

## Population dynamics of a freshwater calanoid copepod: Complex responses to changes in trophic status and climate variability

Hanno Seebens,<sup>1</sup> Dietmar Straile and Rainer Hoegg  
Limnological Institute, University of Konstanz, 78464 Konstanz, Germany

Hans-Bernd Stich and Ulrich Einsle<sup>2</sup>  
Institute of Lake Research, 88085 Langenargen, Germany

### 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.

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. 2005). 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 alter both the abundances and the community structure of copepods (Beaugrand et al. 2002; Jeppesen et al. 2005; Adrian et al. 2006). The influence of climate variability on copepod populations and communities has been especially highlighted in marine systems (e.g., Beaugrand et al. 2002; Rebstock 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). Because of 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 *E. 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 also has a high temporal resolution (two 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

<sup>1</sup> Corresponding author (Hanno.Seebens@uni-konstanz.de).

<sup>2</sup> Deceased.

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different developmental stages and also 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.

## Materials and methods

**Study site and sampling methodology**—Lake Constance is a large (472 km<sup>2</sup>), deep ( $z_{\max} = 254$  m), warm-monomictic lake located in southwestern Germany. The lake has been studied intensively during the last few decades, especially regarding its response to anthropogenic changes in trophic status, eutrophication, and oligotrophication (Bäuerle and Gaedke 1998; Güde et al. 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 center 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 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 1 month (Berger and Maier 2001). Up to 1985, the water column was sampled between 0-m 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. A Nansen closing net (mesh size 105  $\mu\text{m}$ ) was used until 1985; however, this was found to strongly underestimate zooplankton numbers. All subsequent samples were collected using a new, improved net (Hydrobios, mesh size 100  $\mu\text{m}$ ). Comparative hauls with both types of net revealed a difference in zooplankton abundance by a factor of three. All abundance data before 1986 were therefore multiplied by three. Counting categories consisted of all five copepodid stages, males, females, and ovigerous females of *Eudiaptomus*. Subsamples were analyzed under a binocular microscope at  $\times 20$  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 phosphorous concentration ( $\text{TP}_{\text{MIX}}$ ) during the winter mixing period (February, March) as a proxy variable for the trophic status of the lake in a given year (Fig. 1).

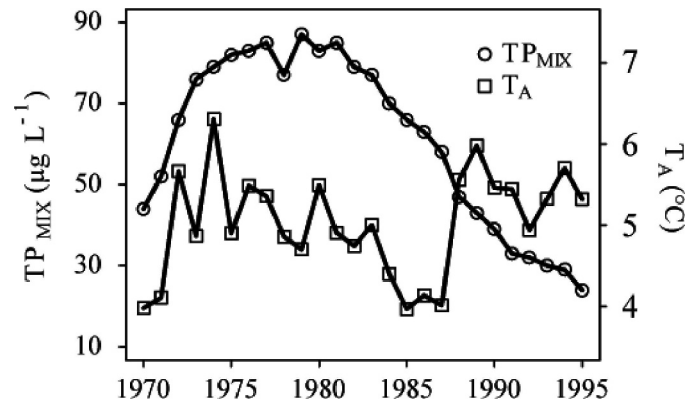


Fig. 1. The development of  $\text{TP}_{\text{MIX}}$  (maximum total phosphorus concentration during winter mixing [February, March]) and April water temperatures ( $T_A$ ) during the study period.

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 monthly during the sampling period at distinct depths. Because *Eudiaptomus* is found at depths from 0 m to 40 m during spring, we used the average  $T_A$  from 0 m to 40 m. Covariation of  $T_A$  with  $\text{TP}_{\text{MIX}}$  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 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 2-week period separately. This allows for seasonal changes in the relationship between environmental variables and *Eudiaptomus*. Although covariation between  $TP_{MIX}$  and  $T_A$  was low, we removed the effects of one variable from the abundance time series by subtracting a LOESS fit to analyze the effects of the other variable. The smoothing parameter of the LOESS fit was chosen based on Akaike's information criterion. We chose this nonlinear method to control for the effects of environmental variables instead of a simple linear least-square fit because 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  $TP_{MIX}$  or  $T_A$ , the influence of the other variable on copepod abundances was analyzed using Pearson correlation coefficients. For a better understanding of the influence of the variable on population dynamics, we plotted the average population dynamics—corrected for the influence of  $TP_{MIX}$  and  $T_A$ , 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 2005).

## Results

*Seasonal cycle of E. 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,  $TP_{MIX}$  was at its maximum, whereas  $T_A$  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 toward 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 (CI) 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 CI abundances in April and higher summer reproduction resulting in low CI abundances.

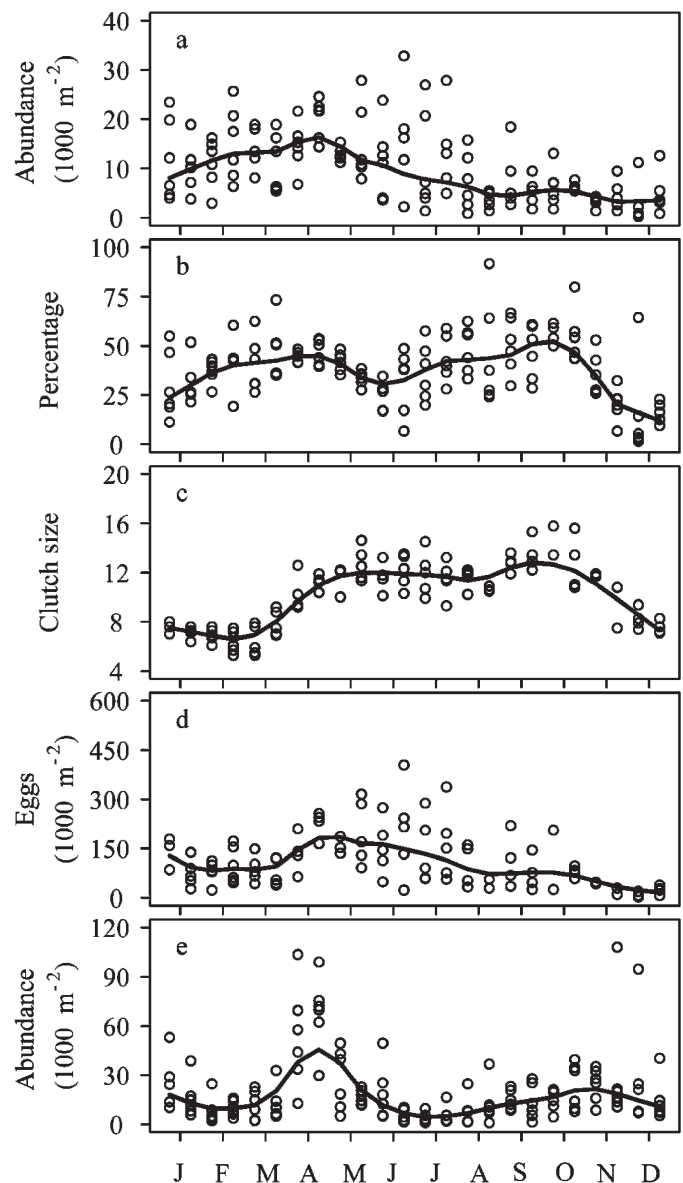


Fig. 2. Seasonal dynamics from 1976 to 1981 of the (a) abundance of ovigerous females, (b) percentage of all females that were ovigerous, (c) number of eggs per clutch, (d) total number of eggs as the product of the number of eggs per clutch and the abundance of ovigerous females, and (e) abundance of first copepodids. The data are represented by circles and the trend by a solid line.

*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 toward summer during the later years (Fig. 3b,f). These seasonal differences in population development were strongly supported by STL decomposition

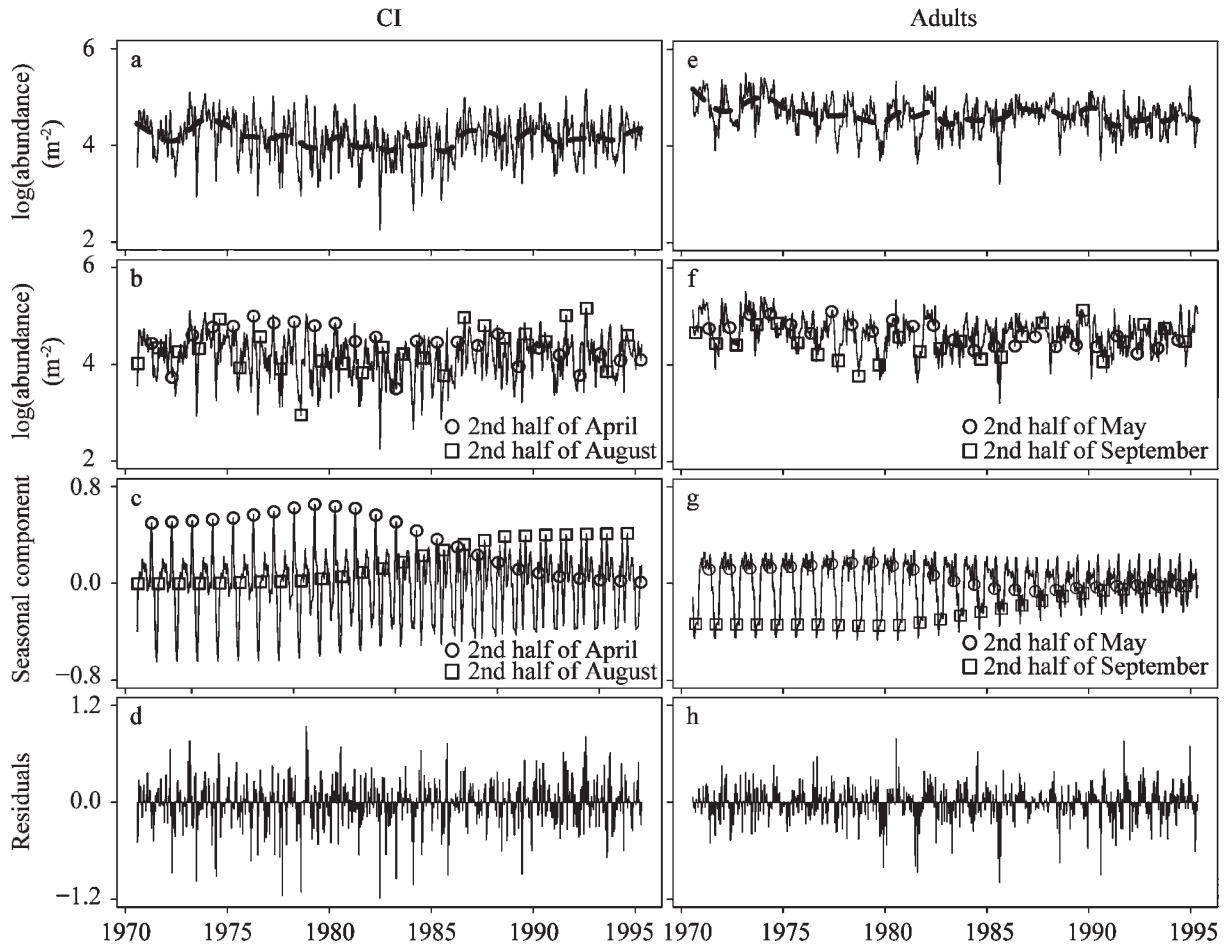


Fig. 3. STL decomposition of the time series of CI (left panels) and adults (right panels) into (a, e) trend component (dashed line), (c, g) seasonal component, and (d, h) residuals. The abundances of CI and adults are shown twice (solid lines in a, e and b, f) in order to compare the population development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

(Fig. 3c,g). Adults showed a similar pattern, with a lag of approximately 1 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 ( $r = 0.70$ ,  $df = 25$ ,  $p < 0.0001$ ), and the seasonal variability, expressed as the coefficient of variation for each study year, was less pronounced in adults than in CI ( $t = 6.2$ ,  $df = 44$ ,  $p < 0.001$ ).

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  $TP_{MIX}$  (Fig. 4a): in April, the abundances were positively related to  $TP_{MIX}$ , whereas from July to October they were negatively related to  $TP_{MIX}$ . Significant correlations were found not only for CI but also for other stages. However,

with increasing ontogenetic stage, significant correlations appeared increasingly later in the season. The abundance and 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 CI and CII (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.

Figure 5 enables 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  $TP_{MIX}$  years than during low



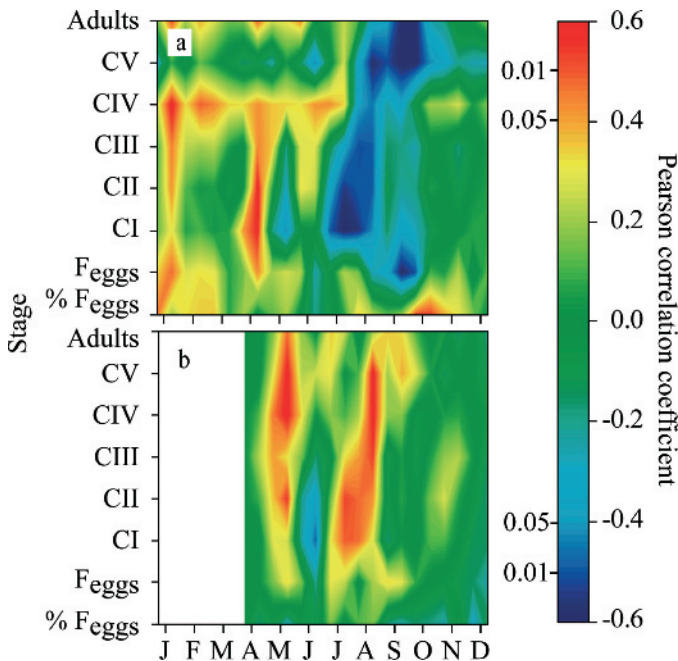


Fig. 4. (a) Seasonal development of Pearson correlation coefficients between the abundances of *Eudiaptomus* copepodid stages, ovigerous females, adults, and  $TP_{MIX}$  (maximum total phosphorus concentration during time of winter mixing [February, March]). (b) As (a), but between the abundances and  $T_A$  (April water temperatures). Before conducting each correlation analysis, the effects of the respective other variable were removed by subtracting a LOESS fit (i.e., before correlating abundances and  $TP_{MIX}$  the effect of  $T_A$  was removed from abundances and vice versa). Correlation coefficients with  $T_A$  before April are not shown in (b). The analysis is based on data from 1970 to 1995.  $F_{eggs}$  = ovigerous females,  $\% F_{eggs}$  = percentage of all females that were ovigerous. Significance levels are shown to the left of the colored scale.

$TP_{MIX}$  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  $T_A$  years are generally comparable to those observed between high and low  $TP_{MIX}$  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  $T_A$ .

## 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 of 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 influences water temperatures, nutrient

availability (Straile et al. 2003a), the abundance of *Daphnia* (Straile 2000), and the year-class 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 food, competitors, or predators of the copepods. The potential influence of the trophic changes of the lake 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) respond to the oligotrophication of the lake. Hence, any significant results obtained by correlation analysis between the abundances of the copepods and either  $TP_{MIX}$  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  $TP_{MIX}$  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 that underwent continuous change during the observation period.

In analyzing the effects of environmental factors, we computed a large number of correlations (2 environmental parameters  $\times$  7 development stages/categories  $\times$  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 done nevertheless 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  $TP_{MIX}$  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

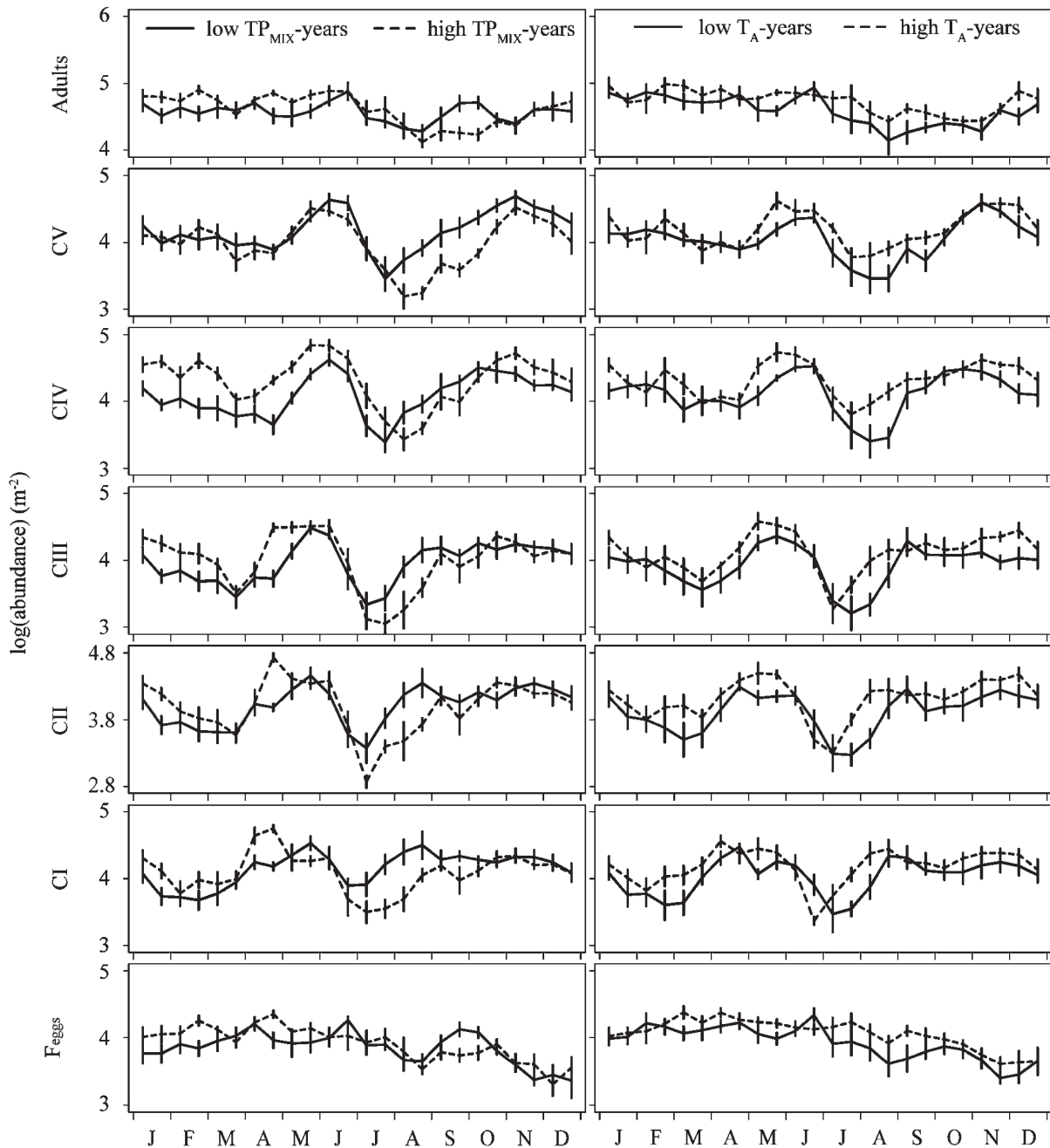


Fig. 5. Left panel: Comparisons of the mean seasonality (with one standard error of the mean) of copepodid abundances in the different ontogenetic stages for those years within the upper quartile ( $n = 6$ ) of  $TP_{MIX}$  (maximum total phosphorus concentration during winter mixing [February, March]) (dashed line) with those years within the lower quartile of  $TP_{MIX}$  (solid lines). The influence of  $T_A$  (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  $T_A$  years after removing the effects of  $TP_{MIX}$ .  $F_{eggs}$  = number of ovigerous females.

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 CI 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 CI and adults during oligotrophication suggests that the increase in CI abundances was accompanied by increased mortality in more advanced stages. Consequently, the abundance of adults increased less than the abundance of CI.

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 (CV and adults) of the cyclopoid copepod *Mesocyclops leuckartii* during spring did increase with oligotrophication, which resulted in a significantly negative relationship between the abundances of the CI of *Eudiaptomus* with *Mesocyclops* ( $r = -0.49$ ,  $df = 25$ ,  $p < 0.05$ ). *Mesocyclops* spp. are 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* is 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 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 toward a seasonality observed during the oligotrophic conditions that prevailed before eutrophication also suggests that the changes associated with TP<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 are 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 (Figs. 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 toward the second maximum in August/September (resulting in positive correlations with April temperatures). Hence, the differences in population dynamics between high and low  $T_A$  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 enable *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, CI 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, whether the two factors had additive or subtractive effects on abundances depended on the season. In July, for example, both oligotrophication and high spring temperatures resulted in increased abundances of CI, 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 enabled 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 because of 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 *E. 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. Whereas 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, because of the cohort dynamics of *Eudiaptomus*, the effects of spring climate variability were transferred far into the season.

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