental stages. This was indeed observed: The timing of maximum abundances of re-emerging C IV₁ copepods was significantly related to the timing of the abundance of the following developmental stage (r = 0.76, df = 22, p < 0.0001, Tab. 1). Also, the timing of the occurrence of the adult maximum was highly related to the timing of the maximum abundances of the offspring copepodids (Tab. 1). A notable exception, however, was the relationship between peak timing of C V and adults: It
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Tab. 1 Pearson correlation coefficients between peak timing of *Cyclops vicinus* stages (copepodid stages (C IV, and C V), adults, ovigerous females (OFM), and offspring copepodid stages (C I, C II, C III, and C IV₂)) within the different study years (n = 23). * p < 0.05, ** p < 0.01, *** p < 0.005, **** p < 0.001.

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was not possibly to predict the timing of maximum adult abundances from the timing of maximum C V abundances (r = -0.02, df = 22, p > 0.1) even after potential outliers were removed (Rstudent > 2). Hence, molting into the adult stage and consequently the timing of reproduction seemed to be specifically triggered by environmental cues. Both, water temperature and the onset of phytoplankton growth, were highly correlated with the timing of maximum abundances of ovigerous females and their offspring stages (Tab. 2). For the latter, however, these relationships were mostly due to the influence of temperature and/or phytoplankton bloom timing on female reproduction: After accounting for the effects of the timing of reproduction in a partial correlation, effects of water temperature and phytoplankton bloom timing were not any more significantly related to the timing of maximum offspring abundances. This is supported by the fact that the timing of offspring stages were more strongly related to water temperature in April (Tab. 2) and not to May temperatures (e.g., peak timing of C I: r = 0.29, df = 22, p = 0.17), the month of their main occurrence (Fig. 2). Correlations with TP revealed no consistent and significant pattern on peak timing (not shown), indicating that the changes in trophic status did not change the phenology of the

Tab. 2 Pearson correlation coefficients between peak timing of *Cyclops vicinus* stages (copepodid stages (C IV₁, and C V), adults, ovigerous females (OFM), and offspring copepodid stages (C I, C II, C III, and C IV₂), and environmental parameters. *(par)* indicates Pearson partial correlation coefficients between parameters while holding the influence of the peak timing of OFM constant. For further details see text. Tₐ = April water temperatures, Phyto = onset of phytoplankton growth in spring. * p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.005, **** p < 0.001.

<table>
<thead>
<tr>
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<th>Tₐ</th>
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<td>CIII</td>
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<td>0.56</td>
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copepod. At the Bay of Bregenz adults and ovigerous females reached their maximum abundances 22 respectively 16 days earlier than at the main station (Tab. 3), whereas no significant differences were found in peak timing of copepodid stages.

To analyse the effects of the phenology of reproduction on offspring performance, we first compared the population development between years of early and late maxima of ovigerous females (in the following early and late OFM years, n = 8, respectively). Please note that the average phytoplankton biovolumes and copepod abundances in early versus late OFM years were calculated after removing potential effects of changes in TP on biovolumes and abundances by substracting LOESS fits within the individual biweeks. To restore the typical seasonal dynamics, the grand mean of the phytoplankton biovolume and copepod abundances in the individual biweeks were then added to the residuals. On average early and late OFM years differed slightly in vernal warming during March and April (Fig. 3a). A higher algal biovolume during April in early OFM years indicated earlier stratification in these years as compared to late OFM years (Fig 3b). However, algal biovolume in early and late OFM years did not differ significantly after April. Also, the start of clear-water phase in early June did not differ between the two year groupings. Early OFM years showed higher abundances of ovigerous females in April, whereas late OFM years higher ones in May/June (Fig. 3c). However, the average abundance of ovigerous females from March to June did not differ between early and late OFM years (r = -0.19, df = 22, p = 0.40). Abundances of copepodids differed significantly between early and late OFM years but, however, only during the build-up phase of the respective stages (Fig 3d-g).

**Tab. 3** Peak timing (day of the year, mean, and standard deviation) of *Cyclops vici nus* stages (copepodid stages (C IV₁, and C V), adults, ovigerous females (OFM), and offspring copepodid stages (C I, C II, C III, and C IV₂)) at the main site and the Bay of Bregenz and differences in peak timing between sampling sites (ANOVA). Only those years were included for which measurements at both sites were available (n = 13 for C IV₁ to OFM and n = 14 for C I to C IV₂). n.s. = p > 0.05.

<table>
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<tr>
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<tr>
<td>CIV₁</td>
<td>47 ± 15.0</td>
<td>40 ± 20.7</td>
</tr>
<tr>
<td>CV</td>
<td>64 ± 15.1</td>
<td>49 ± 29.5</td>
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<tr>
<td>Adults</td>
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<td>109 ± 9.4</td>
</tr>
<tr>
<td>OFM</td>
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<td>124 ± 7.2</td>
</tr>
<tr>
<td>CI</td>
<td>147 ± 8.1</td>
<td>145 ± 8.6</td>
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<td>149 ± 8.2</td>
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<td>CIII</td>
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</tr>
<tr>
<td>CIV₂</td>
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<td>153 ± 7.0</td>
</tr>
</tbody>
</table>
II Modification of single species responses

As a consequence, average C I abundances during the spring bloom (April - June) were significantly related to OFM timing (Tab. 4). This was the case for the main station (model I) and when considering both stations together (model II). TP did not contribute significantly to the two models since the average number of females was also included in the models. The number of females also captures the long-term dynamics of the copepod due to changes in lake trophy, but additionally interannual variability of copepod abundances and thus compete successfully for the variability in C I abundances also explained by TP. When excluding the number of females from the model, TP is a significant predictor (models not shown). The abundance of females also accounts for the reproductive potential of the copepods in a specific year. Consequently, the negative effect of OFM timing on C I abundances suggests a reduced realisation of this potential, either due to reduced productivity of offspring (smaller clutch sizes or number of clutches) or due to offspring mortality. Model II suggests significant differences in C I abundance (higher abundance at the Bay of Bregenz) even after accounting for female abundances and OFM timing. Note, that the estimates for the effect of OFM timing on C I abundances were

Fig. 3 Mean spring development of (a) temperature, (b) biovolume of phytoplankton, and (c) abundance of *Cyclops vicinus* stages (ovigerous females (OFM), and (d-g) offspring copepodid stages (C I, C II, C III, and C IV)) in years associated with an early peak timing of OFM (dashed line) (n = 8) and years of late peak timing (solid line) (n = 8). Bars indicate one standard deviation of the mean. The potential influence of TP on the dynamics of algae and *C. vicinus* stages within the individual biweeks was removed by subtracting LOESS fits. For further details see text.
Modification of single species responses

<table>
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<td>n.s.</td>
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<td>&lt; 0.05</td>
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similar in both models, suggesting higher abundances of C I at the Bay of Bregenz partially due to earlier OFM timing.

The potential mechanisms underlying the timing of the maximum of ovigerous females and abundance of offspring at the main station were summarized in a path diagram (Fig. 4). All goodness-of-fit indices denoted a very good fit indicated by a non-significant $\chi^2$ test with a large Hoelter’s Critical N (giving high confidence in the $\chi^2$ test), a CFI equal one and RSMEA near zero. Moreover, despite of its simplicity the model was able to describe a large amount of the variability of the data set ($R^2 = 0.94$) and hence seemed to provide a reasonable solution of the underlying mechanisms. All estimated path coefficients significantly differed from zero. 61 % of the variability of reproduction timing could be explained by temperature and onset of phytoplankton growth. The latter was significantly related to the onset of stratification. Finally, abundance and peak-timing of ovigerous females determined C I abundances ($R^2 = 0.88$). Considering that all parameters were measured on a rather rough time scale ranging from monthly (temperature) to biweekly (phyto- and zooplankton) sampling intervals the amount of explained variability is high. Furthermore, the path analysis indicated a strong effect of timing of reproduction on abundance of offspring even after including the overall abundance of females.

Discussion

The naupliar stage has been considered as a population bottleneck in several studies of copepod populations (Santer and Lampert 1995; Eiane and Ohman 2004). Consequently, the seasonal timing of reproduction in copepods should be scheduled to minimize naupliar mortality due to starvation and predation. The risk of mistimed
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reproduction seems to be especially high for a copepod species such as *Cyclops vicinus*, which nauplii do have rather high food requirements (Santer and Van den Bosch 1994). In contrast, the freshwater calanoid copepod *Eudiaptomus gracilis* reproduces throughout the year and nauplii can develop also during periods of food scarcity, e.g., in winter (Seebens et al. 2007). However, despite their rather low food requirements, nauplii can be considered as a bottleneck also for the population dynamics of this species. The width of the bottleneck seems to be regulated by predation (Seebens et al. 2007).

In order to not miss the phytoplankton spring bloom, C IV₁ of *Cyclops vicinus* re-emerge well in advance of the bloom and subsequently develop in C V. Development through the C V stage, i.e., maturation at 5°C should take 13.1 and 8.3 days for females and males, respectively (Munro 1974). The average time lag between the maxima of C V and adults is, however, almost 2 months, suggesting that maturation of *C. vicinus* was indeed interrupted. The temperature-dependency of copepod development also suggests that increased food availability due to the onset of the phytoplankton bloom and not increasing temperature is responsible for maturation although we were not able to distinguish statistically between the effects of both factors. This interruption of development is, however, unlikely due to food limitation of C V per se as copepodids re-emerging from diapause usually possess energy reserves, which should allow them to finish development and even reproduce (Santer and Boldt 1998). The timing of maturation seems also not to be triggered by photoperiod as average timing of maturation was 22 days earlier in the Bay of Bregenz than at the main station. This corresponds to an earlier onset of the phytoplankton bloom in the Bay (approximately 2 weeks according to chlorophyll measurements from 2006 and 2007, Kümmerlin, pers. comm.) and suggests that increased food availability due to the start of the phytoplankton bloom acts as a cue for the continuation of development, i.e., for maturation. We are not aware of any other

**Fig. 4** Path diagram summarizing a priori assumptions of the potential underlying mechanisms determining the timing of reproduction of *Cyclops vicinus* and the abundance of offspring. Arrows indicate unidirectional relationships, whereas their strength is shown as path coefficients (**, p < 0.01) estimated by path analysis. For dependent variables R² is given. The goodness-of-fit for the whole model was measured by fitting indices (χ² = 2.0, df = 7, p = 0.96, RMSEA < 0.001, Hoelter’s N = 156). For further details see text.
long-term studies analysing the phenology of development and reproduction of copepods in such a detail, however, Head et al. (2000) reported spatial heterogeneity in maturation rates and egg production for *Calanus finmarchicus* to coincide with the spatial distribution of chlorophyll concentrations in the Labrador Sea. In this case, however, maturation delay was suggested to be due to food limitation *per se*.

Independently of the cues involved in diapause termination and finally maturation, our data suggest that *C. vicinus* uses a two-phase diapause, i.e., diapause as a C IV and developmental retardation as a C V, to ensure a match of their offspring food requirements with the highly variable phytoplankton spring bloom. This complex strategy has not been shown before for this species, possibly because it might be difficult to detect without long-term data on ontogenetic development. Alternatively, this two-phase diapause might be a special adaptation of the *C. vicinus* populations from deep lakes due to the absence of any reliable cues indicating phytoplankton bloom onset at the bottom of these lakes.

Earlier bloom timing seems to cause higher offspring numbers, i.e., increased survival of nauplii. This may be due to various reasons ranging from food availability, seasonal predator avoidance, maternal aging, and the costs of time constraints. Nauplii developing after May probably face food shortage as the clear-water phase usually takes place around June independently whether there was an early or late onset of the phytoplankton bloom (see Fig. 3b). However, number of copepodids declined already during May even in late OFM years although abundance of ovigerous females and food availability in these years was at its maximum during May. This suggests that food limitation seems not to be responsible for the early decline of copepodid numbers in especially late OFM years. Another possibility for this decline might be maternal aging: Decreasing lipid reserves caused a decrease in egg size, clutch size, and C I size with aging females in the copepod *Cyclops kolensis* (Jamieson and Santer 2003). However, as *C. vicinus* seems to postpone maturation until the start of the algal bloom the role of maternal aging might not be the crucial factor for the reduced success in late OFM years. Another possibility might be a seasonal increase of predation pressure during May: This increase might be caused by e.g. the hatching of perch larvae around May (Wang and Appenzeller 1998), cannibalistic feeding of e.g. early C IV copepods (Brandl and Fernando 1981), or predation from *Mesocyclops* (Kawabata 1991). Both C IV₂ of *C. vicinus* and adult stages of *Mesocyclops leuckarti* (unpublished data) have their peak timing in mid May with relatively little interannual variability. Peak timing of adult *M. leuckarti* may be used as an indicator of the interannual variability of diapause.
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termination and hence start of feeding activity of this species, as in this species the C V
performs an active diapause (Elgmork 1980) during winter in Lake Constance. Although we cannot quantify the predation pressure of individual predator species, it is probably safe to assume that the nauplii of C. vicinus will be exposed to strongly increasing predation pressure from May onwards. Finally, reduced survival of nauplii might indirectly result from time stress on development. As diapause migration is controlled by photoperiod (Einsle 1964b; Spindler 1971; George 1973) and usually takes place in early June nauplii hatching late do have considerable less time to complete development towards the C IV stage than early nauplii.

The role of time stress for development has received considerable attention in e.g., insects and amphibians (e.g., Newman 1992; Gotthard et al. 1999). These studies have shown that larvae without time stress do not develop with maximum rates as this involves costs. To speed up development under time stress larvae aim for either an increased uptake of resources or a change in habitat. Both might increase their susceptibility towards predation as predators might be attracted by increased feeding activity or habitat overlap might be larger within the new habitat. For example, copepod nauplii might migrate under time stress towards warmer surface waters, which should allow for faster growth, but may also increase their encounter rate with predators. In addition, larvae may change resource allocation towards increased investment into growth and development. Costs of changes in resource allocation might be immunity suppression (Rolff et al. 2004), increased oxidative stress (De Block and Stoks 2008), or increased fluctuating asymmetry (De Block et al. 2008). Unfortunately, the role of time stress for copepod development has received hardly any attention up to now in studies of copepod ecology. However, a recent modelling study has considered the role of time stress for a marine copepod (Varpe et al. 2007). In addition, there is experimental evidence showing that photoperiod can indeed influence the development of C. vicinus nauplii (Einsle 1964b).

The timing of the C I maximum followed OFM after 7 days at the main station. Given a developmental time of nauplii of 37 days at 5°C and 15 days at 10°C the short interval suggests that the C I peak was not the consequence of the development of the majority of clutches produced but rather corresponds to the successful development of early clutches, whereas the later ones faced increasing mortality. A seasonal through in predation pressure on copepod nauplii at or even before the timing of the phytoplankton spring bloom has also been suggested for the calanoid copepod Eudiaptomus gracilis in Lake Constance (Seebens et al. 2007). In addition, a
disproportionately large contribution of early eggs to reproductive success was predicted by a modelling study of Varpe et al. (2007), which shows that eggs of the subantarctic copepod *Calanoides acutus* have the best prospects when laid even about one month before the start of the phytoplankton bloom. This prediction was based on the assumptions of seasonally increasing predation pressure and time constraints in order to reach a state capable for diapause. Differences in the biology between *C. vicinus* and *C. acutus* and the modelling approach used by Varpe et al. (2007) might explain the presumably differing strategies of the two species. In contrast to *Cyclops vicinus* (Santer and Van den Bosch 1994), the first nauplii stages of *Calanoides acutus* develop without feeding allowing them to bridge a certain pre-bloom period without starvation. However, the results regarding the optimal strategy of *C. acutus* reproduction might depend also on the modelling approach as the optimization model used cannot predict optimal life histories in environments that vary interannually, e.g., in algal bloom phenology (Varpe et al. 2007).

Seasonally increasing mortality and/or differences in developmental rates due to time constraints can also explain the increasing interannual synchronisation of phenological events with life cycle development, e.g., from maturation and egg production towards offspring (see Fig. 2). Comparatively early C I peaks within late OFM years, i.e., a small time lag between the peaks of C I and oovigerous females, might be expected when there is a higher mortality for the late nauplii, and/or when late nauplii develop faster due to time constraints. This synchronisation occurs also when comparing the two sampling stations as there is a large and significant difference in phenology of OFM timing, whereas only a small and non-significant one in e.g. C I phenology. Again, differences in naupliar developmental rate and/or nauplii mortality might contribute to this synchronisation. The latter is supported by significantly lower abundances of the predatory copepod *Mesocyclops leuckarti* in the Bay of Bregenz (unpublished data) and by the fact that the peak timing of adult *M. leuckarti* did also not differ between the two sampling stations (main station: 26th of May ± 10.0 days, Bregenz: 25th of May ± 9.4 days). That is, predation of *M. leuckarti* will increase at both stations rather simultaneously, whereas maturation and reproduction of *C. vicinus* was significantly earlier at the Bay of Bregenz. This should give nauplii of *C. vicinus* at the Bay a longer time window for successful development and consequently contribute to the higher numbers of C I at this site.

To conclude, we have shown that *C. vicinus* copes with the problem of high interannual variability of his reproductive period, i.e., the timing of the phytoplankton bloom, by
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returning early from diapause but postponing maturation until the bloom starts. This suggests that the diapause of the copepod is actually composed of two phases: a dormancy period of the C IV stage and a subsequent developmental retardation of the C V stage until the start of the spring bloom. The copepod benefited from early phytoplankton blooms as this seemed to give the nauplii a longer time window for successful development into C I possibly as a result of reduced predation pressure early in the season and/or reduced time constraints. Simulations with a coupled hydrodynamical – biological model predict that in Lake Constance algal bloom timing will advance up to one month with global warming (Peeters et al. 2007a). This might suggest that C. vicinus will benefit from further warming. However, the life cycle of the species, e.g., diapause induction and termination, is adapted to the current climate and the predicted large shift in phytoplankton phenology might nevertheless result either into a mismatch of the copepods life cycle with the new environmental phenology or microevolutionary adaptations to the new situation.

Acknowledgements

We thank Rainer Kümmerlin for providing phytoplankton data, Henno Rossknecht for data on total phosphorus concentrations and water temperature, and Nelson G. Hairston for valuable discussion. The research was supported by the Deutsche Forschungsgemeinschaft (DFG) (Project CLIMCOPS within the priority program 1162 AQUASHIFT).
Chapter III

‘Ghost of life cycle differentiation past’ determines response of community structure to environmental change

HANNO SEEbens, ULRICH EINSLE, AND DIETMAR STRAILE
Manuscript in preparation

Abstract

The response of ecological communities to environmental changes is commonly investigated by analysing recent interspecific interactions, i.e., competition or predation, while the role of evolutionary processes has received less attention. Here, we analysed long-term (1970 – 1995) dynamics of a freshwater copepod community regarding the role of evolved life cycle strategies in the response to declining nutrient concentrations (oligotrophication). Copepod life cycle strategies differed in the presence and timing of a seasonal diapause, i.e., diapause in summer, autumn, or none at all, resulting in a distinct seasonality of community structure. Their responses to oligotrophication were first observed in juveniles, indicating that oligotrophication mainly acted through offspring mortality. Responses were season but hardly species specific as copepod abundances declined in spring and increased in summer probably due to seasonal opposing changes of invertebrate predation pressure. Consequently, community responses were determined by the seasonal occurrence of offspring depending on the species evolved life cycles, i.e., on the ‘ghost of life cycle differentiation past’, rather than on recent interspecific differences in ecological requirements. The role of life cycle strategies in the community response to environmental changes is widely overlooked.
so far but will be relevant for a broad variety of communities, including species differing in seasonal avoidance strategies such as diapause or migration. Mechanisms observed in this study can not be analysed experimentally, underpinning the need of appropriate long-term data with sufficient high ontogenetic and temporal resolution.

Introduction

The structure of ecological communities results from an interplay of interspecific interactions, i.e., competition (Tilman 2004) and predation (Kurle et al. 2008), and destabilising and stochastic processes such as physical disturbances and variability of the environment (Cloern et al. 2007; Thibault and Brown 2008). However, evolutionary processes such as niche differentiation mitigate or even diminish interspecific interactions and it is a standing debate whether or not the observed community structure reflects recent species’ interactions or the ‘ghost of competition past’ (Connell 1980; Hansen et al. 2007). An experimental approach to address this topic is difficult, however, few studies were performed to analyse the effects of local adaptation on competitive interactions (Hairston et al. 2001; Cousyn et al. 2001; Pritchard and Schluter 2001; Steiner et al. 2007). The role of life cycle differentiation in structuring recent communities is even more difficult to investigate experimentally as different developmental stages and consequently long time scales are involved. Consequently there is no experimental work related to this issue. Life cycle differentiation could, however, play a crucial role in shaping community structures since e.g., many species avoid annual recurring harsh conditions by migrating to more favourable regions, e.g., birds (Webster et al. 2002), insects (Froy et al. 2003), mammals (Berger 2004), fish (Griffiths 2008), or by entering diapause, e.g., mammals (Swenson et al. 2007), insects (Tauber et al. 1986), crustaceans (Alekseev et al. 2007). The structure of communities including species with these complex life cycle strategies thus changes seasonally.

Environmental change such as climate warming or changes in nutrient concentration (eu-/oligotrophication) affects plant and animal communities around the globe (Smith et al. 1999; Walther et al. 2002) and may re-organize these communities (Ruhl and Smith 2004; Morgan et al. 2007). In analysing the influence of environmental change on communities, three major challenges need to be considered: (A) the seasonality of environmental change, (B) the complexity of species’ life cycles, and (C) the demography of populations. Most environmental changes exhibit a strong seasonality,
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e.g., winter warming due to climate change (Stenseth et al. 2002), and even slow, monotonic long-term changes such as oligotrophication may show a striking seasonality in its influence on population dynamics (Seebens et al. 2007). Consequently, the life cycle of a species is of crucial importance whether that species is affected at all by environmental change and whether the new conditions resulted in population changes (Adahl et al. 2006). On a community level, the life cycle might also influence the outcome of interspecific interactions under changing abiotic conditions. For instance, competitive abilities of a resident bird species increased compared to a migratory due to the inability of the latter to adjust its phenology according to climate warming at the breeding habitat, which finally resulted in a change of community structure (Ahola et al. 2007). In many species environmental changes are most influential in juveniles (Lindström 1999), which implies that juveniles mainly determine the response of the whole population to environmental change (Gaillard et al. 2000). Coulson et al. (2001) highlighted the complex interactions of environmental seasonality, life cycle, and demography in a population of Soay sheep, however, studies analysing these issues on community responses are still lacking.

Here, we investigated the role of seasonality, life cycle strategies, and demography in the response of a copepod community to oligotrophication in a lake. This study focuses on oligotrophication, which is known to affect a broad variety of species (Smith et al. 1999), however, the results of this study will also be relevant regarding other environmental drivers with a strong seasonality, e.g., climate change. Copepods are dominant members of zooplankton communities in freshwater and marine ecosystems and a growing body of studies highlights the response of copepods to changes in nutrient loadings (Jeppesen et al. 2005a; Seebens et al. 2007; Anneville et al. 2007). However, no study yet accounted for variations of life cycle strategies and demographical seasonality. Copepod life cycles are complex as they encompass 12 developmental stages (six naupliar, five copepodid stages (C I to C V), and an adult stage) and many species perform a seasonal diapause (Einsle 1993). Particularly, diapausing species exhibit a strong seasonality but, however, population dynamics of non-diapausing species can have a remarkably seasonality as well indicated by the seasonal variation of mortality rates with a magnitude of more than 10-fold (Ohman and Wood 1996; Hirst et al. 2007). However, season-specific responses of copepods to environmental forcing were widely ignored in time series analyses of copepods (but see Adrian et al. 2006; Chiba et al. 2006).
This study is conducted on a unique, highly resolved long-term (1970 - 1995) data set of crustacean zooplankton. In a former study, oligotrophication was found to cause seasonally opposing changes of naupliar mortality in a continuously reproducing copepod (Seebens et al. 2007). Diapausing species, on the other hand, experienced either changes in spring or summer conditions and the long-term consequences of oligotrophication are therefore hypothesized to differ among species conducting a diapause in spring, in summer, or performing no diapause at all. Hence, this study focused on the response of copepods to oligotrophication depending (A) on the seasonality of the species, i.e., timing of reproduction and diapause, (B) their stage structure, and (C) the seasonality of environmental parameters, which potentially affected copepod population dynamics.

Methods

Study site and community
Samples were taken from Lake Constance, a large (472 km\(^2\)), deep (\(z_{\text{max}} = 254\) m), and warm-monomictic lake located bordering Germany, Switzerland and Austria. Lake Constance experienced anthropogenic changes in nutrient loadings during the last decades resulting in a period of eutrophication until the late 70ies and a period of oligotrophication until recent days (Fig. 1). The changes in nutrient loadings strongly affected species composition and abundance of phytoplankton, zooplankton, and fish (Bäuerle and Gaedke 1998).

The copepod community of Lake Constance consisted of three cyclopoid copepods (\textit{Mesocyclops leuckarti}, \textit{Cyclops vicinus}, and \textit{Cyclops abyssorum}) and the calanoid copepod \textit{Eudiaptomus gracilis}. The species differ in their life cycle strategies, i.e., presence and timing of a seasonal diapause and timing of reproduction, resulting in seasonal changes in copepod community structure [supporting information (SI) Fig. 4]. \textit{C. vicinus} diapauses during summer/autumn and reproduces in April/May, while \textit{M. leuckarti} stays in dormancy during winter and reproduces mainly from June to October. In contrast, \textit{E. gracilis} and \textit{C. abyssorum} do not produce any resting eggs or perform any diapause in Lake Constance and reproduce throughout the year (Einsle 1964a; Einsle 1993).
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Sampling
Total phosphorous concentration (TP) during the time of winter mixing (February, March) was used as a proxy for the trophic status of the lake for each year (Fig. 1). Water temperature was measured monthly at consecutive depths (0 m, 5 m, 10 m, 15 m, 20 m, 30 m, 50 m, 100 m, 200 m, 250 m). Since the mean depth of occurrence of most developmental stages of copepods was between 0 and 40 m (Einsle unpubl. data), we used the mean water temperature of this depth interval to account for the interannual variability of climate.

Zooplankton was sampled twice a month at the deepest part of the lake from 1970 to 1995. Sampling and further processing of samples is described in more detail in Seebens et al. (2007). Unfortunately, copepod nauplii were not distinguished to species level. We estimated the seasonality in nauplii species composition using data clutch sizes and abundances of ovigerous females [supporting information (SII) Fig. 5 and Text]. This analysis suggests that during spring (April/May) nauplii should be composed by *C. vicinus* (67 %), *E. gracilis* (21 %), and some *C. abyssorum*, whereas the summer nauplii (July – September) should mainly belong to *E. gracilis* (43 %), *C. abyssorum* (40 %), and to lesser extent to *M. leuckarti* (18 %).

Statistical analysis
Prior to all statistical analysis abundances were log-transformed. To highlight the seasonal changes of naupliar abundance Seasonal Trend Decomposition based on Loess (STL) (Cleveland et al. 1990) was performed. STL uses locally weighted robust regression (LOESS) to decompose a time series into a trend, seasonal, and residual component. In applying STL we strictly followed the recommendations and diagnostic graphical methods given by Cleveland et al. (1990). The method and its application is described in more detail in Seebens et al. (2007) including the choice of the relevant smoothing parameters, which were the same as in this study.

Log-transformed abundances were related to TP as a measure of lake trophy using Pearson correlations for each 2-week interval separately to account for seasonal changes in the copepod - TP relationships. Seasonal time series of Pearson’s r for individuals copepod species and developmental stages were checked for deviations from white noise applying Bartlett's Kolmogorov-Smirnov statistic (Bartlett 1978).

Population dynamics were potentially affected by a variety of environmental parameters, which could differ among season and should be most influential in
offspring. We therefore tested for significant effects of environmental parameters on abundances of nauplii and CI by using univariate (multiple regression analysis) and multivariate (multivariate analysis of variance, MANOVA) linear models, respectively. The linear models were applied on mean values of parameters for spring (April – May) and summer (June – September) separately to account for seasonal differences of the underlying mechanisms. The time windows were chosen according to the results of the correlation analysis and comprised the period of highest (spring) and lowest Pearson’s $r$ (summer), respectively (see Results). The assemblage of active copepods differed between spring ($C. \text{vicinus}$, $C. \text{abyssorum}$, and $E. \text{gracilis}$) and summer ($M. \text{leuckarti}$, $C. \text{abyssorum}$, and $E. \text{gracilis}$) and hence the set of species used as response variable in the MANOVA differed accordingly. Predictors in the linear models were abundance of total eggs, predatory cladocerans (summer), $M. \text{leuckarti}$ (spring), biomass of algae, water temperature, and year-class strength (YCS) of the dominating planktivorous fish species, $C. \text{oregonus lavaretus}$. Both predatory cladocerans $\text{Bythotrephes longimanus}$ and $\text{Leptodora kindtii}$ were active only during summer (June to October) and were therefore not considered in spring models. $M. \text{leuckarti}$ re-emerges from diapause in April/May and its predatory stages (CI to adults) might potentially affect offspring of other copepods during that time. We tested any possible combination of predictors ($2^5 - 1 = 31$) for spring and summer, nauplii and CI separately and computed the corrected Akaike information criterion (AICc). AICc is the appropriate information criterion when sample size is small compared the number of estimated parameters (Burnham and Anderson 1998). The 10 models with the lowest AICc, all single parameter models, and the full model including all parameters are shown [supporting information (SI) Tab. 2]. Statistical analysis was performed with SAS (SAS Institute Inc. 2004) and R (R Development Core Team 2007).

**Results**

Annual means of copepod abundance (all species and stages pooled in one category) did not show any long-term trend during the study period (Fig. 1) and were not related to TP ($r = -0.10, P = 0.67$). However, the copepod community structure changed as percentages of $C. \text{vicinus}$ (sum of CI to adults) declined, $M. \text{leuckarti}$ increased, and $E. \text{gracilis}$ and $C. \text{abyssorum}$ remained rather stable (Fig. 1).
Total abundance of nauplii remained rather stable throughout the study period as indicated by the trend component of the STL despite of considerable intraannual fluctuations (Fig. 2). However, the seasonal component of the STL clearly showed a seasonal opposing pattern with a decrease of abundance in spring and an increase during summer. The abundances started changing mainly in the early 1980ies, i.e., with the onset of oligotrophication.

This strong seasonal pattern was confirmed by correlation analysis as abundance of nauplii was negatively related to TP during summer, i.e., abundances increased with declining TP (Fig. 3). During spring naupliar abundance was positively but weakly related to TP.

This seasonal pattern of opposing relationships in spring and summer was even more pronounced within copepodid stages (Fig. 3). The strength of this relationship, i.e., Pearson’s $r$, differed among species and stages but the pattern was similar in all cases. The effect was less pronounced in the adult stage of all species and in the copepodid stages of *C. abyssorum*. In contrast to the other species, *M. leuckarti* was negatively related to TP during winter in C IV and C V. The period of strong results shifted in time with ongoing ontogenetic development, i.e., low Pearson’s $r$ were first found in nauplii/C I (June to September) and delayed in advanced stages (July/August to October). Clearly, the large number of correlations summarised in Fig. 3 enhances the potential for obtaining statistical significance by chance. Hence, confidence in the ecological significance is mainly given by the seasonal structure of correlations coefficients within and between species.

Therefore, we tested whether the seasonal pattern of Pearson’s $r$ significantly deviated from white noise. This was clearly the case in nauplii, and copepodid stages of *E. gracilis*, *C. abyssorum*, and *M. leuckarti* (Tab. 1). Most copepodid stages and adults of *C. vicinus* were present in the pelagial only during a short period of the year (few
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Months) and thus the number of Pearson’s $r$ used for white noise test was low ($n < 7$ in C I to C III), which strongly reduced the potential to detect a significant pattern. Only C IV of *C. vicinus* is found for a prolonged time period and indeed Pearson’s $r$ significantly deviated from white noise in this stage (Tab. 1).

**Fig. 2** STL decomposition of the time series of naupliar abundance into (A) trend component (thick line), (B) seasonal component, and (C) residuals. In (A) the original time series of nauplii is also shown (thin line). Circles highlight the long-term dynamics during the second halves of May while squares indicate the long-term dynamics in the second halves of August.

I showed positive but low covariation with TP (nauplii: $r = 0.13$, $P > 0.1$; C I (MANOVA): $P > 0.1$) while average summer (July - September) abundances were negatively related to TP (nauplii: $r = -0.52$, $P < 0.05$; C I (MANOVA): $P < 0.005$). To further elaborate potential underlying causes of the TP – abundance relationship we examined in various statistical models the relationships between copepod offspring abundances and temperature, algal biovolumes, year-class strength of whitefish and abundance of invertebrate predators. For the spring period, we considered the average abundance of predatory stages (C IV, C V, and adults) of *M. leuckarti*, for the summer period the average abundance of the predatory cladocerans, *Leptodora kindtii* and *Bythotrephes longimanus*. In addition, we included the estimated average egg abundance into the models. The most important predictor for offspring abundances in both time periods was egg abundance [supporting information (SI) Tab. 2]. As egg abundance was estimated from the abundance of ovigerous females and species specific clutch sizes, egg abundance in the statistical models accounts for potential bottom-up influences on offspring abundance but also for the long-term trends and interannual variability of copepod abundances. In addition to egg abundance, abundance of *M. leuckarti* predatory stages was the second most important predictor of offspring abundance during spring. The models including eggs and *M. leuckarti* abundance were superior to models including other variables or more complex model (e.g., including temperature, STL and Pearson’s $r$ suggest distinct differences between spring and summer in the underlying mechanisms driving copepod dynamics. Average spring (April - May) abundances of nauplii and C
algal biovolumes or year-class-strength of fish). In contrast, during summer no superior model emerged due to the high covariability between factors possibly controlling offspring abundances. However, the abundance of predatory cladocerans was significantly related to offspring abundances and consistently included into the best models according to AICc.

**Discussion**

Our study revealed a number of important insights into the regulation of copepod communities with implications far beyond the response of zooplankton to changes in lake trophy. Nauplii and early copepodids responses to changes in lake trophy were highly season but hardly species specific. Furthermore, the response of copepodids to environmental change was already evident in the dynamics of the nauplii, supporting evidence that this stage - highly vulnerable to starvation (Santer and Lampert 1995) and predation (Eiane et al. 2002) - can be considered as a bottleneck in copepod population dynamics (Santer and Lampert 1995). High sensitivity of offspring is a widespread phenomenon (Lindström 1999) but its consequences for population response to environmental change has been up-to-now mainly analysed in vertebrates (Post et al. 1997; Forchhammer et al. 2001; Coulson et al. 2001). For instance, climate driven reductions in fitness of sheep offspring affected survival and fecundity of adults in the same cohort (Forchhammer et al. 2001). Likewise, survival of offspring driven by
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Tab. 1 Test for white noise (Bartlett’s Kolmogorov-Smirnov statistic) of the seasonal development of Pearson’s $r$ (Fig. 3) for sum of all nauplii, copepodid stages (C I – C V), and adults. Significant results indicate a seasonal pattern of Pearson’s $r$ in Fig. 5 different from white noise. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$, **** $P < 0.001$.

<table>
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<tr>
<th>Stage</th>
<th>C. vicinus</th>
<th>E. gracilis</th>
<th>M. leuckarti</th>
<th>C. abyssorum</th>
<th>Nauplii</th>
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<td>0.57 ***</td>
<td>0.50 *</td>
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<td>-</td>
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<tr>
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<td>0.44 *</td>
<td>0.58 ***</td>
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<td>-</td>
</tr>
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<td>0.53 ***</td>
<td>0.44 *</td>
<td>0.57 ***</td>
<td>-</td>
</tr>
<tr>
<td>C IV</td>
<td>0.62 ****</td>
<td>0.59 ***</td>
<td>0.65 ****</td>
<td>0.60 ****</td>
<td>-</td>
</tr>
<tr>
<td>C V</td>
<td>0.18</td>
<td>0.46 *</td>
<td>0.63 ****</td>
<td>0.71 ****</td>
<td>-</td>
</tr>
<tr>
<td>Adults</td>
<td>0.44 *</td>
<td>0.72 ****</td>
<td>0.28</td>
<td>0.22</td>
<td>-</td>
</tr>
</tbody>
</table>

oligotrophication affected performance of the whole cohort in copepods.

Statistical analysis suggests that declining nauplii and copepodid abundances in spring were the result of increased intra-guild predation by C IV, C V, and adults of *M. leuckarti*. Models including *M. leuckarti* abundances clearly outperformed models with e.g. algal biovolume in explaining spring abundance. Especially during the spring bloom, food abundance and quality is unlikely to be limiting. Furthermore, clutch sizes of adult copepods did not show any response to oligotrophication [supporting information (SI) Text], suggesting that bottom-up control is unlikely during this part of the year. In contrast, especially cyclopoid copepods are known to feed efficiently on copepod nauplii (Fryer 1957; Jamieson 1980; Kawabata 1991) including their own ones (Van den Bosch and Santer 1993). Each cyclopoid copepod species may act as a predator and a prey in these intra-guild interactions. The actual role is thus largely determined by the timing of nauplii occurrence relative to the occurrence of predatory stages, i.e., C IV, C V, and adults. The co-occurrence of spring nauplii of *E. gracilis, C. vicinus* and *C. abyssorum* with increasing abundances of predatory stages of *M. leuckarti* hence suggests intra-guild top-down control to result into the spring population declines with oligotrophication.

This in turn suggests that the opposing copepod responses to oligotrophication during summer and spring actually were linked via the population dynamics and the life cycle of *M. leuckarti* and originated in increased abundances of copepods during summer/autumn. Unfortunately, no clearly superior model emerged for nauplii and copepod abundances during summer probably due to the high covariation of potential drivers. However, the summer abundance increase with oligotrophication is most likely a consequence of reduced nauplii mortality, which is difficult to reconcile with
decreasing algal abundances. Also, water temperature variability has been shown to affect the phenology of copepods but not overall abundances (Seebens et al. 2007) and hence is not expected to influence abundance means covering periods of two to three months. In contrast, the decline of predatory cladocerans, i.e., *B. longimanus* and *L. kindtii*, with oligotrophication may release nauplii from predation pressure. These cladocerans are known to prey on nauplii and copepodids (Dumitru et al. 2001; Pichlova and Vijverberg 2001) and especially *B. longimanus* can have striking influences on zooplankton community structure (Vanderploeg et al. 1993). This is supported by the selection of predatory cladoceran abundance into the best models based on AICc.

All copepod species present during summer benefited from the widening of the naupliar bottleneck. However, for continuously reproducing *E. gracilis* and *C. abyssorum* this summer decrease of naupliar mortality rates had only rather short-term consequences for population dynamics as the offspring of the summer cohort faced a subsequent bottleneck during the winter. In contrast, the low summer mortality resulted in an increased abundance of *M. leuckarti*, diapausing during winter and subsequently emerging from diapause in the next spring. Species with complex life cycles have been suggested to couple the dynamics of different ecosystems via individuals escaping unfavourable conditions by migration (Schreiber and Rudolf 2008). In our study, the complex life cycle of *M. leuckarti* seemed to couple the community dynamics of copepods of different seasons via individuals escaping unfavourable winter conditions by diapause. Although a complex one, this explanation for the opposing responses of copepods in spring and summer to oligotrophication seems to be more parsimonious than invoking two independent explanations for spring versus summer dynamics.

The change in copepod community structure in Lake Constance during 2 decades of changing nutrient supply highlights the importance of life cycle strategies and stage-specific interactions for the understanding of community dynamics. The response of different species to environmental change depended on the seasonal presence of vulnerable offspring, i.e., nauplii, which in turn is a function of species-specific evolved diapause strategies, i.e., of the ‘ghost of life cycle differentiation past’. Species with nauplii present during spring (all taxa with the exception of *M. leuckarti*) suffered from worsened environmental conditions during this time period, whereas species with nauplii present in summer (all taxa with the exception of *C. vicinus*) benefited from enhanced environmental conditions during summer. These seasonal occurrence patterns resulted into rather stable long-term dynamics of the species reproducing.
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during spring and summer (*E. gracilis* and *C. abyssorum*) and declining (increasing) abundances of species reproducing only in spring (summer), i.e., *C. vicinus* (*M. leuckarti*).

Previous research on community dynamics of copepods but also on other communities strongly emphasized the role of competitive interactions and species-specific differences in acquiring resources in determining community structure. Many detailed laboratory studies have been performed to study differences in resource use and growth between copepod species (Muck and Lampert 1984; Adrian and Frost 1993; Santer and Lampert 1995; Hansen and Santer 1995). These species-specific performances have been suggested to result into differences in copepod community structure between lakes (Maier 1996) and time periods (Anneville et al. 2007). In contrast, our study shows that during a 23 year study period encompassing roughly 3 fold variability in total phosphorus concentrations, copepod differences in life cycle strategy and not in resource use determined changes in community structure.

Our study suggests that the importance of species life cycle strategies for community dynamics has been underestimated so far. Clearly, the role of life cycle differentiation for community dynamics is much more difficult to study experimentally than differences in resource use. Furthermore, its detection in the field will require extensive long-term data. Not surprisingly, the only example for the importance of life cycle strategies for community structure we are aware of stems from a well studied animal taxon: birds. Birds as well as copepod species, which evade harsh environmental conditions either spatially by migration (birds) or temporally by diapause (copepods), might be less able to respond adequately to improving environmental conditions at the breeding habitat as species not migrating or diapausing. Consequently, recent winter warming, i.e., improved environmental conditions during winter, resulted in an increased proportion of non-migratory bird species at the expense of migrating species (Schaefer et al. 2008).

Migratory bird populations might respond to the new environmental conditions by rapid microevolutionary change (Berthold et al. 1990). Likewise, behaviour associated with diapause has been shown to respond rapidly to changing selection pressures. For example, autumn warming resulted in the evolution of later diapause entry in the mosquito, *Wyeomyia smithii* (Bradshaw and Holzapfel 2001). It has been also suggested that enhanced food availability with lake eutrophication resulted in the evolution of reduced reproductive allocation into diapausing eggs within the cladoceran *Daphnia hyalina* (Jankowski and Straile 2003). However, selection pressure on the
Lake Constance copepod community were up to now not strong enough to result into changes in e.g. diapause timing or incidence detectable with field data.

To conclude, this study highlighted that oligotrophication affected all copepod species of Lake Constance in the same way through offspring mortality, whereas differences of food thresholds or predator vulnerability seemed to be less important. The responses to oligotrophication strongly differed among spring and summer probably as a result of season specific changes in invertebrate predation pressure. Consequently, the changes of the community structure of copepods largely depended on the seasonal occurrence of their offspring, i.e., on the ‘ghost of life cycle differentiation past’. These insights in mechanisms shaping community structures under environmental change will be relevant for a broad variety of communities, including species differing in seasonal avoidance strategies such as migration or diapause. Hence, this study further underscores the need of appropriate long-term data with sufficient high ontogenetic and temporal resolution.

**Acknowledgements**

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**Supporting material (SI)**

**SI Text**
Clutch size sampling methodology
Clutch sizes were sampled in 1976 - 1981, 1988 - 1990, and 1994 at roughly monthly time intervals. The intensity of clutch size sampling varied among years and species (*E. gracilis*: clutch sizes available for 10 years on average of 25 sampling times per year, *C. vicinus*: 7 years and 9 y⁻¹, *C. abyssorum*: 9 years and 20 y⁻¹, *M. leuckarti*: 6 years and 14 y⁻¹). Although former studies highlighted the relationship between copepod’s clutch size and lake trophy (Einsle 1983), annual averages of clutch sizes in
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this study were not related to TP (E. gracilis: \( r = -0.54, df = 9, P = 0.11 \), C. vicinus: \( r = 0.37, df = 6, P = 0.42 \), C. abyssorum: \( r = 0.27, df = 8, P = 0.48 \), M. leuckarti: \( r = -0.39, df = 5, P = 0.44 \)). We therefore calculated a mean seasonality of clutch sizes for each species and assumed it to be constant over time. The clutch sizes were then multiplied with the number of egg-bearing females to obtain the total abundance of eggs for each date and species.

Diapause of copepod species

At least a part of the population of M. leuckarti remained pelagic during its diapause but also showed typical characteristics of a diapause, i.e., accumulation of globuli, empty guts (Einsle 1968) and is assumed to enter a so-called ‘active diapause’ sensu Elgmork (1980). Water temperature is at least one crucial key in determining the termination and initiation of diapause in M. leuckarti (Smyly 1962). C. vicinus migrated to the sediments to diapause (Einsle 1964a). While photoperiod was assumed to primarily trigger the start of dormancy in C. vicinus (Einsle 1964b; George 1973), the mechanisms leading to the termination of diapause in C. vicinus remained yet unclear.
SI Fig. 4 Mean seasonality of absolute and relative abundances of copepodid stage (C I to C V) and adults for each copepod species. Seasonality of diapausing species, *Cyclops vicinus* and *Mesocyclops leuckarti*, is indicated with lines in the upper parts of the graphs and highlighted the period of diapause (broken line), presence in the pelagial without reproduction (solid line), and presence in the pelagial with reproduction (thick line). ‘Diapause’ marks the timing and the stage of diapause.
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SI Fig. 5 Mean seasonality of absolute and relative abundance of total amount of eggs for each copepod species. Total amount of eggs was calculated as mean clutch size * abundance of egg-bearing females.
SI Tab. 2 Summary of linear models performed to test for an effect of year, total phosphorus concentration (TP), abundance of eggs (sum of all copepods), *Meso*yclops leuckarti* (Meso), predatory cladocerans (PredClad), year-class strength of whitefish (YCS), and biovolume of algae (Algae) on abundances of nauplii (sum of all copepods) and CI (species-specific) in spring (April - May) and summer (July - September). Effects were analysed using univariate linear models for nauplii (multiple regression) and multivariate linear models for CI (MANOVA). Best fitting models (lowest AICc) were highlighted. Significance levels: * P < 0.05, ** P < 0.01, *** P < 0.005, **** P < 0.001.

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First evidence for a zooplankton metacommunity in a lake and its response to environmental change

HANNO SEEbens, ULRICH EINsLE, AND DIETMAR STRAILE
Manuscript in preparation

Abstract

Lakes are commonly treated as homogenous water bodies characterized by high dispersal rates, disabling zooplankton species to respond to local environmental conditions. In analysing a long-term (1972 – 1985) data set of crustacean zooplankton abundances at five sites in a large lake, we highlight that, in contrast to common views, spatial heterogeneity could be persistent for years, despite presumably high dispersal rates. Horizontal variation in zooplankton community structure, species abundances, life history traits, and life cycle strategies were used as indirect measurements to gain a mechanistic understanding of the observed pattern. These measurements suggest that spatial heterogeneity of zooplankton resulted from spatially varying strength of bottom-up (primary productivity) and top-down (vertebrate and invertebrate predation) processes, whereas the relative importance of these factors in shaping local community structure seemed to vary with season. Spatial heterogeneity of zooplankton seemed to reflect primarily local environmental conditions, providing first evidence for a zooplankton metacommunity structure in a lake. Local community structure changed simultaneously at all sites during the study period, suggesting that mechanisms driving the long-term population dynamics did not differ spatially. Consequently, species-
specific responses to oligotrophication observed at one sampling site over an extended sampling period (1970 – 1995) seem to be representative for the lake. Long-term changes in species responses corresponded well to spatial differences within the lake, suggesting that the primary driver in time as well in space was primary productivity. Differences in zooplankton responses between the temporal and spatial dimension seemed to result from inconsistent variation of top-down control in both dimensions. This study provides novel insights in the spatio-temporal dynamics of lake zooplankton communities and highlights that even weak environmental gradients across small geographical scales could have sustaining effects on local community structure.

Introduction

In ecological research much attention has focused on the processes structuring local communities such as interspecific interactions (Tilman 1982), environmental heterogeneity (Chesson 1986), and stochastic processes (Lande et al. 2006). Spatial dynamics, i.e., immigration or emigration, can, however, influence all of these processes when local communities are interconnected (Holyoak et al. 2005). The degree of exchange among communities determines the importance of spatial dynamics over local environmental conditions in structuring local communities and ranges from fully isolated (no effects due to spatial dynamics) to completely mixed communities (no effects due to local environmental conditions). Communities in between these extremes are structured by both local and spatial processes and follow the dynamics of metacommunities (Holyoak et al. 2005). Metacommunities are defined as a set of local communities that are linked by dispersal of multiple interacting species (Leibold et al. 2004). The concept of metacommunities is mostly theoretical (Leibold et al. 2004) and empirical evidences were mainly drawn from systems near the extreme of fully isolated communities characterized by patches with distinct boundaries and low dispersal rates of organisms between patches, e.g., pond systems (Shurin 2000; Howeth and Leibold 2008), islands (Pajunen and Pajunen 2003), water-filled tree holes (Ellis et al. 2006), or patches located over large geographical scales (Meynard and Quinn 2008). In systems close to the extreme of fully mixed communities, e.g., grasslands, oceans, or lakes, dispersal rates among sites are high and local communities are not distinctly separated among each other (Leibold et al. 2004). High dispersal rates in these systems might constrain optimization of communities to local environmental conditions (Amarasekare and Nisbet 2001; Mouquet and Loureau 2002).
Hence, in systems with high dispersal rates and indistinct boundaries among patches, metacommunities might either not exist (no local effects) or not yet described (but see Roberts 1997; White 2007).

Zooplankton provides some classical examples of metacommunities in e.g. lakes (Beisner et al. 2006), separated (Shurin 2000), and interconnected ponds (Cottenie et al. 2003). Even on small geographical scales, local environmental conditions can persistently affect zooplankton community structure, when dispersal among patches was low enough (Cottenie et al. 2003). Also within lakes, especially within large ones, strong and persistent environmental gradients or heterogeneities can exist (Patalas and Salki 1992; Kalikhman et al. 1992; Pinel-Alloul et al. 1999; Romare et al. 2005), but no study up to now was able do document persistent differences in local community structure. In zooplankton, this has been suggested to be due to the high dispersal rates of zooplankton, disrupting species responses to local environmental conditions (Leibold and Norberg 2004). However, most studies of spatial zooplankton dynamics in lakes investigated short periods (mostly a few days), providing only instantaneous snapshots of seasonal plankton dynamics. The short period of investigation strongly reduces the potential to distinguish whether the observed pattern of spatial heterogeneity were of transient nature, e.g., due to wind events, or persistent due to local differences in environmental conditions. Hence, it is not yet clear whether within-lake zooplankton metacommunities are not existent due to inherent high dispersal rates or not yet detected in lakes.

Here, we show for the first time that spatial heterogeneity in lake zooplankton can persist over long time periods (14 years), despite presumably high exchange rates among sites. Local communities are structured by dispersal as well as local environmental conditions, providing first evidence for the existence of a zooplankton metacommunity within a large lake. We analysed a long-term data set of crustacean zooplankton with a high temporal resolution (samples taken twice a month). Sampling was conducted in parallel at five stations along a transect (> 50 km) through a large lake. As far as we know, this combination of a long sampling period with a high temporal and spatial resolution is unique in both freshwater and marine zooplankton time series. We were therefore able to investigate accurately the spatial variation of seasonal zooplankton dynamics and verify interannual variations in these dynamics by comparing the pattern in 14 study years. This study aimed at investigating 1) spatial heterogeneity of zooplankton in large lakes on species and community level, 2) its
seasonal development, and 3) its variability and persistence over long time periods (14 years).

Methods

Study site
The study was conducted in Upper Lake Constance, a large (472 km$^2$), and warm-monomictic lake at the border of Germany, Switzerland, and Austria. Upper Lake Constance may be divided in three morphometrically different parts without any physical barriers (Fig. 1): the large and deep main basin ($z_{\text{max}} = 254$ m, sampling sites: Hagnau, Fischbach, and Langenargen), the fjord-like Überlinger See ($z_{\text{max}} = 140$ m), and the shallow Bay of Bregenz (hereafter BB, $z_{\text{max}} = 60$ m). The five sampling sites were distributed along a transect through the lake (Fig. 1). Lake Constance experienced anthropogenic changes in nutrient loadings during the last decades (Fig. 1, inlay) affecting a broad variety of species and ecosystem functioning (Bäuerle and Gaedke 1998). Recently, climate variability was found to influence the food web of the lake in manifold ways (e.g., Straile 2005; Straile et al. 2007).

Field sampling
Crustacean zooplankton was sampled at all stations twice a month from 1972 to 1985. At Fischbach, the sampling program covered the years from 1970 to 1995. Integrated net hauls were taken with a Nansen closing net (mesh size 105 µm) from a depth of 0 to 100 m (BB, 0 - 60 m). A more detailed description of the sampling methodology is given in Seebens et al. (2007). The zooplankton community of Lake Constance mainly consists of two predatory cladocerans (Bythotrephes longimanus, Leptodora kindtii), two herbivorous cladocerans (Bosmina spec., Daphnia spec.), three cyclopoid copepods (Cyclops vicinus, Cyclops abyssorum, Mesocyclops leuckarti), and one calanoid copepod (Eudiaptomus gracilis). Copepods have a complex life cycle with six

![Fig. 1 Location of the five sampling sites in Lake Constance and change of trophic status (TP) measured as total phosphorus concentration during winter mixing (February, March). The dotted lines border the period from 1972 to 1985.](image-url)
naupliar, five copepodid, and an adult stage, but only adults and copepodid stages were considered in this study. Copepod clutch sizes were recorded rather irregularly. Hence, we only used clutch sizes of *E. gracilis*, *C. vicinus*, and *C. abyssorum* at Fischbach and BB during 1976 – 1980 for which data were more homogenous.

Water temperatures were measured monthly at different depths (0 m, 5 m, 10 m, 15 m, 20 m, 30 m, 50 m, 100 m, 200 m, 250 m) during the whole study period at Fischbach and since 1979 additionally at BB and Langenargen. Mean water temperature of the upper 20 m of the water column was used for statistical analysis. The trophic status of the lake was represented by the maximum total phosphorous concentration (TP) during winter (February, March) mixing. Sampling of algae biovolume and year-class strength (YCS) of the dominating planktivorous fish species, *Coregonus lavaretus*, is described in detail in Kümmerlin (1998) and Straile *et al.* (2007), respectively. TP and biovolume of algae were only measured at the central station (Fischbach).

Statistical analysis
Prior to all analyses abundances were log-transformed. Covariation between abundances and environmental parameters were analysed using Pearson correlation. Analysis of variance (ANOVA) was conducted to investigate differences between sites. Site differences were then compared with Tukey's post-hoc test. Temporal and spatial variations of the zooplankton community were investigated using principal component analysis (PCA). PCA was performed on mean abundances of species in winter (January – March), spring (April, May), and summer (July – September) separately to account for seasonal differences. The time windows were chosen according to the classical chronological sequence
IV Community responses in space and time

Tab. 1 Analysis of variance on the influence of year and sampling site on long-term trends of annual abundances showing in Fig. 2. Effects of independent variables (a) and post-hoc test (Tukey) among sites (b) were presented. For each site, mean abundance of species (Mean) and significant differences among site indicated by lower letters (Sig) were given. Sites with the same lower letter did not significantly differ at the level of $\alpha = 0.95$. Interaction term of 'year x site' was not significant in any species. n.s. (non-significant) $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$, **** $P < 0.001$; BB Bay of Bregenz, LA Langenargen, FB Fischbach, HG Hagnau, ÜS Überlinger See.

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</table>

of annual plankton succession (Sommer et al. 1986) in Lake Constance and represent the periods of winter mixing, spring bloom, and summer development, respectively.

PCA was run on abundances obtained at Fischbach (1971 – 1995) and BB (1972 – 1985) to compare variation among sites (spatial component) with long-term variation at Fischbach (temporal component). Since predatory cladocerans were not present during winter and spring, these species were only considered during summer. The first two axes of PCA were used to analyse covariation between community structure and environmental variables (TP, water temperature, algae, and YCS). All analyses were performed using the statistical software packages SAS (SAS Institute Inc. 2004) and R (R Development Core Team 2007).

Results

The main basin of Lake Constance is characterized by its huge water body, leading to a moderate water temperature regime, whereas shallow BB showed a larger seasonal variability with significantly colder temperatures in February (ANOVA, $F = 7.44$, df = 17, $P < 0.005$), and March ($F = 4.33$, df = 18, $P < 0.05$) and higher values in April ($F = 8.46$, df = 18, $P < 0.005$), May ($F = 8.95$, df = 18, $P < 0.005$) and June ($F = 3.67$, df = 18, $P <$
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The differences of mean temperatures were highest between Fischbach and BB and ranged from 1.2 °C in April to 2.0 °C in June.

The long-term trends of zooplankton populations differed among species. Annual mean abundances of three zooplankton species (Daphnia spec., E. gracilis, and C. abyssorum) declined during the study period, whereas M. leuckarti increased and L. kindtii and Bosmina spec. did not show a clear trend (Fig. 2). Spatial differences in annual mean abundances were present in all species except of C. abyssorum (Tab. 1). In most cases, abundances at BB deviated from the near-by Langenargen in four species and from Fischbach in six species.

Abundances at BB differed significantly from the near-by Langenargen in four species and from Fischbach in six species.

The magnitude of observed differences among sites varied strongly with season (Fig. 3). For instance, low annual means of M. leuckarti at BB were mainly due to the species’ reduced abundances during winter and spring at this site. In contrast, high annual means of Bosmina spec., Daphnia spec., and C. vicinus resulted from elevated abundances during the whole year except of the spring peak. Differences between sampling sites were quite large, e.g., mean winter abundances of Daphnia spec. varied up to 50-fold (10^{1.7}) between sites (Fig. 3), and mean abundances of C. vicinus, M. leuckarti, and Bosmina spec. differed up to one order of magnitude between sites.
Mean abundances in winter were highest at BB for all species except *M. leuckarti* (Fig. 3). During spring and summer this pattern changed as mean abundances of *Bosmina spec.*, *Daphnia spec.*, and *C. vicinus* were highest at the Bay, while abundances of *L. kindtii*, *B. longimanus*, *C. abyssorum*, *M. leuckarti*, and *E. gracilis* were reduced. Sex ratio of copepods did not significantly differ between sites (not shown) except *C. abyssorum* in summer (ANOVA Tukey-post hoc test, df = 65, *P* < 0.05) and *E. gracilis* in winter (ANOVA Tukey-post hoc test, df = 65, *P* < 0.05) and spring (ANOVA Tukey-test, df = 8, *P* < 0.05). In all cases, sex ratio was male-biased at BB. In comparison to Fischbach, clutch sizes of *E. gracilis* were significantly enhanced at BB by 28% during winter (February, March; ANOVA Tukey-post hoc test, df = 8, *P* < 0.05) and 12% in summer (July - September; ANOVA Tukey-test, df = 8, *P* < 0.05). Clutch

![Fig. 4](image1.png)

**Fig. 4** Scores of 1st and 2nd axis obtained from PCA performed on log-transformed zooplankton abundances at Fischbach (dots) and BB (circles) in winter (January – March), spring (April, May), and summer (July, August, September). The percentage of variation explained by each axis is given in parentheses.

![Fig. 5](image2.png)

**Fig. 5** Comparison of temporal (ratio of 6 oligotrophic years/6 eutrophic years during 1970 - 1995) and spatial variation (ratio of sampling sites Fischbach/Bay of Bregenz in 1972 - 1985) of mean zooplankton abundances in winter (February, March), spring (April, May), and summer (July, August, September). Dashed line indicates a perfect agreement between temporal and spatial variations. Species occurring in the lower left quadrant showed high abundances in eutrophic years and at BB while the upper right quadrant represents species with high abundances in oligotrophic years and at Fischbach.
To gain a mechanistic understanding of the observed pattern of horizontal zooplankton distribution, we compared spatial abundance variations with interannual variability at Fischbach for which measurements of environmental variables were available. The first two axes of PCA accounted for 75% (winter), 71% (spring), and 61% (summer) of total variability. PCA clearly separated long-term dynamics in community composition between Fischbach and BB in all seasons (Fig. 4). The 1st axis was significantly related to the abundances of all species except *E. gracilis* in spring and summer and *C. abyssorum* in summer. While most species were positively related to the 1st axis, *M. leuckarti* showed an inverse relationship. *E. gracilis*, *C. abyssorum*, and predatory cladocerans were strongly related to the 2nd axis (Tab. 3). The 1st axis showed considerable covariation with TP and study year, whereas the 2nd axis was related to YCS. Water temperature and biovolume of algae did not correlate with any of the two axes.
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Discussion

This study clearly showed that, in contrast to common views, zooplankton in lakes could show distinct pattern of spatial heterogeneity, persisting for years. Horizontal distribution of zooplankton is usually considered to be mostly driven by passive dispersal due to wind-induced water currents (Jones et al. 1995; Pinel-Alloul et al. 1999; George and Winfield 2000; Thackeray et al. 2004). In Lake Constance, dominating west-winds should indeed blow zooplankton into BB at the eastern part of the lake. However, spatial heterogeneity of zooplankton varied between season and species (Fig. 3), which suggests that displacement due to water currents is unlikely the cause for the observed differences. In addition, we found distinct intraspecific differences between sites, e.g., differences in sex ratio, and clutch size. Furthermore, there is evidence that one species, the cyclopoid copepod C. vicinus, differs in life cycle strategy between sites. Only at BB a reproducing summer population is found, whereas at other sites, the species was in diapause during summer. Hence, the spatial distribution of zooplankton abundances and traits seemed to reflect local environmental conditions, providing first evidence for the existence of a zooplankton metacommunity structure in a lake. Unfortunately, analysis of the mechanisms shaping this metacommunity structure is strongly hampered because no data on the spatial distribution of forcing variables were available, e.g., nutrient concentrations, phytoplankton biovolume, and/or fish distribution with a sufficient spatio-temporal resolution. However, independent data suggests that BB differs from other sampling sites both in increased nutrient influx (IGKB 2000) presumably causing higher primary productivity and in higher fish densities (Hartmann 1984; Appenzeller 1998). Most relevant tributaries of Lake Constance discharge at or near BB with the consequence that in recent years more than 40 % of the whole phosphor loadings entered the lake at the Bay (IGKB 2000). Additionally, the lower depth at BB might result into an increased light availability for phytoplankton and hence higher growth rates during winter and early spring. Fish densities of C. lavaretus in 1993 and catch per unit effort of commercial fisheries (1978 – 1982) were largest in the eastern part of the lake (Hartmann 1984; Appenzeller 1998). In addition, the traits of the species differing between sites suggest that the crustacean metacommunity is primarily structured by regional differences in food availability and secondarily by differences in top-down control. Moreover, intra-crustacean interactions further enhanced spatial differences.
The role of bottom-up control for metacommunity structure

Zooplankton community structure varied between sites but also between years (Fig. 4). Strong covariation between year and the 1st axis of PCA and clear separation of sites in all seasons (Tab. 2) indicates that the 1st axis (35% to 52% explained variability) represents variation of zooplankton abundances coinciding in space and time. Species scores of the 1st axis at BB were significantly higher than species scores at Fischbach in all seasons (Tab. 2). The 1st axis of PCA was also positively related to productivity measured as TP at Fischbach (Tab. 2). That is, the separation of sites along the 1st axis of PCA seemed to reflect variation of zooplankton community structure due to productivity and suggests enhanced productivity at BB. Analysis of covariance conducted on 1st axis of PCA as dependent variable revealed significant effects of both site and TP (or year) in all seasons (not shown), indicating that variations of community structure among sites indeed went in line with variations along TP. The amplified separation of both sites in summer (Fig. 4) might reflect the enhanced significance of phosphorus limitation during that season at Fischbach, as the differences in nutrient concentrations might be especially large during summer due to continuous nutrient influx in the Bay (see above).

Comparing spatial and temporal trends of species abundances revealed a high correspondence (Fig. 5) particularly in winter (R² = 0.94) and spring (R² = 0.70): Abundances of *Bosmina spec.*, *Daphnia spec.*, *C. vicinus*, and *C. abyssorum* were higher at BB and in eutrophic years, confirming the assumption of enhanced productivity at BB. Likewise, *M. leuckarti* increased with oligotrophication and was lowest at the most productive site (BB). However, it should be noted that the correspondence between the temporal and spatial dimension of *M. leuckartii* seems to be due to different mechanisms: Its increase with oligotrophication has been suggested to be due to reduced naupliar mortality during summer (Seebens et al., submitted), whereas its lower abundance at BB seems to result from differences in population development between sites during winter and spring (Fig 3). During summer, spatio-temporal covariation was not consistent (R² = 0.11) as e.g. abundances of *B. longimanus*, and *L. kindtii* were higher in eutrophic years but lower at BB (Fig. 5), which reflects the higher complexity of food web interactions during summer (see below). At Fischbach, interannual variability of zooplankton abundances was already shown to be an albeit indirect consequence of declining productivity (Seebens et al. 2007; Seebens et al. submitted). The strong spatio-temporal covariation of species abundances in winter and spring further indicates that spatial differences in productivity seem to be an important driver for spatial differences of zooplankton.
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Herbivorous cladocerans (Bosmina spec. and Daphnia spec.) are known to respond fast to high food availability, which might explain their elevated abundances at BB (Fig. 3). High abundance of herbivorous cladocerans especially during winter was probably due to further facilitation of phytoplankton growth at BB because of lower mixing depth at this site thereby reducing phytoplankton light limitation. As another indication of bottom-up control, clutch sizes of E. gracilis were higher at BB. In addition, the summer diapause of C. vicinus is suggested to be a response to food scarcity (Santer and Lampert 1995) and the summer generation of this species at BB thus indicated higher food supply at this site. Hence, spatial variability in community structure, clutch sizes, and life cycle strategy suggests that primary productivity is an important driver of metacommunity structure.

The role of top-down control for meta-community structure
A secondary effect of higher primary productivity at BB may be a higher fish density, which distribution is influenced by differences in the distribution of zooplankton. This is supported as species, which are reported to be especially vulnerable to fish predation, i.e., predatory cladocerans (Eckmann et al. 2002) and the large copepod C. abyssorum (Santer 1998), had significantly lower abundances at BB. Additionally, sex ratio of C. abyssorum during summer at BB (ANOVA Tukey-test, df = 65, P < 0.05) - but not at the other sites - was significantly skewed towards males, which might result from selective feeding of fish on conspicuous ovigerous females (Svensson 1997). Consequently, abundances of these species were significantly related to the 2nd PCA axis, which explained 23 % - 25 % variability of zooplankton community structure and also clearly separated the two sampling sites. This suggests that food web interactions originating from spatial differences in productivity further enhanced metacommunity differentiation.

Differentiation along the 2nd axis was, however, more complex as indicated by the significant relationship of PCA scores with the abundances of E. gracilis and whitefish YCS. E. gracilis abundance was positively related to the 2nd axis and was lower at BB despite higher clutch sizes at this site. E. gracilis is a rather inconspicuous species and consequently not an important diet of fishes in Lake Constance (Eckmann et al. 2002). Thus, the cause of E. gracilis covariation with the 2nd axis is presently unclear and may result from interactions within the zooplankton community. The significant positive relationship between the 2nd axis and YCS seemingly contradicts the significantly lower 2nd axis scores at BB as compared to Fischbach. However, the diet of YCS fish most likely differs from that of larger ones due to their gape limitation. For example, the large
spina of *B. longimanus* is suggested to efficiently reduce the predation of small fish on *Bythotrephes spec.* (Barnhisel 1991; Straile and Hälßch 2000). Large YCS hence might not affect the abundance of *B. longimanus* but reduce abundances of smaller species, e.g. *Daphnia*. Consequently, the ratio *B. longimanus*/*Daphnia* is significantly related to YCS (ANOVA Tukey-test, df = 65, *P* < 0.05). In contrast, high abundances of larger non-gape-limited fish at BB seem to have resulted in lower abundances of predatory cladocerans (*B. longimanus* and *L. kindtii*) thereby releasing smaller crustaceans from predation pressure (Dumitru et al. 2001; Pichlova and Vijverberg 2001) and contributing to the observed higher abundances of e.g. *Daphnia* at the Bay. Consequently, the abundance ratio *Bythotrephes/Daphnia* was significantly lower at BB as compared to the other stations (ANOVA Tukey-test, df = 65, *P* < 0.05). Hence, predator defenses against YCS and cascading interactions may explain why 2nd axis scores were positively related to YCS, but inversely with adult fish distribution, i.e., lower scores at BB.

Spatial heterogeneity of zooplankton community structure in Lake Constance could be explained by an interplay of spatially varying bottom-up (productivity) and top-down (predation pressure imposed by both vertebrates and invertebrates) processes. Although zooplankton community structure seemed to be strongly influenced by the local environment, the sampling sites clearly are not isolated. Water currents in Lake Constance (Appt et al. 2004) should affect spatial heterogeneity of zooplankton and prevent abrupt transitions in community structure. Consequently, the station Langenargen located between BB and Fischbach is also intermediate regarding its zooplankton abundances (see Figs. 2 and 3), suggesting a supply of individuals from BB. Thus, local communities seemed to be structured by both spatial and local processes, providing first evidence for a zooplankton metacommunity structure in a lake. The lack of studies investigating metacommunities in lakes (or other systems with indistinct boundaries and high dispersal rates) seems to be mainly due to the lack of appropriate data. In these systems, species abundances change gradually and differences in community structure among sites are low, which strongly hampers the potential to distinguish local communities (Leibold and Norberg 2004). Nevertheless our study suggests that also in these systems a metacommunity structure can persist even during periods of environmental change.

The metacommunity in Lake Constance fundamentally differs from that reported in other zooplankton studies in the degree of (1) connectivity among sites and (2) heterogeneity of local patches. In systems with a low connectivity, e.g., different lakes,
dispersal among sites is considered as a limiting factor, potentially preventing species from colonization of new patches (e.g., Shurin 2000). Moreover, local community structures could be highly resistant to the invasion of new species (Shurin 2000; Forrest and Arnott 2006). In contrast, in interconnected ponds, local community structure was persistently affected by dispersal (Cottenie and De Meester 2004; Howeth and Leibold 2008) and dispersal did not act as limiting factor but rather homogenizing factor, reducing variation among local communities (Cottenie et al. 2003). Although we found evidence for the homogenizing effect of dispersal (i.e., intermediate abundances at Langenargen), it was not strong enough to prevent a metacommunity structure within this single water body. Secondly, within-lake environmental heterogeneity is likely smaller than between-lake or pond environmental heterogeneity. Consequently, community structure varied spatially regarding the relative abundance but not the presence of species. Hence, the dynamics of the zooplankton community in Lake Constance did not follow common paradigms of metacommunities, i.e., species sorting or patch dynamic (Leibold et al. 2004), and is probably best categorized as a special case of source-sink metacommunity: The sink (main basin of Lake Constance) should be considered as a quasi sink (sensu Nee 2007) since local communities were able to retain their population – with the exception of the summer population of C. vicinus –, however on a lower level, without the need of immigration from the source (BB).

Zooplankton community structure changed during the study period at all five sampling sites simultaneously (Fig. 2), which is further supported by non-significant interaction terms ‘year x site’ in regression models (Tab. 1), even when distinguishing between seasons (data not shown). This indicates that the mechanisms shaping zooplankton long-term dynamics did not substantially differ between sites. Consequently, it seems to be sufficient to concentrate on one site for the analysis of e.g. oligotrophication on food web dynamics.

Spatial gradients of environmental parameters are often used to analyse potential influences of future environmental changes of this parameter, i.e., to perform a space-for-time substitution (Fukami and Wardle 2005). Here, we were able to test the potential of applying a space-for-time substitution on closely related sites, i.e., within the same food web: Is it possible to predict the response of the zooplankton community to oligotrophication by comparing sites differing in productivity within a lake? The strong spatio-temporal covariation in winter and spring indeed suggests this possibility (Fig. 5). However, in summer a space-for-time substitution would be misleading as e.g.
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summer abundances of predatory cladocerans and spring abundances of *E. gracilis* and *C. abyssorum* were reduced at BB but enhanced in eutrophic years (Fig. 5). This shows that even within one food web ecological processes do not always vary in space in the same way than they do in time (Dunne *et al.* 2004). The choice of closely related sites might increase the predictive power of a space-for-time substitution but does not prevent false predictions. In contrast, most space-for-time substitutions were performed on completely separated habitats with apparent structural differences between food webs, e.g., different lakes (Jeppesen *et al.* 2003), forests (Carreiro and Tripler 2005), grasslands (Dauber and Wolters 2005), soils (Ross *et al.* 2000), in some cases over large geographical scales (e.g., Meerhoff *et al.* 2007). Our study suggests that inferences drawn from those space-for-time substitutions should be made carefully as within site food web interactions might change the effects of environmental gradients on food webs.

In conclusion, this study provides first evidence for a planktonic metacommunity structure within a lake. Even within a small geographical scale in a rather well-mixed system, local environmental conditions - possibly enhanced by food web interactions - can generate spatial differences in community structure. These differences were not due to overall differences in food web structure but resulted from differences in the relative abundance of species exposed to spatial differences in bottom-up (primary productivity) and top-down (fish predation) control. Metacommunities hence should be expected to develop and may also be prevalent in comparatively homogenous and open environments.

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General discussion

During the last decades, the Lake Constance ecosystem experienced strong changes in trophic status and high climate variability and both environmental changes are likely to affect all trophic levels of the food web simultaneously. For instance, oligotrophication in Lake Constance was shown to alter abundance and community composition of algae (Gaedke 1998), ciliates (Gaedke and Wickham 2004), crustacean zooplankton (Straile and Geller 1998a), and fish (Eckmann and Röschr 1998). On the other hand, climate variability was found to influence hydrodynamics, nutrient availability (Straile et al. 2003a), stratification and spring bloom timing (Peeters et al. 2007b), phenology of the key stone species *Daphnia* (Straile 2000), and year-class strength of whitefish (Straile et al. 2007). Any significant covariation between copepod abundances and TP or water temperature might therefore be due to large number of potential mechanisms. It is thus a difficult task to elucidate the mechanistic relationships between copepods and their environment and whether observed changes in abundances were due to top-down or bottom-up regulations.

This thesis clearly shows that the mechanisms affecting copepod population dynamics are complex and vary between season, species, and developmental stages. Seasonal differences can be striking and even result into contrasting responses to oligotrophication in spring and summer (chapter I). In Lake Constance, environmental changes seem to affect population dynamics of copepods mainly via changes in offspring survival as responses to environmental changes were strongest and first observed in nauplii and early copepodid stages (chapter I and III). This seems to be true for all four copepod species analysed in this study (chapter III) probably due to similar ecological niches of nauplii. However, although the mechanisms did not vary among species, the consequence of oligotrophication for the maintenance of a population fundamentally differed between species depending on the seasonal occurrence of their offspring, i.e., on the specific life cycle strategy (chapter III). Consequently, mean annual abundances declined in species reproducing in spring,
increased in summer reproductive species while seasonal opposing trends resulted in rather stable annual means in continuously reproducing species. The responses to declining trophic status could, however, be modified by climate variability as *C. vicinus* had higher reproductive output in warm years, which at least partly compensated its decreasing long-term trend due to oligotrophication (chapter II). Moreover, stage-specific adaptations to environmental factors such as food availability or photoperiod additionally modify responses to oligotrophication and climate variability (chapter II). Zooplankton abundances varied among sampling stations, which at least partly went in line with interannual variability (chapter IV). This correspondence of spatio-temporal dynamics was probably due to concomitant changes of productivity, indicating that mechanisms driving this amount of variation coincided in space and time. Inconsistent spatio-temporal variations of zooplankton abundances might be due to spatially varying fish densities, confounding a potential substitution of spatial and temporal mechanisms as commonly performed in space-for-time substitutions. In conclusion, this thesis provides novel insights in (1) the interaction of environmental changes and the consequences for copepods population dynamics, (2) the interactions of environmental seasonality and species’ seasonal niche, (3) stage-structured interactions, (4) and spatio-temporal variations of zooplankton responses to productivity.

**Interaction of oligotrophication and climate variability**

During the last decades many lakes experienced changes in trophic status and water temperatures (Jeppesen et al. 2005b; Blenckner et al. 2007). However, most studies only investigated the influence of a single environmental change while studies on the interacting effects of oligotrophication and climate variability are scarce in limnological research (but see Straile and Geller 1998b; Massol et al. 2007). It can be challenging to disentangle their influences on population dynamics if both factors changed simultaneously and the influence of one parameter modified the influence of the other parameter. A clear differentiation of the influences of two simultaneously changing parameters might be possible if (1) the parameters affect different aspects of population dynamics, e.g., timing or abundance, or (2) the parameters exhibit a distinct different interannual variability, e.g., a monotonous long-term trend in one parameter and highly variable trend in the second. Both seemed to be true for oligotrophication and climate variability in Lake Constance: TP declined monotonously while spring water temperature showed a high interannual variability (Fig. 1, chapter I). A monotonous trend in species abundance is therefore more likely to be associated with oligotrophication while a trend with high interannual variability seemed to be linked to climate variability. Moreover, oligotrophication mainly affected species abundances,
whereas climate variability influenced the phenology of species (chapter I - III). However, both environmental changes also interacted as reproductive output of *C. vicinus* was higher in warmer years, i.e., temperatures affected abundances in that species, too (chapter II). This effect of warming seemed to modify the declining trend of *C. vicinus* due to oligotrophication. In other lakes, the interactions of both environmental factors may be even more complex making a clear differentiation of their influences difficult. For instance, the strength and duration of mixing events are prone to climate variability (Peeters et al. 2007a) but also affected nutrient availability, i.e., lake productivity, in the epilimnion throughout the subsequent stratified period (Straile et al. 2003a). Weakened or shortened mixing events due to increasing water temperatures should change nutrient availability of plankton, affecting abundances of plankton communities throughout the year. Mixing events and their consequences for food web dynamics thus represent an example of a tight coupling of both environmental changes with the potential to affect whole food web processes. Recently, it could be shown that climate variability and oligotrophication in fact strongly interact in determining the long-term dynamics of the phytoplankton spring bloom (Huber et al. 2008). These interactions are even more important in shallow, polymictic lakes where stratification is not stable throughout the year and irregular mixing events within the warm season strongly affected abundances of organisms (Wilhelm and Adrian 2008).

**Interaction of environmental seasonality and species' seasonal niche**

The strength of environmental forces on population dynamics of species is usually not constant throughout the year and consequently environmental changes did not act in equal manner at every time of the year. For instance, climate variability associated with the North Atlantic Oscillation (NAO) affected water temperatures of Lake Constance in winter and spring more strongly than during summer (Straile et al. 2003a). Even the consequences of changing lake trophy showed a distinct seasonality (chapter I, III, and IV). However, long-term studies analysing the role of seasonality of environmental changes on species’ population dynamics are rare in ecological research, which is mainly due to the lack of appropriate data. Detailed studies were mainly available for mammals, e.g., lynx (Stenseth et al. 1997), red deer (Post et al. 1997), lemmings (Turchin et al. 2000), and sheep (Forchhammer et al. 2001). For the latter population, it could be shown that climate variability is most influential during the time of offspring occurrence in spring and affect fitness components, i.e., survival and fecundity, until adulthood (Forchhammer et al. 2001). Since offspring in many mammals is born during a specific period of the year, the environmental conditions during that time are of crucial importance for the fitness of the whole population (Gaillard et al. 2000), and
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regulators of population dynamics could differ between breeding and non-breeding seasons (Sæther 1997). In Lake Constance copepods, the timing of offspring occurrence primarily depended on their life cycle strategy and mainly coincided with the periods of non-diapause (chapter III). Hence, the regulators of copepod population dynamics differ between diapausing and non-diapausing seasons. As a consequence, the interaction of seasonality of environmental change and life cycle strategy of copepods explained almost exclusively their response to oligotrophication (chapter III). However, in both groups of animals, mammals and copepods, the influences of environmental changes mainly acted through survival/fitness of offspring.

Abundances of copepod species showed similar long-term trends at all sampling sites in Lake Constance, indicating that the mechanisms shaping these long-term trends did not substantially differ among sites (chapter IV). However, a substitution of the temporal gradient of lake productivity with the presumed spatial gradient between sampling sites revealed a more heterogeneous picture. Based on the analysis of long-term trends of copepods, one might expect a clear seasonal separation of differences in abundances among sites, i.e., abundances at the Bay of Bregenz (BB) should be elevated in spring and reduced in summer, which could not be confirmed. *E. gracilis* and *C. abyssorum*, for instance, showed reduced abundances in both seasons (chapter IV). These inconsistencies in space and time might be due to variety of reasons. The most important point might be the inconsistent variation of predatory cladocerans probably due to elevated fish densities at BB. Changing abundances of predatory cladocerans were assumed as the ultimate cause of long-term changes in copepods (chapter III) and inconsistent variation in space and time should result in inconsistent variation of predation pressure on copepods. Additionally, the life cycle strategy of *C. vicinus* differed among sites as a part of the population skipped the summer diapause at BB. *C. vicinus* was already suggested to suppress the population of *M. leuckarti* in Lake Constance (Einsle 1983) and its summer generation probably caused the comparatively low summer response to varying productivity of *M. leuckarti* at BB (Fig. 5, chapter IV). However, on the temporal dimension the increasing summer abundances of *M. leuckarti* were suggested to cause the long-term declining trend of copepod abundances in subsequent spring (chapter III). Consequently, enhanced predation pressure on summer abundances imposed by *C. vicinus* at BB might result in a reduced response of *M. leuckarti* to oligotrophication and finally in reduced responses of other copepod species in subsequent spring at this site. An apparent small change in population dynamics of one species, i.e., summer generation of *C. vicinus*, thus seemed to affect responses of the whole copepod community. Hence, although the
long-term trends of copepods did not substantially differ among sites, the comparison of variation along spatial and temporal gradients of productivity is confounded by concomitant but inconsistent changes of fish densities and life cycle strategies.

**Stage-structured interactions**

Most long-term studies on copepods focused on adults, ignoring potential differences in juvenile responses. However, the effect of environmental change might be stronger in juveniles than in adults as, in Lake Constance, responses to oligotrophication were first observed in youngest developmental stages, i.e., nauplii and early copepodid stages, and delayed in more advanced stages. This indicates that the observed changes in adults were actually a consequence of responses of juveniles (chapter I and III). This coincides with findings of other studies showing that mortality is highest in copepod offspring (Santer and Lampert 1995; Eiane and Ohman 2004). High sensitivity of juveniles is a wide-spread phenomenon in nature and was shown to determine fitness of the whole cohort in many species (Lindström 1999). Consequently, performance of offspring under environmental change determined the response of the whole population. For instance, fitness changes in lambs due to climate variability affected responses of a sheep population (Forchhammer et al. 2001) while recruitment performance in fish determined its response to oligotrophication (Massol et al. 2007). In invertebrates, this mechanism was not yet shown. One problem might be that in studies of large animals individual-based changes in fitness components could be easily tracked through the cohort, whereas in copepods consequences of changes in juvenile fitness are difficult to measure although such cohort effects are likely to happen as well. For instance, Varpe et al. (2007) showed in model study that egg fitness of copepods strongly varies throughout the year due to environmental seasonality. Hence, harsh environmental conditions could result in low egg fitness, probably affecting fitness and reproductive output of the whole cohort. However, these effects remain to be shown empirically.

The sheep population addressed above also served as model organisms investigating the role of demography in the response to environmental change. Coulson et al. (2001) highlighted that the contribution of sensitive stages, i.e., young and old individuals, affected the population response to winter weather conditions. Harsh conditions were more influential when the amount of sensitive individuals was high. A similar mechanism was also found in the response of copepods to oligotrophication although only in the extreme case of presence/absence of sensitive stages, i.e., nauplii. The influences of oligotrophication mainly acted indirectly through naupliar survival (chapter
III). Hence, populations are most vulnerable when offspring is present. The consequences were best seen during a short period in spring when all species were reproductive except *M. leuckarti*, *E. gracilis*, *C. abyssorum*, and *C. vicinus*, decreased in spring with declining TP while *M. leuckarti* did not (chapter III). While Coulson et al. (2001) highlighted the role of sensitive stages for the response to environmental conditions within a single population, this thesis showed that similar patterns seemed to be important for community responses as well. However, research on this topic is just starting and copepod dynamics need to be analysed in more detail.

Timing and performance of offspring plays a crucial role in the response to environmental forcing in copepods. Their responses can, however, be modified by stage-specific adaptations to other environmental parameters. This was shown for *C. vicinus*, which adapted its timing of reproduction to the onset of phytoplankton growth, whereas ontogenetic development of offspring seemed to be influenced by photoperiod (chapter II). The copepod thus adjusted its phenology to environmental triggers others than temperature, which at least partly compensated or superimposed the effect of climate variability. This adaptation enabled the copepod to respond sufficiently to interannual variability of phytoplankton growth, ensuring a match of high food availability and offspring occurrence. Stage-specific adaptations to environmental conditions and their role in modifying responses to environmental changes are not yet investigated in copepods. However, it is known that diapausing copepods often trigger the onset of their dormancy to photoperiod (Marcus 1982; Hairston and Kearns 1995). Hence, photoperiod is likely to modify potential shifts in phenology due to rising temperatures in many copepods and is assumed to be of primary importance in order to adapt to future climate warming in other species as well (Bradshaw and Holzapfel 2008).

**Spatio-temporal dynamics**

Spatio-temporal dynamics of zooplankton in a lake were usually analysed over short time periods of a few days and most studies stressed the importance of transient environmental conditions such as water currents, shaping the horizontal distribution of zooplankton. For the first time, this thesis highlights that the pattern of spatial heterogeneity could be persistent for years (chapter IV). A large amount of this spatial variation in zooplankton abundances (32 % - 52 %) coincided with interannual variability most likely due to similar changes of productivity in both dimensions. This high correspondence resulted in similar trends of mean abundances along the spatial and temporal dimension, e.g., both, in eutrophic years and at BB, abundances were
elevated in *C. vicinus* and reduced in *M. leuckarti*. However, the comparison of spatial and temporal dynamics of copepods was confounded by inconsistent variations of predator abundances, i.e., vertebrates (fish) and invertebrates (*B. longimanus* and *L. kindtii*), and the life cycle strategy of *C. vicinus*. Both resulted in slightly different outcome of interspecific interactions under changing productivity.

In accordance to the findings shown in chapter III, the responses of copepods to spatially varying productivity seemed to be influenced by the species life cycle strategies as well. For instance, a part of the population of *C. vicinus* skipped summer diapause at BB and was active throughout the year (chapter IV). *C. vicinus* is known to affect population dynamics of a broad variety of other planktonic organisms (Brandl and Fernando 1981; Plassmann et al. 1997) and its occurrence in summer may therefore explain the reduced abundances of *E. gracilis*, *C. abyssorum*, and *M. leuckarti* at BB. This might also be due to enhanced fish predation at BB, however, fish predation should also reduce abundances of *C. vicinus* as this copepod is larger than e.g. *M. leuckarti*. As another example for the role of life cycle strategy, abundances of *M. leuckarti* were reduced during its winter diapause at BB. Its state of inactivity seemed to prevent this copepod to respond accordingly to environmental conditions, i.e., the copepod was not able to exploit the presumably enhanced food availability at BB during winter nor it was able to escape enhanced predation imposed by other cyclopoids, e.g., *C. vicinus* (chapter IV). This does not have to be contradictory to former findings of this thesis, i.e., seasonal occurrence of offspring is of primary importance, but highlights another aspect of the role of life cycle strategy in the response of copepods to environmental change.

Spatial variations of species abundance, community structure, or ecosystem functioning along environmental parameters were commonly used to predict the influences of future environmental changes, i.e., to perform a space-for-time substitution (Fukami and Wardle 2005). For example, a space-for-time substitution was conducted on 466 lakes to analyse the influence of oligotrophication on lake food webs (Jeppesen et al. 2003). Lakes of varying latitude (Meerhoff et al. 2007) or altitude (Karlsson et al. 2005) were compared to predict their response to future climate warming. Although space-for-time substitutions have proven to reveal many insights of ecosystem functioning, their application in predicting the influences of future environmental changes is constrained by the underlying assumption that ecological processes vary in space in the same way than they do in time (Dunne et al. 2004). Moreover, compared habitats in most space-for-time substitutions greatly differ in
abiotic and biotic factors others than the focal one. However, this thesis shows that even in closely related sites, i.e., located in the same food web with the same food web structures, species responses to environmental changes were not fully comparable in space and time. The application of a space-for-time substitution would reveal some misleading results. For instance, the response of *E. gracilis* in spring to declining lake trophy would be predicted to decrease considering temporal variations and increase while analysing spatial variations (Fig. 5, chapter IV). A false prediction would also be obtained in summer abundances of predatory cladocerans. This stressed that the prediction of future species responses to environmental changes is difficult to obtain from space-for-time substitutions and implications should be done carefully.

**Concluding remarks and perspectives**

While this thesis provides many insights in the population dynamics of copepods some important aspects still remained unexplained. In this thesis, fluctuations of environmental parameters were always related to changes in abundances. However, fluctuations in abundances resulted from changes in fecundity and/or mortality and the knowledge, which of these traits is affected, is of crucial importance for the understanding of the mechanisms driving population dynamics. While fecundity expressed as clutch size and the number of egg-bearing females is comparatively easy to measure, estimations of mortality rates in stage-structured populations are still challenging. For this purpose, diverse demographic estimation procedures have been developed (Rigler and Cooley 1974; Braner and Hairston 1989; Caswell and Twombly 1989; Wood 1994; Aksnes et al. 1997) but they often require strong assumptions and high temporal sampling and ontogenetic resolution. Nevertheless, the application of Wood’s (1994) population surface method on the copepod data set from Lake Constance revealed promising tentative results, deserving to be analysed in more detail. This should enable a more detailed investigation of the underlying mechanisms. While the latter method estimated mortality rates independent of environmental fluctuations, Caswell and Twombly’s (1989) inverse matrix method is based on an underlying mechanistic model, which directly related environmental conditions to vital rates. The most recent study using this method confirmed results of this thesis that copepods were affected by a set of factors, i.e., predation, competition, and density-dependence, which vary with developmental stages (Twombly et al. 2007). However, seasonal variations of these sets of factors were not yet analysed. The copepod data of Lake Constance seemed to be well suited to apply such demographic estimation procedures and to analyse the inter- and intraannual variation of regulators of copepod population dynamics in greater detail.
Many studies have shown that time series analysis is valuable to gain new insights in population dynamics and ecosystem functioning but, however, these findings remain hypothetical since the assumed mechanisms could not be verified in controlled scenarios. Hence, a time series analysis provides a first step in analysing long-term dynamics and reveals many hypotheses, which have to be tested experimentally. For instance, this thesis suggests complex interactions between the phenology of *C. vicinus* and its environment, i.e., stage-specific adaptations to phytoplankton growth and photoperiod (chapter II). While these findings were only correlative, their ecological significance has to be proofed experimentally. Another interesting issue might be the interaction of photoperiod and temperature in modifying species response to climate variability (Bradshaw and Holzapfel 2008). The results of this thesis suggest that *C. vicinus* seemed to be an appropriate model organism in analysing this interaction and its consequences for offspring survival in detail. Furthermore, the onset of population growth in spring is known to result from the onset of stable stratification, while it is not yet clear whether phytoplankton growth or temperature determined the onset of population growth. In *C. vicinus*, phytoplankton seemed to be the primary trigger but this remained to be tested for other zooplankton species. Finally, inter- and intraspecific interactions of copepods seemed to be very complex due to ontogenetic shifts in diet, omnivory, cannibalism, and density-dependence. Many of the findings in this thesis are based on assumptions on these interactions and a close investigation should be done to verify these assumptions.

This thesis highlighted many novel insights in the population dynamics of copepods particularly in the role of seasonality, life cycle strategy, and stage-structured interactions in their responses to environmental changes. The fact that most of these insights were overlooked or less investigated in the past seemed to be partly due to quality of the data available in this thesis. For instance, many copepod long-term studies analysed mean abundances for each year to capture the mean long-term dynamic of a species, while ignoring potential differences among seasons. The study of *E. gracilis* showed that these attempts are likely to fail since at least in Lake Constance the use of e.g. annual means did not reveal any relationship to oligotrophication although the copepod strongly responded to this environmental change (chapter I). Furthermore, most studies did not distinguish developmental stages or even species and analysed subfamilies of copepods, i.e., Calanoida and Cyclopoida. However, an analysis of subfamilies is not able to capture the diverse responses of cyclopoids since long-term trends in abundances of these species were negatively, positively, or not
related to oligotrophication (chapter III). Moreover, the analysis of the role of life cycle strategies in population dynamics required stage-specific data over long time periods, i.e., more than one annual cycle. The use of data with low seasonal or taxonomical resolution strongly reduces the potential to elucidate the underlying mechanisms driving population dynamics of copepods. Hence, this thesis stressed the necessity of highly resolved long-term data in analysing population dynamics of copepods in particular but also of other species with complex life cycles in general.

Although, much effort has been invested during the last decades to reveal more insights in the processes shaping population dynamics of copepods, we still did not fully understand how these species responded to environmental changes. As long as this lack of knowledge still exists, we will not be able to predict their responses to future environmental changes such as further climate warming or further nutrient increases/decreases. This thesis provided an additional piece of the puzzle, mapping the mechanisms driving population dynamics of copepods. By using a unique long-term data set of copepods, it was highlighted that the life cycle and the stage structure of a population could be of crucial importance in order to predict the responses of a species to future environmental changes. These findings are not restricted to copepods but will be relevant for a broad variety of species and communities, exhibiting a strong seasonality and/or stage-structured populations.
Summary

Copepods are exposed to a variety of external forces, which at least partly drive inter- and intraannual population dynamics. However, the underlying mechanisms, translating a change of an external force to population dynamics of copepods, are less understood, which hampered the prediction of future environmental influences such as climate warming or nutrient increase/decrease. This thesis represents an attempt to improve the knowledge on this topic while its primary focus lies on the role of seasonality, life cycle strategy, and stage-structured interactions of freshwater copepods in the response to declining phosphorus concentrations (oligotrophication) and climate variability. For this purpose, I analysed a long-term (1970 to 1995) data set of crustacean zooplankton abundances with a high sampling frequency (samples taken twice a month) and ontogenetic resolution (advanced developmental stages of copepods were distinguished). The four copepod species under investigation differed in their life cycle strategies particularly in the presence and timing of a seasonal diapause, i.e., summer diapause (*Cyclops vicinus*), winter diapause (*Mesocyclops leuckarti*), or without a diapause (*Cyclops abyssorum* and *Eudiaptomus gracilis*).

Although the study lake (Lake Constance, Germany) experienced changes in trophic status and climate variability simultaneously, it was possible to disentangle the responses of species to both environmental changes. Hereby, oligotrophication was found to primarily cause changes in abundances while climate variability expressed as spring water temperature mainly affected copepod’s phenology, i.e., timing of peak abundance, maturation, and reproduction. However, both environmental stressors were also able to interact in some species as reproductive output of *C. vicinus* was affected by timing of reproduction and abundance of reproductive females. Timing of reproduction in this copepod was coupled to phytoplankton growth in spring and reproductive output was higher in years with advanced phytoplankton growth, i.e., in warm years, counteracting the declining trend of abundances due to oligotrophication.
The responses of copepod species to oligotrophication were of complex nature and varied between ontogenetic stages and season. Offspring of all species was affected stronger than advanced developmental stages, coinciding with other studies, which regarded offspring as a bottleneck in ontogenetic development of copepods. However, the mechanisms, mediating the effect of trophic changes into changes of population dynamics, strongly differed among seasons, resulting in declining abundances in spring and increasing abundances in summer. These seasonally opposing long-term trends seemed to be a consequence of seasonally contrasting changes of invertebrate predation pressure on copepod offspring, affecting all species similarly. Non-diapausing species were able to compensate the losses in spring with the rises in summer, resulting in rather stable long-term dynamics during the study period. Diapausing species, on the other hand, were either present in spring (C. vicinus) or in summer (M. leuckarti), and thus their annual mean abundance decreased (C. vicinus) respectively increased (M. leuckarti). Hence, the consequences of oligotrophication for the maintenance of a copepod population mainly depended on the species’ evolved life cycles, i.e., on the ‘ghost of life cycle differentiation past’. Species-specific ecological requirements such as food thresholds or predator vulnerability, which were suggested in other studies to be of primary importance in the response of copepods to oligotrophication, seemed to play a secondary role in Lake Constance.

In addition to the described sampling program, zooplankton was also sampled for 14 years (1972 to 1985) at four other sites in Lake Constance. In contrast to former studies, which regarded horizontal distribution of zooplankton as a transient phenomenon mainly driven by wind-induced water currents, here, it could be highlighted that spatial heterogeneity was persistent for years. Zooplankton community seemed to be structured by both local environmental conditions and dispersal, providing first evidence of zooplankton metacommunity structure in a lake. The interannual variation of abundances observed in former chapters corresponded to a large amount in space and time most likely due to concomitant changes of productivity. The correspondence was highest in winter and spring and less consistent in summer, probably reflecting the higher degree of complexity of interspecific interactions in summer. However, a potential space-for-time substitution to analyse the effect of declining productivity along both dimensions seemed to be confounded by inconsistent variations of fish densities and life cycle strategies of copepods. This highlights that inferences drawn from space-for-time substitutions even across closely related sites with the same food web structure should be interpreted carefully.
This thesis represents one of most detailed studies of copepod population dynamics and revealed many novel insights in the role of seasonality, life cycle strategy, and stage-structured interactions in the response of copepods to environmental changes. The observed mechanisms are not restricted to copepods and will be relevant for a broad variety of communities with stage-structured populations, complex life cycle strategies, and a strong seasonality.
Zusammenfassung


Zusammenfassung des Nachwuchs' und wirkten damit dem abnehmenden Trend des Copepoden aufgrund von Oligotrophierung entgegen.


Zusammenfassung


Zusammenfassung


Zusammenfassung


Zusammenfassung


Wang, N. and A. Appenzeller. 1998. Abundance, depth distribution, diet composition and growth of perch (Perca fluviatilis) and burbot (Lota lota) larvae and juveniles in the pelagic zone of Lake Constance. Ecology of Freshwater Fish 7:176-183.


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All analyses presented in this thesis were exclusively performed by myself. Interpretation, discussion, and presentation of the results in the scientific context were mainly done in cooperation with Dietmar Straile. The long-term data set was sampled and determined by Ulrich Einsle.

Abgrenzung der Eigenleistung